

## Part 4    Manipulation of the Biological Environment for Insect Pest Suppression

The modern concept of biological insect pest suppression encompasses more than just the practices of classical biological control as presented in the preceding chapters. We may also include within our current thinking a host of old and very new techniques which all come under the umbrella of biological pest suppression in that they involve human manipulation of the biological environment of the pest. Through judicious interference, we can beneficially modify the species characteristics (i.e. internal environment) of the pest or some of the density-independent conditioning forces in its external environment. For convenience we may generally divide the techniques used into two groups: those involving other members of the ecosystem, and those concerned directly with the pest itself. In the former group we may include such ancient and time-tested practices as breeding hosts for pest resistance (Chap. 4.1) and various cultural manipulations (Chap. 4.2) which together constitute a system for modifying the density-independent conditioning elements of the environment in order to reduce its potential carrying capacity for the pest. The latter group includes a number of more recently developed techniques that are basically aimed at modifying species characteristics of the pest, such as alteration of genetic makeup or reproductive capacity (Chap. 4.3), or interference with normal behavioral and developmental functions (Chap. 4.4).

### 4.1 Host Resistance to Pest Insects

As suggested in Chapter 2.1 the recognition and encouragement of crop strains showing some degree of resistance to damage by insects may well be the oldest form of biologically-based pest suppression. Certainly the history of agriculture has been coextensive with the improvement of domesticated plants and animals in various ways, including increased resistance to depredation by pest insects. However, the earliest published references to the phenomenon date only to the late eighteenth century in suggestions of possible resistance in wheat to the Hessian fly, *Mayetiola destructor* (Say) (Painter, 1951). Lindley (1831), in England, also took note of varietal resistance in apples towards the woolly aphid, *Eriosoma lanigerum* (Hausman), and during the 1880s the vineyards of France were saved from destruction by the importation of phylloxera-resistant rootstock from the United States (Howard, 1930; Ordish, 1972). Recent reviews have dealt with resistance in cereals (Gallun et al., 1975), forest trees (Hanover, 1975), and a variety of crop plants (Maxwell et al., 1972). As an energy efficient method of pest control it is difficult to exceed host resistance, which provides "protection and

insurance against insect damage at no extra cost in materials or labor, and with no danger from chemicals or chemical residues" (Painter, 1968). In fact, it has been called the ideal method of controlling insects (Packard and Martin, 1952; Luginbill, 1969).

#### 4.1.1 Mechanisms of Resistance

The term resistance means different things to different people, and a number of workers have attempted to define the concept and analyze its various aspects. Mumford (1931) was one of the first, and although he recognized and discussed the most important characteristics of resistance, his division of the phenomenon into epiphyllaxis (due to externally occurring factors) and endophyllaxis (due to internal biochemical factors) has found little favor. Later, Snelling (1941) defined resistance as those characteristics which enable a plant to avoid, tolerate, or recover from attacks of insects under conditions that would cause greater injury to other plants of the same species. He illustrated the complexity of the subject by enumerating 15 categories which he felt constituted the broad concept of resistance at is was presented in the literature. Chesnokov (1962) emphasized the significance of specific host properties which prevent or reduce insect damage on a particular plant form, or make it tolerant to the damage suffered, in contrast to properties of other forms of the given culture which are subject to severe damage under the same conditions and suffer a decrease in yield. He recognized two main forms: immunity or a comparatively slight affliction of the species or variety, and resistance to injury that would result in loss of yield (i.e. tolerance). Due to a heavy emphasis on the importance of environmentally conditioned acquired characteristics, the ideas presented by Chesnokov have not received wide acceptance outside the Union of Soviet Socialist Republics in areas which favor the theories of Mendelian genetics.

Certainly the most widely accepted and best known ideas about plant resistance are those of Painter (1936, 1951, 1966). Emphasizing the fact that resistance is definable only in relative terms, and that it is the result of interaction between insect and plant, Painter suggested that, practically speaking, it represents the ability of a certain variety to produce a larger crop of good quality than do ordinary varieties at the same level of insect population. This is the result of the relative amounts of heritable qualities possessed by each variety which influence the ultimate degree of damage done by the insect. The degree of resistance exhibited by specific hosts to specific pests was recognized to vary from immunity, indicating no consumption or injury under any condition, to high susceptibility, indicating the potential for much greater than average damage by the insect to the plant. Painter's analysis of the causes of resistance was based on practical observations made under field conditions and included the three basic mechanisms: nonpreference, antibiosis, and tolerance. Sweetman (1958) presented a basically similar classification, but called the three aspects physical, chemical, and physiological. Nonpreference denotes a plant character (or characters) which adversely affects the insect's behavioral response toward the plant for use in oviposition, as food, or for shelter. Antibiosis exerts an adverse influence on growth and survival

of the pest by preventing, injuring, or destroying the insect's normal life, often, but not always, by chemical means. Tolerance allows the plant to support the same sort of insect population as less resistant varieties but still maintain normal vigor, growth, reproduction, and yield by rapidly repairing or overcoming injury. These elements of resistance are interrelated, and many times vaguely delimited (Beck, 1965). Although resistance in a host may be due to any one of them, it usually results from some combination of the three. For example, Horber (1965, 1972) found all three elements active in the roots of several alfalfa strains collected from fields severely infested with white grubs, *Melolontha vulgaris* F. Hairiness of legumes has long been considered basic for resistance to leafhoppers (Hollowell et al., 1927), but sometimes it only accounts for part of the resistance (Jewett, 1932; Johnson and Hollowell, 1935).

Most recently Beck (1965, 1974) has redefined resistance to exclude tolerance from consideration. Thus, plant resistance is the collective heritable characteristics by which a plant species, race, clone, or individual may reduce the probability of successful utilization of that plant as a host by an insect species, race, biotype, or individual. Although tolerance is an important agronomic characteristic, Beck feels that in this restrictive sense it implies a biological relationship substantially different from the other two mechanisms.

One other group of occurrences somewhat related to resistance have been called pseudoresistance (Painter, 1951). The term is applied to apparent resistance in potentially susceptible hosts resulting from some transitory situation. Host evasion takes place when the most susceptible stage of the host is ephemeral or occurs when pest populations are at a low ebb. For example, early sowing of susceptible varieties may evade significant injury if pests do not build up to large populations until late in the season. Induced resistance is a temporary condition resulting from a beneficial alteration of some condition in the plant environment, as fertility or water supply. Escape refers to the improbable but occasional lack of injury or infestation on a susceptible host in a heavily infested population because of some unusual circumstance.

#### 4.1.2 Factors Affecting Resistance

True host resistance is the result of inherited characteristics rather than ecological conditions such as those promoting pseudoresistance. As such, it is the most desirable and most studied of the two because it is theoretically exhibited wherever the target insect is a potential pest. However, even genetic characters are expressed only in reference to a given environment, and therefore resistance will be influenced to a greater or lesser extent by various environmental factors, some affecting the host and some concerning the insect. The simple examples studied in an introductory genetics course are mostly those which are little affected by the environment. Plant breeders know that many times they are not working with a specific character, but instead with the tendency of the organism to react in a particular way to a certain environment. Applying this idea to insect resistance we find that if the environment is changed the host-pest relationship may or may not change also.

#### 4.1.2.1 Factors Modifying Expression in the Host

Edaphic and climatic factors have considerable effect on the expression of resistance (Painter, 1951; National Academy of Sciences, 1969a). High humidity facilitates odor detection, thus perhaps influencing the preference-nonpreference response of insects to attractive or repellent host emanations. Onions grown on soils high in organic matter are twice as pungent as those grown in sand (Yarnell, 1942). Thus, if an insect is attracted (or repelled) by the smell of onion, the type of host substrate alone could be indirectly responsible for a large difference in infestation rate. Soil moisture levels may affect the resistance of plants to insects through the agencies of water balance and osmotic pressure (Withycombe, 1926). Such influences are mostly effective against sucking insects, and are probably expressions of induced resistance although they are accentuated by varietal differences (Painter, 1951). Many researchers have noted the relationship of soil fertility to plant injury by insects (review by Painter, 1951). In some cases, additional fertility increases resistance to insect attack (Keen, 1936; Chesnokov, 1962; Leuck, 1972; Goyer and Benjamin, 1972; Smirnoff and Valéro, 1975), whereas in others it has precisely the opposite effect (Huber et al., 1928; Shaw and Little, 1972). At present, only two conclusions may be drawn: under no conditions of soil fertility has a resistant plant become susceptible, or a susceptible one become highly resistant (National Academy of Sciences, 1969a), and each insect species and each host species constitutes a unique problem requiring separate analysis (Painter, 1951). The effect of temperature has also been documented (Dahms and Painter, 1940; Albrecht and Chamberlain, 1941), with the indication that, at higher temperatures, aphid-resistant strains of alfalfa perform better than at low temperatures, perhaps due to increased growth rate. Similar effects were noted with the greenbug, *Schizaphis graminum* (Rondani), on resistant sorghum (Wood and Starks, 1972). However, high temperature may have the opposite effect on aphid-resistance in wheat (National Academy of Sciences, 1969a).

A number of biological factors also affect resistance expressed by the host. Age of the host may be important (deWilde et al., 1969). For instance, a corn variety may be repugnant to grasshoppers once it is tasted, but a single bite on a seedling may prove fatal to the plant whereas a half grown plant would be essentially unaffected. Only the current year's growth of foliage of jack pine, *Pinus banksiana* Lambert, is unacceptable to two species of *Neodiprion* sawflies normally restricted to this host (Benjamin and All, 1973). Harvey and Hackerott (1974), working with sorghums, found that as long as seedlings showed a high degree of resistance to greenbug, maximum yields could be obtained. Insects are often vectors of plant diseases (Carter, 1973), and the presence of a sublethal infection in a plant may make it more attractive to pest attack (Baker, 1960; Whitten and Swingle, 1958; Fleming, 1972), or less able to resist chemically or tolerate such attack. Other biological factors that may affect resistance in plants are evasion by varieties selected for genetic earliness in maturity, and hybrid vigor (Painter, 1951). The presence or absence of adjacent individuals may also have an effect on resistance. In domestic cattle, significant differences have been demonstrated in the preference of the horn fly, *Haematobia irritans* (L.), and the stable fly, *S. calcitrans* (L.), for dark over light hair coat (National Academy of Sciences, 1969a). Thus, if light



breeds and dark breeds are pastured together, the light breeds show relative nonpreference; but light-colored animals by themselves may be heavily infested.

#### 4.1.2.2 Factors Modifying Responses of the Insect Pest

Foremost among the factors affecting the response of insect pests to their resistant hosts is the development of biotypes. For purposes of this discussion, these are defined as usually morphologically indistinguishable biological strains of a pest species displaying diverse physiological reactions to a genetically stable variety of host. The development of races of pathogens capable of attacking disease-resistant crop varieties has long been recognized. For a recent example one need only consider the devastation to the United States corn crop in the early 1970s caused by the fungal pathogen, *Helminthosporium maydis* Nisikado and Miyake (southern corn leaf blight). In insect pests the phenomenon is less common than in pathogens, but several examples are known (Singh and Painter, 1965; Briggs, 1965; Hatchett and Gallun, 1970; Nielson et al., 1970; Wood, 1971). There are also indications of biotypes in the European corn borer on corn (Chiang et al., 1968) and the frit fly, *Oscinella frit* (L.), on wheat (Chesnokov, 1962). There appear two basic kinds of insect biotypes. The least common is that represented by the pea aphid, *Acyrtosiphon pisum* (Harris), on peas, where resistance is apparently overcome simply by greater vigor and larger size in the successful biotypes (Harrington, 1945). The other kind is represented by the spotted alfalfa aphid, *Therioaphis maculata* (Buckton), on alfalfa, in which the so-called "lock and key" theory (Painter, 1951) or gene for gene relationship (Flor, 1956) is illustrated. For example, each of the 6 recognized biotypes of *T. maculata* varies in its virulence toward clones of "Hayden" alfalfa (Nielson and Don, 1974). Thus, a particular clone may be susceptible to biotype A, but resistant to biotype H and the other biotypes because only A carries a gene allowing it to overcome a particular gene for resistance in the plant. In like manner, another clone may be susceptible to biotype H but not to A or the others, and so on. Other examples of this kind of biotype development occur in the Hessian fly on wheat (Hatchett and Gallun, 1970), and the aphid, *Amphorophora rubi* (Kaltenbach), on raspberry (Briggs, 1965). The discovery of the existence of biotypes emphasizes the importance of combining several genetic factors for resistance into each variety in order to overcome problems with gene for gene relationships, which arise through selection in much the same manner as insecticide resistance (Painter, 1951).

Other important characteristics modifying the response of the pest to the resistant host include its stage of development, the size of the pest population, and generational differences. Some kinds of insects feed only during the immature stages and thus the adult causes no direct injury to any host. Others feed on the host as a nymph or larva and on a completely different food source as an adult. Some cause injury in all stages of development. Early instars are usually much less injurious than are late instars. Frequently superimposed upon the increased damage caused by an aging pest population is that caused by reproduction and a numerically larger sized population as the season progresses in those species with multiple generations. These effects are particularly visible in regard to the tolerance aspect of resistance. Many host varieties may tolerate low numbers of small

insect pests, but only the most tolerant will sustain high populations of large insects without significant yield loss. Sometimes insect voltinism is important in modifying the expression of resistance in the host (Guthrie et al., 1970). Inbred lines of corn resistant to feeding by first generation European corn borer larvae are not necessarily resistant to that by the second generation, and vice versa. This is partially a result of differential feeding behavior; the first generation larvae attack the whorl leaves which contain a repugnant chemical, whereas those of the second are sheath feeders.

Finally, the opportunity arises again to emphasize proper identification and thorough knowledge of the insect pest. Because of inaccurate identification many observations on insect resistance are open to question (Painter, 1951). Mixtures of pest species cannot be studied as a whole unless they are known to cause identical injury, prefer the same food plant varieties, and react the same way to these varieties. A statement that a variety is resistant to "thrips" or "borers" is of little significance unless specific identifications are made. For instance, the raspberry variety "Herbert" is resistant to the aphid, *A. rubi*, but not to *Aphis rubicola* (Oestlant) (Winter, 1929). As in other aspects of biological pest suppression it is important here to *know your insect*.

#### 4.1.2.3 Factors Affecting the Permanence of Resistance

A brief mention is also in order regarding the permanence of genetic host resistance to pests. Whereas the factors discussed in the two preceding sections may cause temporary discrepancies in the expression of resistance, the fact remains that such resistance is genetically determined and heritable from generation to generation. However, potential does exist for changes in the genetic constitution of either the pest or the host which may prove detrimental to the status quo. The problem resolves to the question of whether the plant (or animal) breeder can keep satisfactorily ahead of nature. Can suitable resistant variants be found in the gene pool of the host to offset new mutations for virulence arising in the pest? If a resistant variety sustains a mutation to susceptibility will it be recognized and removed before it is widely distributed? Problems such as these are, at present, largely hypothetical, but must be kept under consideration by breeders. Also, the selective pressure exerted by resistant varieties against those pests exhibiting biotypes would appear to bestow advantage onto a virulent biotype, eventually leading to its ecological success and complete displacement of other biotypes. As yet, this situation has not been encountered as a serious problem with insects in the field either. Another theoretical possibility is that of learning by the pest to utilize a nonpreferred host (Painter, 1951). If nonpreference were based on a repellent odor or feeding deterrent, it might be feasible for the pest to become habituated to the odor (Cushing, 1941) in the face of universal availability of only the nonpreferred host and imminent starvation. Coupled with the fact that some insects are known to prefer ovipositing on the same host they utilized in their immature stages (Hovanitz, 1969), this could result in a permanent shift in the ability of the pest to use the previously resistant host. This idea leads to consideration of the large and complex subject of host selection and specificity, a subject well reviewed by Fraenkel (1969), Dethier (1970), and Beck (1974), but too broad for discussion here.

### 4.1.3 Principles and Procedures in Utilization of Host Resistance

The successful development and utilization of resistant varieties in agriculture first and foremost demands cooperation between at least one competent breeder and one competent entomologist. Each should attempt to become familiar with the problems faced by the other when working within his area of expertise. The interdisciplinary approach assures better understanding of the pest, the host, and the relationships between the two. Additional insect pest resistance should be strived for in every breeding program directed toward improving quality or yield of domestic plants or animals, and in the introduction of known varieties or breeds into new geographical areas (National Academy of Sciences, 1969a). With but a few exceptions, past entomological literature has given, at best, inadequate consideration to resistance for pest control, although the story of the grape phylloxera is every bit as fascinating as that of the cottony cushion scale.

After becoming thoroughly familiar with the methods practiced in each other's discipline, the breeder-entomologist team must gain a detailed knowledge of the particular host, pest, and host-pest interaction to be studied. In plant research, a series of plots is usually sown with available varieties at different dates in order to study the biology and behavior of the pests, and determine the properties of the varieties, especially those chosen to represent the maximum range in time of maturity. Observations such as these allow for the later recognition of pseudoresistance and other ecological effects separate from genetically-based resistance in the host varieties. Although these tests are usually subjected to natural infestations in field-plots, much of the subsequent testing is done in the greenhouse or laboratory where both environmental conditions and infestation levels can be controlled, so that consecutive tests in a series may be most comparable. Further field-plot tests are then essential to corroborate the experimental results.

Another initial problem in the research program is to find inherited factors for resistance. The probability of locating such resistance is largely proportionate to the number of individuals and varieties examined, but thus far, genetic resistance has been discovered wherever adequate search has been made (Painter, 1966). For several reasons, the development of arthropod-resistant animal breeds has not proceeded as rapidly as that of resistant plants (National Academy of Sciences, 1969a). Progress is retarded by much greater costs (e.g. pigs vs corn plant), longer generation times with fewer offspring per generation, and the more limited availability of a large number of breeds from which to select. Plant material, by contrast, is much easier to investigate. Of the various sources available, the locally-grown and adapted varieties should be the first investigated, because they are known to possess many desirable qualities a priori (with the exception of the desired resistance). Also included in the screening should be other varieties being used as sources of disease resistance or other improved characteristics for incorporation into the new variety. Although it is difficult to locate resistant factors in a locally adapted variety grown for other reasons, such fortuitous results have occurred (National Academy of Sciences, 1969a). Individual plants or strains showing less injury, greater yield, or supporting fewer pests than individuals or strains of the same species nearby may be suspected of carrying resistance factors. If such

genetic potential is not available in local varieties, researchers look further afield (Sullivan et al., 1974), even to the ancestral home of the pest and/or crop, or to an area of maximum morphological variability in the crop. Long association of insect and plant in the place of origin and evolution may have resulted in ample time for natural selection of resistance characteristics. On the other hand, plants from areas supporting highly diverse physical characteristics in the population may also contain the potential for diverse physiological characteristics useful in selection for resistance. Plants bearing close phylogenetic relationships to the host may also be sources of resistant genes in extreme instances. Germ plasm for the exotic varieties is obtained from colleagues working with the same species, from the storage facilities of organizations (Gallun et al., 1975) such as the United States Department of Agriculture, or through the cooperation of the United Nations Food and Agriculture Organization (FAO). Finally, useful mutations may sometimes be induced by radiation or other means (Micke et al., 1973).

Upon location of suitable resistance potential by inspection in these early tests, it is necessary to obtain evidence for the inheritability of the factors responsible. It must be kept in mind that some degree of resistance is the goal, not total immunity. Therefore, it is best to compare varieties at pest infestation levels suitable to elicitation of the greatest differential in injury: not so low as to allow numerous escapes and not so high as to mask any of the components of resistance, particularly tolerance. Evidence for genetically induced resistance comes from breeding studies and examination of the progeny of the suspected host. This frequently involves self-pollination of the plant for a number of generations and eventual cross-fertilization amongst resistant selections. The varieties under study are constantly compared against a standard, either a known susceptible variety or the original resistant parent, and always under the same environmental and infestation conditions. In addition, retention of resistance under a variety of environmental conditions lends further credence to the supposition of inheritable resistance factors. Whenever a large number of varieties is available, it is wise to consider the possibility of finding complementary resistance to more than one insect pest at a time, even though primary emphasis is centered on one species.

Practically speaking, a detailed understanding of the actual bases of host resistance to insects has not been necessary. Research toward that understanding has not progressed as far as the practical utilization of the method (Painter, 1966). However, such information is of great theoretical interest, and may have significant influence on the future development of insect pest suppression (Beck, 1965, 1974). Current practice dictates complete genetic, biological, and ecological analyses of the components of the system, after which a biochemist may profitably be added to the research team. Although a number of biochemical bases have been identified for host selection between plant species (Beck, 1965; Hsiao, 1969), substantial examples of such differences between varieties are rare (Beck, 1960; Da Costa and Jones, 1971). In general, and under current conditions, the most economical, rapid, and effective way of locating resistance is through an actual bioassay of the candidate varieties against the potential insect pest, as opposed to any chemical test procedure (Agarwal, 1969).

Identification of the chemical bases of resistance and host selection should have other applications, however. Naturally occurring host chemicals responsible

for preference, nonpreference, repellency, or feeding deterrence might have broad appeal for use in behavior modification of the pest insect (Gilbert et al., 1967; McMillian et al., 1969; Munakata, 1970; Benjamin and All, 1973). Synthetic analogues of these chemicals might be even more potent. Chemicals associated with antibiosis could serve as the bases for new more specific kinds of insecticides (National Academy of Sciences, 1969b; Klun, 1974; Shaver, 1974). Finally, knowledge of the chemical basis of resistance and a test for its presence would be most beneficial for animals and woody perennial plants, where each generation takes several years and screening by bioassay is less practical. Plant pathologists have made significant advances in this area, and are now able to rapidly screen for resistance of individual sugarcane plants to eyespot disease by simply spraying the plants to be tested with a toxin identified from the spores of the causative fungal pathogen (Strobel, 1975).

If suitable resistance factors are fortuitously located in a locally adapted cultivar, they may be most easily selected or combined to yield a new variety for immediate testing and distribution. If, however, the genes for resistance are found in a nonadapted source, they must be combined into the genotype of an acceptable variety by cross-breeding with plants of satisfactory varieties and reselecting the resistance in succeeding generations. The best parental sources of resistance are those exhibiting more than one component of resistance, and, better yet, those carrying more than a single gene for resistance. If possible, resistance factors from several sources should be accumulated in the new variety simultaneously, for although it is easier to manipulate a single gene in the breeding program, the multiplicity of resistance genes will greatly reduce the probability of natural selection to an insect biotype capable of overcoming the resistance. In the end, the new variety produced must be *at least* equal to those commonly grown locally in all agronomic characteristics, or it has little chance of acceptance by growers despite superior resistance properties.

#### 4.1.4 Examples of Host Resistance

To illustrate the importance and effectiveness of insect pest suppression through the use of resistant varieties we have chosen to briefly discuss the following three classic cases: grape phylloxera on grape, leafhoppers on cotton, and Hessian fly on wheat. In these examples host resistance is the principal method of suppression employed, but there are many other examples in which resistance is but one vital component in an integrated approach to reducing pest problems (Maxwell, 1972).

##### 4.1.4.1 Resistance in Grapes to the Grape Phylloxera

Of all the examples of pest suppression through the use of resistant hosts, the story of the invasion and defeat of the grape phylloxera, *Phylloxera vitifoliae* (Fitch), in France is the most outstanding. It compares favorably with the control of cottony cushion scale on citrus as one of the classic cornerstones of modern applied entomology, and according to Ordish (1972), this "triumph ... saved wine

for the world.” Curiously, the great American entomologist, C.V. Riley, again played a leading role.

The grape phylloxera is an aphid indigenous to eastern North America. It is restricted to hosts in the plant family Vitaceae and exhibits a very complex life cycle, which may be briefly and simply summarized as follows: On native American vines the life is passed in galls both above and below ground and sexual and asexual reproduction both occur. On the European vine, *Vitis vinifera* L., the cycle takes place almost wholly underground and only parthenogenetic reproduction occurs. Most important is the fact that American vine species vary in their susceptibility to the insect, with the most resistant being those which sustain lengthy leaf gall infestations but relatively brief root gall infestations. Whereas, on American vines the root galls and deformities simply stop growth and increase in root diameter, on *vinifera* the continuous infestations kill the root. When this happens the aphids abandon the desiccating food source and move to the surface of the soil through available fissures and cracks. There, they seek another vine and, if they find one, descend to its roots and again begin feeding. Thus the destruction spreads.

The presence of *P. vitifoliae* on *V. vinifera* was first discovered in an English greenhouse in 1863, and perhaps it arrived on ornamental Virginia creeper (*Ampelopsis*) imported from America (Ordish, 1972). The insect was probably also present in France at about the same time, but the year of its first appearance is usually designated as 1867 (Howard, 1930; Ordish, 1972). In 1868, the problem became of such proportion that a French commission was appointed to investigate. One of the commissioners, J.E. Planchon, discovered the insect which, in fact, was responsible for what had been considered a disease. Unaware of its identity with the American phylloxera, he named it *Rhizaphis vastatrix*, a most appropriate appellation for the European form, meaning the devastating root aphid. Shortly thereafter it was discovered that the insect was, in fact, a member of the genus *Phylloxera*, and by 1869, Planchon, his brother-in-law J. Lichtenstein, and C.V. Riley had determined the exact identity of the American and European forms. Although *P. vitifoliae* is the scientifically correct name, *P. vastatrix* has been so widely used in the literature that it too is an acceptable name.

Next came the problem of working out the life history and biology of the pest and finding a weakness in it to attack. This work was principally accomplished by Signoret, Lichtenstein, Cornu, and Balbiani in France, Westwood in England, and Riley in the USA. Planchon and Riley exchanged visits with each other to examine the insect's habits in both countries. The French government offered at first a prize of 20000 francs (later a 300000 franc prize was approved) for a cure to the problem, which brought forth a plethora of absurd suggestions from every sector of society. Much investigation and argumentation was required to sort through the suggestions. Considerable wasted effort resulted when all proved useless, especially when one considers the simplicity of the final solution.

The solution was simply to graft the European *vinifera* vines, with their highly desirable fruits, onto resistant American rootstocks. As early as 1524, the Spanish settlers in “New Spain” (Mexico) were encouraged to establish vineyards rapidly by grafting Spanish *vinifera* cuttings onto established native plants (Ordish, 1972). Unfortunately there were no phylloxera present in Mexico, so the importance of

the resistant rootstocks remained obscure, as did an early record in a Philadelphia herbarium by Buckley, an American botanist, which indicated that the introduced (European) vine flourished only when grafted to a strong native stock (Ordish, 1972). American vines had been imported and established in France in the 1840s in search of a mildew resistant variety, and it was not long after the phylloxera scourge arrived that the continuing vigor of these vines was noted. As the pest grew in importance, consideration was given to growing only American species; but they made poor wine. The idea of grafting the good fruit to the resistant root arose naturally from these considerations.

There was considerable dispute as to whom should deserve the honor (and the prize) for developing the idea (Howard, 1930; Ordish, 1972). M. Leo Laliman of Bordeaux was the first to draw attention to the resistance of American vines to the scourge of the French vineyards, and he later claimed the prize. However, M. Gaston Bazille first proposed the practical solution of grafting in 1869, and by 1871 had succeeded in carrying out his suggestion. About the same time, Planchon and Lichtenstein achieved similar success, and the following year Riley dispatched a number of specially chosen vines to France from America. Gradually the old dying roots of the European vines were replaced by resistant American species and the French wine industry was on the way to recovery. Other countries suffering the same difficulties found relief in the same solution. Laliman's claim to the 320000 franc prize money was disallowed, ostensibly because he had not *cured* the phylloxera, only found a way of preventing its occurrence. The prize should have gone to him or been shared with Bazille, but most likely went unrewarded because of governmental reluctance to part with money (Ordish, 1972).

The true value of the contribution may be gathered from the following quotation (Howard, 1930):

The alarm caused in France by the Phylloxera is difficult to exaggerate. It had many disastrous effects. Aside from the absolute destruction of the vines as early as 1884 over a territory comprising 1200000 hectares, a monetary damage which is estimated at 7200000000 francs, there must be added the consequent necessary importation of wine and of dried grapes to make wine, which cost France over 2800000000 francs, and the total loss by 1884 of ten billion francs (two billion dollars).

The solution to this problem once again illustrates the importance of a thorough knowledge of the life history, biology, and ecology of the pest insect in all its aspects.

#### 4.1.4.2 Resistance in Cotton to Leafhoppers (*Jassids*)

The leafhopper, *Empoasca fascialis* Jacobi, was formerly one of the most serious pests of cotton in Africa (Smit, 1964). Worldwide the family Cicadellidae, and particularly the genus *Empoasca*, contains a large number of important cotton pests (Husain and Lal, 1940). The insects are extremely polyphagous, but the problems on cotton have been greatly alleviated through the use of resistant hairy varieties beginning with the highly successful discoveries of Parnell and his co-workers in South Africa.

The cotton jassid, *E. fascialis*, is a small bright-green sucking insect which causes damage characterized by leaf burn, an initial yellow discoloration of the

leaf edges which turns red and spreads rapidly into the tissues between the main veins. The leaves eventually dry out and turn brown from the edges inward in severe infestations, and may fall from the plant. Young leaves become curly and brown. The insect was especially destructive in wet seasons in the lowveld of the Transvaal and in Zululand cotton areas, and was also a pest in northern and central Africa and in India (Evans, 1952; Smit, 1964). The use of insecticides against it was not economically feasible in South Africa because of its great reproductive potential on a large variety of crops and wild plants. The first widespread outbreak of *E. fascialis* occurred in South Africa in 1922–1923 causing at least a 25% reduction in yield of cotton over the next few years (Worrall, 1923, 1925). The first indications of varietal resistance were noted at that time (Worrall, 1923). Several varieties were rapidly and severely injured, but American Upland varieties of *Gossypium hirsutum* L. were less prone to injury, although they varied considerably even between plants of the same variety. Without exception the resistant plants were more hairy than the susceptible ones. A selection of the Cambodia variety of *G. hirsutum* from India was extremely hairy and practically immune to leafhopper injury (Worrall, 1925; Parnell, 1927).

The program for breeding leafhopper-resistant cotton began in 1925. Parnell (1925) observed that “all resistant plants are distinctly hairy, though all hairy plants are not necessarily highly resistant.” In that year, a single plant (designated U.4) was selected for propagation, and it became the basis for all jassid-resistant varieties grown in South Africa since 1929. By 1930, jassid populations had declined notably in Southern Rhodesia, perhaps due to the planting of resistant cotton (Peat, 1930). The selection of the single resistant plant made it possible to profitably grow cotton in areas previously considered unusable because of injurious jassid populations. The initial U.4 bulk selection was not everything the growers desired in other respects, but considerable improvement was obtained by selection within the line and a hybridization program (Parnell, 1935; Parnell et al., 1949).

The most important cotton leafhopper in Pakistan and India is *Empoasca devastans* Distant (Husain and Lal, 1940). No plant without resistance to *E. devastans* has a chance of survival in parts of India (Sohi, 1964). Injury to the plant is similar to that noted for *E. fascialis*. As early as 1913 it was recognized that hairy plants of Dharwar-American cotton were resistant to leafhopper damage (at that time considered to be a disease), and the strain was selected and maintained as Gadag I for many years. The true cause of the so-called “red leaf blight” was recognized in the early 1930s, and by 1937 a coordinated government program was under way in India to breed for jassid resistance. Local Desi varieties (*Gossypium arboreum* L.) were highly resistant to jassids but many upland varieties were susceptible (Sohi, 1964). Some introductions of resistant U.4 cotton from South Africa proved to be susceptible to *E. devastans* in the Punjab and Madras although they were profusely hairy (Husain and Lal, 1940). In any case, most hairy varieties were resistant; but some were susceptible and a few sparsely hairy varieties were resistant.

In Queensland, similar damage to cotton is caused by another species of leafhopper, *Empoasca terra-reginae* Paoli (Sloan, 1938). Breeding for resistance began about 1937, with the examination of various imported varieties including



U.4 from South Africa and Ferguson from Trinidad. These were bred to locally adapted more susceptible varieties such as Miller, and commercially useful high quality resistant selections were obtained (Marriott, 1943). Again it was noted that resistant plants were usually hairy, but not exclusively so.

Similar observations and breeding programs have been undertaken elsewhere (Painter, 1951). In Sudan, breeding for hairy-leaved varieties of cotton resistant to leafhoppers has been less successful due to difficulties in combining factors for high yield and quality with hairiness, and to the fact that hairy varieties favor injury by whiteflies. A different jassid species, *Empoasca libyca* (deBergevin and Zanon), is involved, although *E. fascialis* does occur in southern Sudan where it is relegated to minor status on the hairy upland African varieties grown there (Schmutterer, 1969).

Observations and experience worldwide have confirmed the fact that leafhopper resistance in cotton is generally associated with dense hairiness, particularly on the leaves. Work in South Africa has gone so far as to demonstrate a direct relationship between hairiness and resistance to *E. fascialis* (Parnell et al., 1949). Both density and length of hairs are implicated, but the latter appears to be the most important factor. It appears that resistance involves nonpreference by adult leafhoppers for hairy leaves, although tolerance in resistant plants is also seen (Parnell, 1927; Sloan, 1938; Afzal et al., 1943). In Queensland, the relationship between hairiness and resistance to *E. terra-reginae* is also strong, but not as complete as the situation in South Africa (May, 1951). Nevertheless, the association has proved useful in breeding for jassid resistance. Resistance of cotton to *E. devastans* in India appears to have a partially different basis, in that U.4 and some other hairy varieties are susceptible there, and a number of more glabrous varieties show resistance. The toughness of the leaf veins of resistant strains appears to be a very important characteristic in this instance (Lal and Husain, 1945; Afzal and Ghani, 1948), but this characteristic is also closely linked to hairiness. Whether or not reduced leafhopper injury to hairy cotton is due to mechanical prevention of feeding by the hairs, or some other factor, it is clear that genes for resistance are usually linked to those for hairiness, and that this characteristic may be used as an aid in more efficient development of resistant strains until the actual basis for resistance is understood.

#### 4.1.4.3 Resistance in Wheat to the Hessian Fly

Wheat is the major bread grain of the world and is grown on large acreages in North America, Europe, Asia, Argentina, and Australia (Painter, 1951). The Hessian fly, *Mayetiola destructor*, is a mosquito-like fly which was formerly a leading pest of wheat, and to a lesser degree, barley and rye in the Northern Hemisphere. At present, there is no Hessian fly-infested major wheat-growing area where at least one adapted fly-resistant wheat variety cannot be grown (Painter, 1966), and there is no need for losses to occur.

Damage caused by the Hessian fly to susceptible varieties results from the feeding habits of the larvae, and takes several forms. Larvae attack the wheat culms (stems), secreting a substance which causes the cells immediately beneath

the site of attack to cease growth. The surrounding cells continue to grow about the insect leaving a depression within which the larva feeds and develops. Finally it changes to a puparium ("flax seed"), and then emerges as the adult fly. There are usually 2-5 generations per year. Plants may be killed outright by the damaged stem or only partially incapacitated. Infestation may also increase winterkill of weakened plants or decrease yield through reduction in the actual number or size of grain heads which mature. The most noticeable damage is lodging of plants shortly before harvest when the stem breaks at the point weakened by larval attack.

The first reference to Hessian fly-resistant wheat was in an anonymously-authored farm paper in 1785 (Painter, 1951). During the late 1700s about 10 varieties were found to exhibit resistant qualities, but the first extensive studies did not occur until the 1880s and 1890s in California (Woodworth, 1891). By this time, *M. destructor* was playing havoc with wheat harvests from North America to Europe and Russia (Chesnova, 1968). Over 100 seed sources from all over the world were tested, and 22 were considered as moderately resistant, resistant, or immune. Resistant varieties tended to mature earlier than susceptible ones.

During the 1920s and 1930s major screening and breeding programs were undertaken in California (Packard, 1928) and Kansas (McColloch and Salmon, 1923; Painter et al., 1931), and also in Russia (Chesnokov, 1939). The result of these experiments was a series of new wheat varieties highly resistant to Hessian fly which were released to farmers in the early 1940s. Varieties such as Poso 42 and Big Club 43 were so successful, and replaced susceptible varieties to such an extent in California, that it became difficult to collect enough Hessian flies for seasonal history studies. In Kansas and Nebraska, the variety Pawnee was widely used, and by 1948 eliminated the fly problem in many counties. Research is continuing in this area to provide still better varieties. According to Painter (1966), between 6000 and 9000 varieties of wheat have already been screened for resistance, and at least 6 genes for resistance have been identified. Today there are 29 varieties resistant to the Hessian fly (Gallun and Reitz, 1971). Continuing changes in plant disease conditions, milling and baking requirements, and availability of varieties improved in other characteristics, results in replacement of old fly-resistant varieties by new ones superior in resistance or other respects.

As indicated earlier (4.1.2.2), the Hessian fly is an insect pest exhibiting biotype development, a fact first noted by Painter (1930). The genetics of the insect biotypes are now nearly as well-known as those of the host plant (Hatchett and Gallun, 1970). There are eight races, determined by various combinations of three pairs of alleles, and this knowledge has prompted Gallun (1974) to suggest that Hessian fly might be completely eliminated or ineffectualized over areas the size of entire states if strict governmental regulation were allowed over the variety of wheat to be planted in those areas.

The actual basis for fly resistance in wheat is still not entirely clear, although Painter (1951) implicates all three components: nonpreference, antibiosis, and tolerance. But, in any case, the ultimate goal of developing desirable resistant varieties was successfully achieved without this knowledge, and even before genetic information about its inheritance was precisely understood.

### 4.1.5 Value and Limitation of Host Resistance for Insect Pest Suppression

A number of the values and limitations of host resistance have already been touched upon, but it seems wise at this point to summarize them again along with some additional information.

The development of resistant hosts is a long range process requiring investment in the present for benefits received in the future. It is no place for short-sightedness and political whimsy. The time required to find and utilize resistance factors may be considerable; 15–20 years or more for a wheat variety (National Academy of Sciences, 1969a). Developmental time is frequently considered in comparison with that required for a synthetic insecticide, and until recently that comparison was unfavorable. Now, with greater environmental concern and demands for voluminous data supporting registration of new chemicals for insecticidal application, host resistance presents a better image. Another comparison to insecticides is appropriate (Painter, 1966). The effect of a resistant variety is cumulative, selective, and persistent on the pest population in contrast to insecticides, which are sudden, often dangerously unselective, and decreasing in effectiveness unless reapplied. Some resistant varieties are usable immediately on discovery, and once found can be utilized as rapidly as the time required in determining correct dosage of a new insecticide. Persistence is such that farmers frequently tend to forget about the insect and how it is controlled until they switch to a susceptible variety and must relearn.

The prior existence or natural selection of pest biotypes may prove detrimental to the success of a resistant host variety. Although instances of biotype development against host resistance are known in insects, the problems faced by plant pathologists are much more severe and pervasive, as are those faced by toxicologists studying insecticide-resistant strains of pests. The components of antibiosis or nonpreference can exert a strong selective pressure on pest populations, enhancing the chances for biotype development. The question of the permanence of such resistance is thus raised. The artificially accelerated process of evolution which characterizes the development of resistant varieties is essentially a forceful attempt to remove the protected plant population from the host range of the pest insect by disrupting existing host plant specificities (Beck, 1974). Eventual readaptation seems highly likely unless steps are taken to prevent it. One method of doing this is to breed-in resistant qualities from several sources, and preferably carried by different genes (Pathak, 1970; Dahms, 1972). Alternatively, genetic diversity in a single crop planted over a large area may be gained by using several resistant varieties, thus making it less likely that a mutant in a far-ranging pest species which is capable of overcoming resistance in one variety will be able to sustain its virulent gene in the total population.

The defensive nature of tolerance should be emphasized (Horber, 1974). Thus far no mechanism has been recognized in insects to overcome this component of resistance, in contrast to the aggressiveness of new biotypes in overcoming nonpreference or antibiosis. Highly tolerant varieties are fine, especially in forest or forage crops, but even a limited degree of tolerance is valuable, and may be sufficient to “buy time” for the crop until natural enemy populations build up or

other natural processes reduce pest numbers (Wyatt, 1970; Starks et al., 1972). In fact, it is not necessary, or perhaps even desirable, for any component of resistance to approach 100% effectiveness, because of the rapidity and efficiency with which such resistance screens the pest population for virulent biotypes. A low degree of resistance may accomplish all that is needed. The leading Hessian fly-resistant wheat in Kansas during the 1950s, Pawnee, was only at best 50% resistant, and yet the fly population there was nearly exterminated (Painter, 1966), providing another example of the cumulative and persistent effect of host resistance.

Another potential limitation of resistant varieties is the incompatibility of other desirable agronomic properties with resistance factors. For instance, does insect resistance in legumes affect the nutritive value of forage produced? If domestic animals or humans feed on the same parts of a resistant plant as the potential pest, what is the potential for harm? Chemicals postulated to be responsible for antibiosis or nonpreference may be especially suspect and require close scrutiny, but so far no instances are known in which a pest-resistant host proved deleterious to the well-being of humans or domestic animals (Painter, 1951). Insects are distantly removed phylogenetically from warm-blooded animals and also, apparently, in their responses to resistant plants. Resistance may be localized in tissues or plant parts not used by humans, or the causes of resistance may be active only during a short time in the life of the host, well in advance of harvest and utilization (Horber, 1974). A number of studies of resistant alfalfa cultivars show them to be equivalent in nutritive value to susceptible varieties for livestock feed (Barnes et al., 1970; Kindler et al., 1971), and often superior in quality because of decreased loss of protein and vitamins to resisted pests (Sorensen et al., 1969). The hairiness of cotton associated with resistance to leafhoppers may present difficulties in ginning because of leaf fragments mixed with cotton fibers; and the hairy leaves are reportedly more prone to attack by the cotton aphid, *Aphis gossypii* Glover (May, 1951), and cotton whitefly, *Bemisia tabaci* (Gennadius) (Schmutterer, 1969). The incompatibility of phylloxera-resistant American rootstocks with fruit suitable for wine-making was overcome by grafting (Ordish, 1972).

Farmer acceptance of a new pest-resistant variety may be a stumbling block unless it is clearly superior to the old susceptible varieties in other respects. For this reason, it is wise to constantly attempt to combine increased resistance to one, or preferably several insect pests with any breeding program aimed at improving yield or other agronomic characteristics of domestic plants or animals (e.g. Pathak, 1969, 1970).

Resistant varieties have their greatest value in crops of low value per hectare or in situations where yields vary greatly due to the uncertainties of weather or other intermittent hazards (National Academy of Sciences, 1969 a). They are also valuable in developing countries or in other situations where holdings farmed by individuals are small, and the use of insecticides is unknown, unavailable, or too expensive. An insect-resistant variety of one crop may have a beneficial effect upon another crop attacked by the same insect in the area. Use of a corn earworm-resistant corn variety in the southern United States has reduced damage by the same insect to cotton also, where it is known as the bollworm, because of the smaller total population (National Academy of Sciences, 1969 a).

Let us close this discussion with some cost-benefit analyses of host resistance for insect pest suppression. Some idea of the monetary importance of the practice has already been given in regard to the grape phylloxera situation in France during the 1880s, where the cumulative loss of over \$ 2 billion was overcome through the introduction of resistant rootstocks. More recently the idea of using host resistance to its fullest extent has gained considerable impetus elsewhere. Hanson (1961) estimated a 100:1 return on dollars invested to find resistance in alfalfa to spotted alfalfa aphid. The increased emphasis resulted in a 50% increase in manpower between 1963 and 1969 in the United States Department of Agriculture Plant Science Research Division for the purpose of studying plant resistance to insects (Sprague and Dahms, 1972). A recent estimate (Council on Environmental Quality, 1972) places the total cost of research conducted by Federal and State agencies and private companies to develop resistant varieties for Hessian fly, wheat stem sawfly, European corn borer, and spotted alfalfa aphid, at about \$ 9.3 million. The estimated annual savings in reduced losses to the farmer was \$ 308 million. This means that over a 10-year period the research has a net worth of about \$ 3 billion, or a return in reduced losses of approximately \$ 300 for every research dollar invested. More specifically, the use of Hessian fly-resistant wheat saves at least 5 million bushels of grain per year in Kansas alone (Painter, 1966). Over a 20-year period (1950–1970) every dollar invested by the USDA on the development of earworm [*H. zea* (Boddie)] resistance in corn realized a \$ 20 return in the value of increased yields (McMillian and Wiseman, 1972).

## 4.2 Environmental Manipulations and Cultural Practices

A diverse and widely used assemblage of environmental manipulations and cultural practices (Isely, 1941) is of great importance as a component of biological insect pest suppression. The principal common function involved in all of these practices is a purposeful alteration of the environment of the pest insect to make it either less acceptable to that pest, or more hospitable for its natural enemies. The desired result is a reduction of the pest to subeconomic population levels, or at least a suppression of its rate of increase and damage. Many, or most, of our native pest insects are pests because of some change made by man in their environment (e.g. extensive monoculture) which allows them to become extremely numerous and destructive. But as Tothill (1958) said, “we have changed the environment once; we have it within our power to change it again ...” Cultural practices alone are rarely sufficient to hold pest populations at low levels satisfactorily, but they are very important adjuncts within the framework of integrated pest suppression (Strayer, 1972).

Above all else, the utilization of environmental manipulations and cultural practices requires a thorough understanding of the life history, biology, and ecology of the pest and its natural enemies. The most vulnerable points of the insect pest’s life cycle must be accurately determined, and measures devised to exploit

them; alternatively, methods may be developed to buttress weaknesses in the life cycle of beneficial organisms present in the pest's environment. The methods employed are usually technical or temporal modifications of operations already utilized in the normal course of crop production, and are aimed at preventing a problem from developing at some future time rather than curing one which has already occurred. For this reason, it is sometimes difficult to evaluate the effectiveness of the measures employed. Changes in land use, planting time, tillage methods, or water management must be sound agronomic practices in other respects, or their widespread adoption by farmers has little chance. The effectiveness of many cultural and environmental manipulations often depends on their successful practice throughout a given geographic area, and therefore universal cooperation should be encouraged. If recommended cultural practices aimed at insect pest suppression are at odds with recognized sound agronomic policy, then the potential advantages and disadvantages of change must be carefully evaluated and a decision made on the basis of which combination offers greatest benefit. Careful consideration must also be given to the fact that a given environmental modification may be inimical to one pest species while at the same time encouraging to another. Perhaps the single most advantageous feature of any cultural manipulation is its low cost. In general, they require little or no additional monetary or energy expenditure because they are simply modifications of preexisting practices.

## 4.2.1 Changes in the Environment Adversely Affecting the Pest

### 4.2.1.1 Land Use

Probably the first required environmental decision which has bearing on future insect problems is the selection of a site for raising crops, or trees, or livestock, or people. For example, in the latter case, it would be simply common sense for people to settle in or inhabit areas where the risk of attack by biting flies and mosquitoes is low. A farmer does not, as a rule, locate his house immediately adjacent to a barn or livestock pen where fly infestations are most likely to be heavy. Likewise, campers prefer not to set up their tent too near a marshy area or water course with the associated problems of mosquitoes, tabanids, and black flies. However, many settlements are developed in similar locations without apparent prior thought to potential problems, only to discover too late that mosquito control with either repeated chemical treatment or expensive filling-dredging operations is required to make the place habitable. Numerous silvicultural examples may be cited. Healthy, vigorously growing trees are usually much less prone to insect attack, and certain combinations of climatic and edaphic factors are important to each particular tree species in promotion of such vigorous growth (Graham and Knight, 1965). Knowledge of these factors may be used in selecting the proper site for growing each kind of tree with the minimal risk. Thus, black locust trees are subject to less injury by the locust borer, *Megacyllene robiniae* (Forster), on a good site than on one which supports only slow-growing

trees (Wollerman, 1962). In the Great Lakes region of North America, the pine root collar weevil, *Hylobius radialis* Buchanan, causes severe damage to jack pine and Scots pine primarily on sandy, well-drained sites. Planting these species on alternate sites greatly reduces the problem (Wilson and Schmiede, 1965). Finally, in the production of grapes in California, it has been shown that vineyards established in the Napa Valley have a greater chance of escaping injury from the grape leafhopper, *Erythroneura elegantula* Osborn, than those planted elsewhere because of the abundance of wild blackberries in the Valley. The blackberries support a population of non-economic leafhoppers which serve as overwintering hosts for an important parasitoid of *E. elegantula*, thus providing a headstart for the parasitoids in the spring (Doutt and Nakata, 1965).

Crop spacing can be used in some cases to minimize insect damage (President's Science Advisory Committee, 1965; National Academy of Sciences, 1969a). Spacing may affect the relative rate of growth of the crop and its associated pest population, or the behavior of the pest insect in searching for a feeding or oviposition site. Close spacing may encourage disease epizootics in the pest population, or increase the effectiveness of predators and parasitoids. Alternatively, in other crops or in livestock, lower density spacing may make it more difficult for insect pests to locate and completely utilize the available hosts. The damage caused by the European pine shoot moth, *R. buoliana* (Schifferrmüller), to pines is one example of how plant spacing can be beneficially manipulated. Injury by this insect is greatly reduced in stands exhibiting a closed canopy. Therefore, suitable spacing in plantations to most rapidly promote canopy closure and straight growth is of definite advantage in minimizing the effects of *R. bouliana* (Graham and Knight, 1965).

A land use pattern known as crop rotation is probably one of the oldest and most widely practiced forms of cultural insect suppression. The simple idea behind this practice is to break the continuity in the readily available food supply of a pest insect. This objective is usually accomplished by alternating the kinds of crops grown in each field from year to year on a regular basis. Crop rotation is most useful against crop diseases, nematodes, and insects with a restricted host range and limited powers of dispersal. For example, legumes of various sorts are a favored host of whitefringed beetles, *Graphognathus* spp., in the southern United States, and many more eggs are produced by adults feeding on them than by adults feeding on graminaceous crops. The beetles cannot fly, and therefore are limited in their ability to move when a corn or small grain crop is planted in an area where the population has increased on peanuts or soybeans. Damage to grain crops is relatively insignificant and populations decrease rapidly. When wise crop rotation practices are followed, excluding two successive crops of legumes, these insects need not be of serious concern (Anonymous, 1969). Corn rootworms, *Diabrotica longicornis* (Say) and *Diabrotica virgifera* LeConte, arise mainly from eggs laid in cornfields in the fall. Since newly emerged rootworms the following spring cannot move very far in search of their corn host, significant population suppression can be obtained by following a corn crop with at least one, and preferably two, years of alfalfa or oats (Chiang, 1973). A rotation of cotton with sorghum or some other row crop is preferable to a non-row crop like barley or alfalfa to promote "suicidal emergence" of the pink bollworm, *Pectinophora gos-*

*sypiella* (Saunders). The minimal shading provided by a row crop allows the soil to warm more rapidly in the spring, which, in turn, causes many diapausing *P. gossypiella* pupae in the soil from the previous year to emerge before nearby cotton plants are at the susceptible fruiting stage (Mueller et al., 1974). One of the most extreme and effective rotation systems is shifting, or slash-and-burn, cultivation as it is practiced in the tropics (Nickel, 1973). Forests are cut and burned, crops are grown for 1–3 years, and then the forest is allowed to regenerate for 4–25 years as the farmer moves on to a new site. Such practices are used on about 30% of the world's exploitable land and support about 10% of the world's human population (Anonymous, 1970). Shifting cultivation maintains the long-term usefulness of the land by minimizing soil erosion and allowing for rejuvenation of soil fertility, as well as holding pest populations at low levels. The land becomes a mosaic of small plots in various stages of regrowth, and those areas which are currently under cultivation are devoted to a mixed culture of several interplanted crops. The ecological diversity thus engendered leads to an environmental stability that resists massive pest outbreaks associated with long term monoculture.

Several other land use related cultural practices may be mentioned (National Academy of Sciences, 1969a). Livestock will suffer less injury from tabanid flies if the wooded lowland haunts of these pests are pastured only in the spring and early summer when the flies are less active; upland pastures with few trees are preferable in the late summer fly season. In the Great Plains of North America, strip-cropping is practiced to reduce wind erosion and retain snow for water conservation. Wheat stem sawflies, *Cephus cinctus* Norton, are encouraged by the practice because they need move only a short distance from fallow stubble strips to adjacent growing plants. In western Kansas, migratory grasshoppers, *Melanoplus sanguinipes* (F.), behave similarly. However, strips and rotations can be designed to avoid juxtaposition of growing wheat and stubble. In fact, increased distance between crop plantings may be beneficial in other agronomic systems as well. For example, first generation chinch bugs, *Blissus leucopterus* (Say), breed in small grains and migrate to corn and sorghum when the grains mature. Migration takes place by crawling and if corn is planted at sufficient distance from the grain field, then few bugs will reach and damage it.

#### 4.2.1.2 Sanitation

Frequently, destruction of crop residues is an important technique for reducing the injury potential of insect pests by removing breeding and overwintering sites. To be used to greatest advantage, the method requires an intimate knowledge of the biology of the pest so that effective steps are taken at the proper time. Various species of injurious bark beetles (Scolytidae) are able to build up large populations in slash left behind after logging operations. Similar build-ups may occur in wind-damaged forest areas, and densities may become great enough to overcome the defenses of nearby healthy trees. Removal or destruction of slash and windthrows before a high population can develop is an effective preventative measure (Schwerdtfeger, 1955; Vité, 1972). Similarly, debarking or burning of logs and branches infested by the smaller European elm bark beetle, *Scolytus multistriatus* (Marshall), and the native elm bark beetle, *Hylurgopinus rufipes* (Eichhoff), is a



primary control measure recommended against these vectors of Dutch elm disease, *Ceratocystis ulmi* (Buisman) C. Moreau (Whitten and Swingle, 1958). Removal of cotton plant debris and early plowdown are very influential in reducing the emergence of pink bollworms, *P. gossypiella*, the following spring. Of several combinations tested, complete removal of debris, disking, and early plowdown was the most effective, whereas shredding, disking, and later plowdown combinations were much less so (Watson et al., 1974). Similar measures are useful against the boll weevil, *A. grandis* Boheman (Anonymous, 1960). Population suppression of tobacco hornworm, *M. sexta* (L.), tobacco budworm, *H. virescens* (F.), and tobacco flea beetle, *Epitrix hirtipennis* (Melsheimer), by sucker control and improved stalk destruction immediately after harvest can be so effective that insecticide treatments are no longer required (Aycok, 1974). Many fruit insects such as the codling moth, *L. pomonella* (L.), plum curculio, *C. nenuphar* (Herbst), and apple maggot, *Rhagoletis pomonella* (Walsh), maintain their populations in orchards by utilizing decaying or dropped fruit. One of the major methods of suppressing such pests in Nova Scotia (MacPhee and MacLellan, 1972) and in small orchards elsewhere is through destruction or utilization of this fruit (National Academy of Sciences, 1969a). In Florida and Georgia, burning, mowing, or heavy grazing serves to keep down the dense mat of dry grass in coastal Bermuda grass pastures where spittlebugs (Cercopidae) seek refuge (Strayer, 1972). The pasturing of livestock on crop residues is another recommended means of pest destruction which appears to have some merit (National Academy of Sciences, 1969a). Proper sanitation is the most important element in any program to lower house fly, *M. domestica* L., populations; and only cleaned storage facilities, free of old pest infested grain, should be used for storing a new crop (President's Science Advisory Committee, 1965). An important aspect in mosquito control in Africa (and elsewhere) is proper sanitation and refuse disposal in the human environment (McClelland, 1974).

Another important aspect of sanitation is the elimination of alternate hosts of the pest and nearby weedy areas which may serve as overwintering sites or some other sort of pest reservoir. This is usually accomplished by direct mechanical or chemical destruction, but Piemeisel and Carsner (1951) have advocated an indirect method which they call "replacement control." The method is based on the natural process of secondary plant succession and applies almost exclusively to uncultivated land, usually grazing land. The primary example has been the reduction of beet leafhopper, *Circulifer tenellus* (Baker), problems on beets and other crops in the western United States (Piemeisel, 1954). If desert rangeland adjacent to cultivated fields is allowed to support a weedy flora, it provides an excellent breeding and maintenance site for *C. tenellus*, which then moves to the nearby sugar beets or beans, bringing with it the virus of curly top disease. One principal weed host of the leafhopper is Russian-thistle, *Salsola kali* var. *tenuifolia* Tausch, and well over 40 500 ha of rangeland which formerly supported dense populations of this weed have been successfully seeded to suitable nonhost perennial grasses (Gibson and Fallini, 1963). Crested wheatgrass, *Agropyron desertorum* (Fischer) Schult., proved particularly useful, and it has replaced the weeds in large areas, resulting in decreased leafhopper migrations and lower incidence of curly top disease (National Academy of Sciences, 1969a). In most cases, however, alternate

hosts are destroyed mechanically or chemically. The sorghum midge, *Contarinia sorghicola* (Coquillett), overwinters in Johnsongrass, *Sorghum halepense* (L.) Pers., which grows on the borders of fields and other waste places. In the spring the midge can proliferate through one or two generations in these areas before moving into fields of grain sorghum. One of several recommended cultural practices is early cultivation or burning of Johnsongrass in waste areas to destroy hibernating midges (Walter, 1928). In India and Pakistan, various species of sugarcane borers utilize semicultivated or wild grasses and sedges near cane fields as alternate host plants (Nagarkatti and Ramachandran Nair, 1973). This frequently leads to rapid pest increases in sugarcane at the beginning of the rainy season (Carl, 1962). Mechanical removal of plants, such as wild sorghum, can reduce border infestations in sugarcane by as much as 50% (Gupta and Kulshreshtha, 1957), although increased cultivation of sugarcane with two crops a year has made the borers less dependent on alternate wild hosts (Nagarkatti and Ramachandran Nair, 1973). Injury by adults of the Japanese beetle, *P. japonica* Newman, to corn is increased in amount and extent if favored weed hosts are allowed to persist in the field (Woodside, 1954). Destruction of the forest ecosystem and replacing it with grassland has effectively reduced tsetse fly (*Glossina*) problems in parts of Africa (Ford, 1968). A particularly severe form of alternate host destruction is mandated by law in several tropical countries. The so-called "dead season" lasts four months in the Sudan and Lesser Antilles, during which time no alternate hosts for certain cotton pests, such as the cotton stainers (*Dysdercus* spp.), may be allowed to grow (Evans, 1952; Ripper and George, 1965; Schmutterer, 1969).

Judicious timing of selective pruning with suitable disposal of the waste can also be useful in reducing pest insect problems, especially on ornamental woody plants, Christmas trees, and in orchards. Weakened and dead elm branches may be infested with bark beetle larvae, and pruning and burning of this material at the proper time will destroy the brood before emergence. Selective pruning has been useful for aphid control on street trees in California (Olkowski, 1974). Many twig and shoot insects, such as the European pine shoot moth, *R. buoliana*, may be eliminated from Christmas trees if pruning and shaping are done properly. Twigs and branches of fruit trees heavily infested with scale insects may be removed from the trees and burned.

#### 4.2.1.3 Planting Dates and Harvest Times

Observation of proper planting dates and harvest times is a recognized method of avoiding severe insect pest infestations on crop plants. Often this practice (a form of pseudoresistance) is dependent upon the availability of crop varieties suited to the required schedule. The best known example of the technique is provided by the use of so-called "fly-free" planting dates in avoiding the Hessian fly, *M. destructor* (Metcalf et al., 1962). Before the development of fly-resistant varieties this was the most effective method of combating the pest. In the major wheat-growing area of the midwestern United States it is nearly always possible to sow winter wheat late enough to avoid any but a light infestation and still attain adequate plant development before winter begins. Japanese beetle injury to corn silks may be avoided by planting the crop to silk either before (Woodside, 1954) or after

(Cory and Langford, 1955) the peak of adult beetle activity in the field. In the absence of resistant varieties, Wiseman and McMillian (1969) suggest serious consideration be given to early planting dates for protection of grain sorghum from the sorghum midge, *C. sorghicola*. In southern Georgia, the method is effective before May 20, or a flowering date before July 10–15. Similar recommendations are made for sowing sorghum in Sudan, where early planting avoids heavy incidence of the central shootfly, *Atherigona varia* Meigen, and various grasshoppers, as well as *C. sorghicola* (Schmutterer, 1969). Damage by the weevil, *Hyllobius pales* (Herbst), to young pines planted in areas recently cleared of pine stands by harvest or fire, can be minimized by delaying reforestation for 9 months in the southern United States, and at least two years in northern areas (Speers, 1967). The delay allows weevils to breed and mature in stumps and remnant escape trees, and then disperse from the area when suitable habitats are no longer available. Careful attention to proper planting date is used to control rice, wheat, and millet insects in The People's Republic of China (Cheng, 1963; Nash and Cheng, 1965).

Harvesting crops as soon as proper maturity is attained usually increases yields due to the avoidance of unnecessary insect injury. This is particularly important for fruits subject to infestation by fruit flies, but also applies to such varied crops as tobacco which is subject to many leaf-feeding insects, legumes subject to weevil (Bruchidae) attack, and potatoes which may be damaged by potato tuberworm, *P. operculella* (Zeller), if left in the field too long. Damage from a number of insect pests of alfalfa can be reduced by harvesting at the early-bloom stage, which is sooner than the traditional method. New techniques allow utilization of the forage, and early harvest makes the habitat less favorable to pests like the potato leafhopper, *Empoasca fabae* (Harris), and alfalfa weevil, *H. postica* (Gyllenhal) (Casagrande and Stehr, 1973).

#### 4.2.1.4 Tillage Methods

The physical characteristics of the soil environment have great impact on some insect pests, and are themselves determined by the time and way in which the soil is cultivated (Fleming, 1957). Temperature, texture, moisture content, and organic content are all important factors which may be beneficially manipulated at low energy cost in the course of good agronomic practice. During periods when no crop is upon the land, cultivation can be used to destroy crop residues, volunteer plants, or weeds which might harbor pest insects until a new crop is sown. Deep plowing may bury some insects too deeply for successful emergence from the soil, or conversely may expose some species to high levels of parasitization, predation, or climatic mortality at the soil's surface. Examples of insect pests suppressed by proper soil preparation techniques include the corn earworm, *H. zea* (Boddie), European corn borer, *O. nubilalis*, the migratory grasshopper, *M. sanguinipes*, and the wheat stem sawfly, *C. cinctus* (National Academy of Sciences, 1969a). The grape berry moth, *Paralobesia viteana* (Clemens), is particularly susceptible to the method of plowing right up to the bases of the vines, thus burying overwintering cocoons to a depth sufficient to prevent emergence in the spring (Still, 1962). In the Prairie Provinces of Canada, the long-accepted method for suppressing the

pale western cutworm, *Agrotis orthogonia* Morrison, is to till summer-fallow in late July and leave the soil undisturbed so that a crust forms. This prevents oviposition by the adults which fly in August and September (Corbet, 1974). As with many other cultural practices, the key to the successful use of cultivation for insect control is in knowing the pest's biology well enough to time the action with the weak link in its life cycle.

#### 4.2.1.5 Fertilization

The potential effect of fertilization upon pseudoresistance in plants to insect pests has already been briefly discussed (4.1.2.1). Fertilizers are, of course, applied to enhance the growth and yield of crop plants, and in this respect their application is a cultural method of modifying the environment of the pest. In fact, plant nutrition is known to influence greatly the feeding, longevity, and fecundity of insect pests, but unfortunately the effect is not always beneficial. It appears that the effect of high fertility or large amounts of nitrogen, phosphorous, or potassium in the soil must be evaluated separately for each pest-host system. In some cases, additional fertility has direct or indirect benefit for pest suppression, whereas in others it has precisely the opposite effect (Painter, 1951; National Academy of Sciences, 1969a). Soil pH also affects population density of some insect pests. For example, research in Ohio indicated that raising the pH of soil with the application of hydrated lime consistently reduced grub populations of the Japanese beetle in test plots (Polivka, 1960).

#### 4.2.1.6 Trap Crop/Logs

In certain instances, small plantings, usually made earlier than the main planting of a crop, may be effectively used to draw insect pest attack away from the major host crop. To be effective, this trap crop must be very attractive to the target pest, and capable of sustaining a temporarily heavy infestation; it must be destroyed before pest offspring are produced and/or the main crop is available. In Ontario, the production of tobacco is dependent upon a rotation with rye for enhancement of soil nutrient and erosion prevention. However, darksided cutworm larvae, *Euxoa messoria* (Harris), begin development in the rye and are ready to attack the tobacco seedlings when they are put out in May. Bucher and Cheng (1970) suggested early interplanting of single rows of tobacco in the rye to concentrate the cutworms and make them more easily treated with a minimal amount of pathogenic virus spray. Either four or sixteen-row trap plots of cotton may be planted two weeks early to concentrate and suppress low density overwintered populations of the boll weevil, *A. grandis* (Scott et al., 1974). Stern (1969) suggested interplanting alfalfa with cotton to protect the less attractive cotton from damage by lygus bugs. Japanese beetles are known to feed on plants which are actually toxic to them (Ballou, 1929; Hawley and Metzger, 1940). Flowers of bottlebrush buckeye, *Aesculus parviflora* Walter, and cultivated geranium, *Pelargonium* spp., cause beetles feeding on them to become paralyzed, fall from the plant, and in many cases die. Although both species flower during the time of peak beetle activity, neither is attractive enough to draw significant numbers of the pest away

from favored host plants and thus protect them. Some species of bark beetles are strongly attracted to newly cut logs. In places where beetles pose a threat to standing timber, a number of trap trees may be felled and closely monitored until they have become infested with reproducing adults. The logs may then be utilized, treated with insecticide, or destroyed, thus significantly reducing the bark beetle population in the area (Thatcher, 1961; Schmid and Beckwith, 1972). Suppression of *Oryctes rhinoceros* L., a pest of coconut and other palms in the Far East, is aided by arranging heaps of decaying plant parts near the palm trees as attractants. At regular intervals, the attracted beetles are gathered, or the trap pile is treated with insecticide (Fröhlich and Rodewald, 1970).

#### 4.2.1.7 Water Management

The importance of water management in pest suppression is probably best illustrated by the fact that malaria was indirectly eliminated from much of Europe and North America before the development of synthetic insecticides, because urban and industrial development had destroyed many mosquito breeding sites (Conway, 1971). Canalling, proper impoundment, and judicious drainage of water resources all have a place in the systematic reduction of populations of aquatic insect pests such as mosquitoes, biting midges, and tabanids (National Academy of Sciences, 1969a). In addition to controlling water levels, it is frequently necessary to remove shore line vegetation which harbors and protects these pests. Such manipulations increase the exposure of the insect larvae to wave action and predation by fish and other predators. Water management is a significant tool for mosquito control in the salt marshes of Florida, but there as elsewhere, it is necessary to consider with great care the potential effects of manipulation on the total ecosystem, including its fish, wildlife, and vegetation (Provost, 1974).

Time and duration of irrigation can sometimes be manipulated to the detriment of agricultural pests. The Chinese have traditionally flooded their rice paddies at the proper time to suppress several species of rice borers (Nash and Cheng, 1965). In some cases, similar steps can be used against moth borers, *Diatraea saccharalis* (F.) and *Castnia licoides* Boisduval, in sugarcane (Ingram et al., 1951; Charpentier and Mathes, 1969). Strategically timed irrigation of alfalfa fields may be instrumental in promoting fungal epizootics among aphid pests therein (Hall and Dunn, 1957). However, proper practice and design in irrigation systems must be followed to avoid the creation of aquatic habitats which produce insect pests needlessly (National Academy of Sciences, 1969a).

## 4.2.2 Changes in the Environment Encouraging

### Natural Enemies

#### 4.2.2.1 Better Pesticide Utilization

Many beneficial natural enemies of pest insects live in very close association with their host. This circumstance frequently results in widespread wholesale destruction of the natural enemy complex when pesticides are used indiscriminately against a pest population. In fact, pesticides are probably the most important

adverse factor to be faced in the environment of a beneficial organism today (DeBach, 1974). As such, we shall have more to say about the wise use of pesticides later (Chap. 5.1), but for now we may suggest that this chemical environment is one aspect of the total environment which one can modify most easily and effectively to promote the usefulness of natural enemies. Misuse of insecticides can so disrupt the natural enemy complex of a pest that biological suppression can never be maintained; and worse, in the process, pesticide treatment can create new pests from previously unimportant insect species by destroying the complex of natural enemies which previously kept them in check.

The techniques which may be used to mitigate the adverse effects of pesticides on natural enemies include the search for chemicals with greater specificity, new modes of action, and more rapid degradability; the development of formulation, delivery, and application methods which minimize the exposure of beneficial organisms to the pesticide; and more thorough ecological understanding of the temporal interrelationships of the pest and its natural enemies. Data of this magnitude will allow a wise decision on when it is most advantageous (and least destructive) to make a pesticide application.

To illustrate how the judicious use of pesticides may enhance the benefits derived from natural enemies we may cite an example from South Australia (F. D. Morgan, pers. comm.). Both the Noolook and Bundaleer Forest Reserves sustained localized outbreaks of *Chlenias auctaria* Guenée, a geometrid defoliator of pine plantations (*Pinus radiata* D. Don). Extremely high populations of the moth larvae occurred within a central focus of infestation which was surrounded by a larger peripheral area supporting lower densities. Parasitization by the ichneumonid, *Lissopimpla excelsa* Costa, in the central infestation amounted to about 35% of the pupae, while the attack rate in the surrounding areas varied between 5 and 22%. A detailed knowledge of the host-parasitoid interaction showed that approximately two months time elapsed between the hatching of the last eggs of *C. auctaria* in the spring and the emergence of the first *L. excelsa* from parasitized host pupae in the summer. In addition, it was known that *C. auctaria* larvae were much more susceptible to DDT than were *L. excelsa* adults. During this two month period, a very low volume application of DDT was made with fogging equipment to the central infestation only. The result was a very substantial reduction of host populations in the central area. Upon emergence, the large numbers of highly mobile *L. excelsa* adults in the treated area found few hosts available nearby and moved outward into the surrounding untreated forest. Parasitization rates jumped to between 75 and 100% throughout the infested area after one careful, well-timed insecticide treatment in only a small crucial area.

#### 4.2.2.2 Land Use

As we have seen, land use patterns can be modified to the detriment of pest insects; however, proper land use can also serve to encourage the beneficial functions of natural enemies. The same can be said for a number of the other environmental manipulations discussed previously in regard to their use against pests. Crop spacing may be manipulated to the benefit of natural enemies, especially those which have limited locomotory powers. A closely spaced crop plant-

ing will make it easier for them to move from plant to plant in search of prey or hosts. The practice may also have similar effects on the transmission of pathogenic microorganisms within the pest population. A type of crop rotation known as strip-harvesting may be used to advantage in California and other warm regions of the United States for alfalfa production (van den Bosch and Stern, 1969; Council on Environmental Quality, 1972). The procedure involves dividing the alfalfa field into three broad strips, and harvesting it  $\frac{1}{3}$  at a time, allowing the remaining  $\frac{2}{3}$  to progressively regrow. This results in a more stable environment for beneficial insects because they can quickly move from the harvested strip to adjacent growing alfalfa where a reservoir of hosts or prey is readily available. When properly carried out, the procedure quadrupled the numbers of beneficial insects present, increased spider populations by one order of magnitude, and increased yield of alfalfa by nearly 15%.

#### 4.2.2.3 Habitat Provision

Strip-harvesting of alfalfa could be considered as a method of providing shelter for displaced beneficial organisms, as well as a type of land use. An analogous method of shelter provision has been devised for encouragement and conservation of parasitoids and predators of pestiferous flies in chicken houses (Hartman, 1971). Instead of frequent and complete removal of manure accumulations from under the chicken cages, the program calls for only partial removal twice a year. The residual manure harbors a sufficient number of natural enemies to maintain a greatly reduced density of manure-breeding flies, instead of temporarily allowing a pest population spurt. The encroachment of humanity upon the forest ecosystem has greatly modified it in many areas. In most cases, the result is a simplification of the environment, with entire species and/or age classes of trees harvested and removed. In some instances, the entire forest is replaced by a monocultural even-aged stand. Even orchard trees are more heavily pruned and managed for increased efficiency. The loss of shelter, nesting, and roosting sites for insectivorous birds and mammals is enormous in such habitats. In decrying the losses of "natural" or "public services" performed by the environment due to human intrusion, Holdren and Ehrlich (1974), stated it this way, "productivity is achieved at the expense of stability." Shrubs, hollow trees, brush piles, and windfalls are eliminated, and with them go many beneficial species of vertebrate predators. Such problems have been recognized in Europe longer than anywhere else, and have been dealt with, particularly in Germany, through the provision of fabricated shelters and nest boxes for the encouragement of birds (Franz, 1961b; Hagen and Franz, 1973) and bats (Buckner, 1966). Similarly several species of *Polistes* paper wasps are beneficial predators on hornworms, *Manduca* spp., which attack tobacco. Modern intensive agroecosystems tend to eliminate suitable nesting sites in woods or fencerows near the tobacco fields, but in North Carolina, the wasps accept small wooden boxes attached to fence posts as alternative nest sites (Lawson et al., 1961). This situation increased predation on hornworms and reduced the use of insecticides.

In general, environmental diversity favors the conservation and increase in numbers of beneficial organisms (Glen, 1954). Floral diversity should be most

easily realized in the forest environment (President's Science Advisory Committee, 1965). Graham (1928) found that better drained portions of tamarack swamps supported a more diverse plant community than wet sites. In such areas, small mammal populations were higher and the existing larch sawfly, *P. erichsonii* (Hartig), cocoon population was subject to much heavier predation. This suggested that lowering water levels in tamarack swamps would indirectly have a beneficial influence against larch sawfly. Healthy, diverse forest structure also encourages small mammals, and benefits are derived from them against the gypsy moth, *P. dispar* (L.) (Bess et al., 1947), and other forest pests (Hamilton and Cook, 1940).

In other agroecosystems, diversity may be more difficult to obtain because of efficiency benefits derived from the practices of monoculture (President's Science Advisory Committee, 1965). We have discussed the potential advantages of clean cultivation, destruction of crop residues, and elimination of weedy and waste areas that provide alternate host plants sustaining reservoir populations of pest insects. But such practices are not always advantageous. Again we may emphasize the necessity for a complete understanding of the biology and ecology of the target pest and its associated complex of beneficial organisms. The very same measures that are used to discourage high pest densities may be more detrimental to beneficial species, and in the long run may be ill-advised (van Emden, 1965a). Many parasitoids and invertebrate predators pass the winter in debris, or within their host in crop residues or weedy alternate host plants. If the residues are plowed under, or the debris and weeds destroyed before their emergence in spring, then many beneficial organisms will be lost. The so-called "dirty-field technique" may be advantageously applied to maintain these parasitoids and predators (Rabb et al., 1974). There is much discussion and considerable support for a shift of agricultural practices toward a more complex polyculture (Brookhaven National Laboratory, 1969), but the choice of plant mixtures, rotation schedules, and other cultural practices aimed at increasing diversity must be made intelligently to be useful (Southwood and Way, 1970).

#### 4.2.2.4 Food Provision

The availability of a reliable supply of food for each feeding stage in the entomophage's life cycle, at the proper time of the year, is another essential feature of the environment necessary for the encouragement of beneficial insect species. The provision of a suitable diet for the adults is an important and frequently overlooked requirement. Particularly in the parasitic groups (e.g. Diptera, Hymenoptera), only the immature forms subsist at the expense of the host, whereas the adults require alternate food sources, frequently pollen and/or nectar from flowering or weedy plants (Wolcott, 1942). For example, of 27 species of flies collected from the flowers of a goldenrod patch, *Solidago virgaurea* L., in England, 17 were beneficial parasitic Tachinidae (Grensted, 1946). Hymenopterous parasitoids (Fig. 3) appear to be particularly attracted to umbelliferous flowers (Leius, 1960), and one study incidence a direct numerical relationship between the number of flowers present and the incidence and activity of parasitic Hymenoptera (van Emden, 1962b). Adults of *Orgilus obscurator* (Nees), a common hymenopterous parasitoid of the European pine shoot moth, are dependent on the flowers of wild



carrot, *Daucus carota* L., in Ontario, for maximum effectiveness (Syme, 1966). Unfortunately, provincial statutes designated the plant as a noxious weed, thus making it illegal to foster its growth or allow it to flower. A plant of open spaces, *D. carota* grows wild in many pine plantations only until closure. This coincides with the period of greatest tree susceptibility to shoot moth, and by the 1970s its weed status had apparently been emended. This allowed growers to plant it and thus encourage *O. obscurator* (Corbet, 1974). Similar flower requirements have been recently demonstrated for other parasitoid species (Syme, 1975). Dietary supplements may also be important to adult predators to initiate reproduction, as in the lacewings (Tauber and Tauber, 1974).

Studies in Great Britain have shown the importance of hedgerow plants in determining the abundance and effectiveness of beneficial insects (van Emden, 1962a, 1965a, b; Pollard, 1968). Flowers in the hedges were visited by parasitic hymenopterans and tachinids, and by adult syrphid flies. Predation by syrphid larvae on cabbage aphids, *Brevicoryne brassicae* (L.), infesting Brussels sprouts was greatest near the edges of the fields where wild flowers were most numerous. Some insects, such as mirid bugs, feed on pest insects in the crop, but supplement their diet with plant food from weeds in nearby hedgerows, particularly in the absence of sufficient prey. Van Emden (1965a) called the hedges a "bridge for failures in the synchronization of parasite and pest generation and a source of prey when the pest species becomes scarce." He even went so far as to suggest that pest problems are more pressing in the USA than in Britain, because no part of a small English field is far from a weedy area, whereas the large acreages of American fields allow only minimal access to a few scattered wild areas.

Entomologists in the USSR advocate the use of weed plants in providing nectar for increased parasitoid effectiveness (Cherepanov, 1969). A cover crop of the weed, *Phacelia* sp., in orchards, greatly increased the rate of parasitization of San Jose scale, *Aspidiotus perniciosus* Comstock, by the parasitic wasp, *Aphytis proclia* (Walker). Addition of quick-flowering mustard species to cabbage fields greatly enhanced the effect of the parasitoid, *A. glomeratus* (L.), upon its cabbage-worm hosts, *Pieris* spp. Success has been reported in the use of an artificial food supplement for entomophagous insect adults which sustains them and may increase reproduction (Hagen et al., 1971). The "food spray" simulates honeydew and/or pollen, and is utilized by lacewings, *C. carnea* Stephens, and several species of Syrphidae and Coccinellidae. It consists of a commercial preparation of a yeast and its whey substrate (Wheat), sucrose, and water. Sucrose or molasses sprays utilized by Carlson and Chiang (1973) appeared to concentrate available natural predators in a treated corn field, and thus reduce European corn borer populations. The beneficial predatory ant, *Oecophylla longinoda* (Latreille), is heavily dependent for success on honeydew from a scale insect, *Saissetia zanzibarensis* Williams, in the coconut plantations of Zanzibar (Way, 1954).

The unavailability of an alternate host may limit the success of a natural enemy, rather than the absence of a food source for the adult stage. A good example of this has already been discussed briefly in another regard (4.2.1.1). *Anagrus epos* Girault, an important parasitoid of the grape leafhopper, *E. elegantula*, in California requires an alternate host in which to pass the winter when eggs of *E. elegantula* are unavailable (Doutt and Nakata, 1965). A nonecon-

omic leafhopper, *Dikrella cruentata* Gillette, which occurs on wild blackberries, actively reproduces all year long and provides a suitable alternative host. Programmed establishment of blackberries and *D. cruentata* in and near commercial vineyards significantly increases the effectiveness of *A. epos* on the grape pest by keeping parasitoid populations at a high level year-round. A similar situation occurs in Oklahoma with the greenbug, *S. graminum*, on sorghums (Eikenbary and Rogers, 1974). Low greenbug populations at two intervals during the summer create a critical situation for survival of an important parasitoid, *Lysiphlebus testaceipes* (Cresson). However, when the alternate host, *Aphis helianthi* Monell, is available on sunflowers or other host plants nearby, the parasitoid is able to maintain its population until *S. graminum* is again abundant. Much of the success in suppressing insecticide resistant *H. virescens* (F.) (see 2.1.3) on cotton in the Cañete Valley of Peru resulted from a change in the cropping system throughout the valley. This change increased the diversity of crop plants grown (Hambleton, 1944) and, in turn, provided many alternate host insects for the build-up and maintenance of a large complex of polyphagous natural enemies which attacked *H. virescens*.

#### 4.2.2.5 Tillage Methods and Dust

We have discussed how tillage and cultivation may be efficiently used to reduce pest numbers, but in some instances these practices may be inadvisable because more beneficial insects are destroyed than pests. This is especially true in the more permanent crops such as orchard fruits and citrus. Disking and cultivation, especially at the wrong time of year, may either destroy parasitoids or predators overwintering in the soil (Steiner, 1938), or reduce weeds and ground cover that protect the beneficial insects or their alternate hosts and prey (Pepper and Driggers, 1934; Muma, 1961). Dust, produced by cultivation or vehicles on nearby unpaved roads, appears far more detrimental to small beneficial parasitoids and predators than to the pests they attack, such as scale insects (Bartlett, 1951; DeBach, 1958a). Less cultivation, better road surfacing, and/or a sprinkler system to wash dusty foliage will counteract this problem.

#### 4.2.2.6 Reducing the Enemies of Beneficial Insects

Beneficial insects also suffer from natural enemies. Predators, secondary parasitoids (hyperparasitoids), or disease organisms may prove detrimental to the beneficial species and to the pest population balance they maintain. Although there are few quantitative studies to prove the point, it would appear from qualitative observation that any agency which substantially reduces the viability of beneficial organisms is detrimental to the objectives of biological insect pest suppression (Hodek, 1973). For instance, a braconid parasitoid, *Perilitus coccinellae* (Schrank), attacks and kills several species of ladybird beetle adults (Fig.42) at a rate of about 12% parasitization (Balduf, 1926). Examples of hyperparasitism are not difficult to find in entomological literature (Muesebeck and Dohanian, 1927; Sweetman, 1958; Mertins and Coppel, 1973; Ackerman et al., 1974), but the exact consequences of these occurrences is difficult to assess. Although the obvious



Fig.42. A dying lady beetle, *Coleomegilla maculata* (DeGeer), parasitized by the braconid, *Perilitis coccinellae* (Schrank), whose cocoon is visible beneath the host abdomen

answer might appear that they are destructive (Coppel, 1952), perhaps they sometimes serve a beneficial dampening function in keeping the natural enemies of pests from becoming too numerous for stable efficient population regulation. In a similar fashion, Coppel and Sloan (1971) suggested that bird predation helped stabilize populations of the larch casebearer, *C. laricella* (Hübner), and its parasitoids by selectively removing a high proportion of parasitized host larvae. De-Bach and Bartlett (1951) suggested that it may sometimes be feasible to use insecticides selectively to reduce hyperparasitism.

Benefit has been demonstrated from reducing natural enemies of beneficial organisms. A fungus disease organism, *Entomophthora sphaerosperma* Fresenius, periodically causes heavy mortality among caterpillars of the diamondback moth, *Plutella maculipennis* Curtis, on crucifers in South Africa (Ullyett, 1947). During long periods of high environmental moisture, fungal disease epizootics decimate the *P. maculipennis* population, and along with it the parasitoid populations as well. Parasitoids succumb either directly to the fungus within the host, or indirectly through the drastic reduction in available hosts for reproduction. Recurrent outbreaks of *P. maculipennis* then are released until the parasitoid population once again takes hold. Ullyett recommended fungicide application to reduce the incidence of fungal infections and the attendant problems. In Zanzibar, a predaceous ant, *O. longinoda*, is capable of regulating populations of the coreid coconut pest, *Pseudothraupis wayi* Brown, in a suitably diversified environment (Way, 1953). Interplanting of clove trees with the coconut palms affords better nesting sites and supplementary food in the form of coccid honeydew for the *Oecophylla*. However, a rich and varied ground cover is also essential, because it discourages

colonization of the area by three other ant species which do not attack *P. wayi*, although they attack and completely eliminate *O. longinoda* in clean culture groves. Other species of ants are often responsible for inhibiting the effectiveness of aphid predators and parasitoids by interfering with oviposition or actually killing the beneficial insects (Way, 1963). For example, suppression of the Argentine ant, *I. humilis* (Mayr), in citrus groves, is essential to obtain full benefit from parasitoids and predators of the scale insects, aphids, mealy bugs, and mites which attack the trees (DeBach, 1958a).

#### 4.2.2.7 Water Management

As noted earlier, water levels may be adjusted at certain times to the detriment of pest insects. Beneficial organisms may also be encouraged, however, by the judicious management of water levels. For example, mosquito fish, *G. affinis* (Baird and Girard), are far more effective predators of sparse populations of mosquito larvae in open water than in weedy areas (Danielsen, 1968). Changing the level of impounded water to reduce weedy shallows and shorelines could add greatly to their efficiency. Another scheme involves the use of properly timed irrigation to increase the incidence of disease infection of a pest. Several species of entomogenous fungi, which occur naturally in California alfalfa fields, can be enhanced in their effectiveness against the spotted alfalfa aphid, *T. maculata*, by extra periods of irrigation (Hall and Dunn, 1957). In well-drained fields which can withstand the additional water, a "blanket of humidity" is thus created to encourage more rapid and complete spread of the fungi throughout the aphid population.

### 4.3 Autocidal Control and Genetic Manipulation

The biological environment of any living thing consists of two components: external and internal. Most aspects of insect pest suppression by biological or other means concern themselves with the external environment and how it can be managed or modified to the detriment of the pest (e.g. increased mortality). However, the internal biological environment also lends itself to manipulations which can work against the pest insect. In this regard, particular attention has been accorded to the pest's genetic constitution and its potential for useful modification (e.g. decreased fertility). It is surprising that more attention has not been given to the application of genetic principles in insect pest suppression. This is especially true when we consider that so much of modern genetics has its foundation in work done on insects, particularly a vinegar fly, *Drosophila melanogaster* Meigen, the honeybee, *Apis mellifera* L., and the silkworm, *Bombyx mori* (L.). Genetics has found wide practical application in many phases of modern agriculture exclusive of insect control. However, the very characteristics which made insects ideal basic research subjects are not fully recognized for their equivalent value in applied areas of pest suppression. High reproductive potential, short life cycles, and relative ease in mass rearing are all qualities that can be used against insect pests. Also important are both the great genetic plasticity of insects (witness

the widespread development of insecticide resistance) and their genetic diversity, either in naturally occurring races, or induced with various mutagenic agents to which they are vulnerable. Finally, as suggested by Whitten (1970), the successful use of genetic manipulation for insect pest suppression sometimes requires far less basic biological and ecological information about the target organism (aside from numerical data) than other forms of biological control, at least when overwhelming numbers are available for release. The most critical factor is that random mating can be demonstrated between the liberated insects and the wild population (Whitten et al., 1973; Rai et al., 1973; Young et al., 1975). Hindsight indicates, however, that extensive basic ecological research might avoid many of the problems inherent in genetic manipulation programs on a limited budget (Whitten and Foster, 1975).

Genetic manipulation is easily included under the broad definition we have adopted for biological insect pest suppression because it involves the use of a living organism (the pest itself) for the population suppression of a pest insect considered detrimental to man. In fact, a basic tenet of the method is that the most efficient way of seeking out and attacking a pest female is with males of its own kind (Knipling, 1960a). The great specificity and environmental safety of the technique are also unsurpassed by other methods. In this chapter we will discuss briefly the theory and practice of genetic manipulation of pest insects, and also the use of induced sexual sterility for population suppression. The somewhat related subject of competitive displacement of pest insects with less noxious forms will also be treated, and we will close with a discussion of the potential for genetic improvement of beneficial organisms.

### 4.3.1 Suppression or Eradication Through Induced Sexual Sterility

In most aspects of biological control we deal in relativity; that is, we strive for the suppression of pest numbers to an economically acceptable level relative to a previously existing unacceptable high level. The application of the principles involved with induced sexual sterility has allowed us to think in terms of absolute eradication of a pest, a rare pleasure.

The hypothesis upon which the so-called sterile-male technique is based was first conceived and developed by E. F. Knipling in the late 1930s (Knipling, 1955; Baumhover et al., 1955; Lindquist, 1955). A number of recent extensions and elaborations of Knipling's early simple models have appeared recently (Weidhaas, 1973; Miller and Weidhaas, 1974). Simply and briefly summarized, the argument is as follows: The reproductive capacity of many animals is barely adequate to overcome the environmental resistance which is expressed in various forms of natural mortality. Under normal conditions they can maintain their population size, but a drastic reduction in their reproductive potential would be an intolerable blow. If sterility can somehow be induced in individuals of the species without destroying their sexual competitiveness, and overwhelming numbers of these sterile individuals can be introduced into the natural population over a period of

several generations, then a drastic reduction in reproductive potential will be realized, and the natural population will disappear. The simplicity of the method belies its effectiveness, and the passage of this so-called autocidal technique (Knippling, 1960a) beyond the hypothetical to full realization in regard to the screwworm fly, *Cochliomyia hominivorax* (Coquerel), has been called "one of the most remarkable biological achievements of our time" (Christenson, 1966).

#### 4.3.1.1 *Screwworm Eradication Program*

The history of the eradication of the screwworm from the southeastern United States is well known to most entomologists and the informed public, and has been documented and recounted numerous times (Knippling, 1959, 1960a, b; Bushland, 1960; Ball, 1961; Baumhover, 1966). A brief summary will suffice here.

The larval form of the blow fly, *C. hominivorax*, is the screwworm, a maggot which gregariously infests open wounds of wildlife and livestock, increasing them in size and eventually causing death of the host. The resulting annual monetary losses ran into the hundreds of millions of dollars in the southern USA. The twenty years, between the hypothesis of Knippling and its realization in fact, were filled with discussion, theorization, and research by the men involved. Necessary biological and ecological information regarding the suitability of *C. hominivorax* was accumulated (Smith and Skipper, 1952; Bushland and Hopkins, 1953; Bushland, 1960), a means of mass rearing was developed (Melvin and Bushland, 1940; Graham and Dudley, 1959), and a safe practical means of sterilization was devised and evaluated (Bushland and Hopkins, 1951; Lindquist, 1955). Pilot tests on Sanibel Island, off the Florida coast, and on Curacao in the Caribbean, were successful and helped develop release procedures and methods of evaluation (Bushland et al., 1955; Baumhover et al., 1955).

By 1957, the stage was set for an attempt at eradicating *C. hominivorax* from the state of Florida. As it turned out, eradication from Florida meant elimination of the insect from the entire southeastern USA, because the winter of 1957–58 was particularly severe and screwworm survival north of Florida that winter was nil. Headquarters for the project was Sebring, Florida, where an old aircraft hanger was converted to an automated fly factory which operated 24 h a day, seven days a week, producing 54 million sterile flies per week. Fly pupae were exposed to a predetermined dose of gamma-radiation from a cobalt-60 source and the resulting sterile flies were dispersed by air drop over the entire southern half of Florida. The program was considered a complete success when, after 18 months of activity, researchers were unable to find any wild screwworms in the entire Southeast. To the present, the same situation is in effect, and although occasional infections occur in the area in association with imported livestock from infested areas, these are quickly and easily eliminated. The cost of the entire project was \$ 10.6 million, or approximately half of the annual losses caused in previous years by screwworms (Davidson, 1974).

With the encouraging success in the Southeast behind them, U.S. Department of Agriculture personnel set about a much more difficult task, the projected eradication of *C. hominivorax* from the Southwest, and eventually from all of North America. In addition to the much larger area to be covered, the terrain in

the Southwest was more rugged and inhospitable to released flies. There was no natural isolation of the infested area as in the East, and reinfestation from climatically favorable havens in Mexico was a constant threat. The plan was to first eradicate the flies from the USA, and then maintain a 160-km-wide barrier zone across northern Mexico with sterile fly releases to keep migrant wild flies from reentering. A new fly factory was constructed at Mission, Texas, and the program was begun in 1962. Subsequent observations showed that wild flies were capable of traversing the barrier zone, and its width was increased in some places to 560 km. The Mission facility employed 300 people and had a capacity of more than 150 million flies/week. The first objective, that of eradicating the screwworm from the USA, was apparently accomplished, but maintaining the barrier zone of 2900 by 560 km has proven to be a difficult task (Anonymous, 1973c). By 1970, only 153 cases of screwworm were confirmed in the United States, apparently all directly resulting from Mexican invasions. This compares to 50000 estimated cases in 1962, the year the program began. However, by 1972, analysis of published records in the Cooperative Economic Insect Report of the U.S. Department of Agriculture showed a total of 92000 cases for the year (Anonymous, 1973c). (The final official USDA total was 95642.) Reasons for the increased screwworm activity have been adequately discussed by Bushland (1974, 1975). This alarming situation led to a redoubled release effort, and an announcement of a 5-year cooperative plan between the USA and Mexico to eradicate the screwworm from northern Mexico. A new fly factory is under construction near Tuxtla Gutierrez, Mexico, with a capacity of 300 million sterile flies/week (Bushland, 1975). Cooperating with the Mission factory, the objective is to push the barrier zone at least as far south as the narrow Tehuantepec Isthmus, where it will require far less effort to maintain. In the meantime, sterile fly releases of up to 200 million/week in the barrier zone of northern Mexico, and the areas of the United States adjacent to it on the north, are once again slowly reducing the number of reported and confirmed screwworm cases. The total for 1973 was 14976 and for 1974, 7267 (U.S. Department of Agriculture, 1974, 1975), representing a decrease of 84.4% and 92.4%, respectively, against the 1972 record total.

Like the introduction of the vedalia beetle into California citrus groves, and the use of phylloxera-resistant American rootstocks in French vineyards, the success of the screwworm eradication program marks a milestone in applied entomology and biological insect pest suppression. It has shown the way toward a new rational solution to pest problems. Again a theory has been formulated and has successfully survived the test of practical application, and in the process, established a philosophical basis for the further understanding and extension of its principles (see International Atomic Energy Agency, 1969, 1970, 1971; Smith and von Borstel, 1972; Davidson, 1974; Pal and Whitten, 1974).

#### *4.3.1.2 Principles and Methods in the Autocidal Technique*

A summary of the basic requirements for application of the sterile-insect technique was presented by Knipling (1964, 1967). These included: a method of mass rearing the target insect, availability of a method of inducing sterility without adverse effect on competitiveness and mating behavior, quantitative information

on natural-population density at the low level in the population cycle, a practical way to reduce natural populations to levels treatable with sterile insects, and data on rate of population growth to determine release ratio required to overflow with sterile insects. The cost of current suppressive measures plus losses caused by the insect must exceed the cost of reducing the natural population to manageable size plus the cost of rearing, sterilizing, and releasing the required number of insects. If immigrating insects undergo a successful eradication, then the cost of maintaining control through continuing releases of sterile insects must be favorable in comparison to the cost of other methods plus additional losses caused by the insect. Even if cost comparisons show sterile insect releases in an unfavorable position, such a program may be justifiable if it shows advantages in reducing environmental hazards attributed to other suppressive methods. Released sterile insects must not cause undue losses to crops or livestock, or create hazards for humans that outweigh the benefits of achieving or maintaining pest population suppression.

As illustrated by Knippling (1960a, 1964, 1967), the release of sterile insects is unusual among pest suppressive methods in that it becomes increasingly efficient with decreasing population density. That is, the lower the density of wild insects becomes in the release area, the greater will be the ratio of sterile to wild attained with a given number of released insects. With all of its advantages, however, the method does have some limitations. For example, it is useless against insects reproducing by asexual means. Also, some serious pests occur in such abundance and have such wide distribution that, at present, it is not feasible to rear sufficient numbers of sterile insects to overflow the natural population. However, improved methods of population reduction by other means may bring their numbers within reach, and, on the other hand, improvements in rearing technology may soon make massive rearing programs more feasible (Knippling, 1966; Gingrich, 1972; Davidson, 1974). A third alternative solution is the sterilization of the wild population in situ (see following discussion on chemosterilization).

The very successful screwworm eradication program has, of course, inspired widespread research interest and a number of imitative and innovative programs against other important insect pests. Major emphasis appears to have fallen upon insects of public health importance, particularly Diptera (Pal and Whitten, 1974; International Atomic Energy Agency, 1975). This emphasis stems principally from the more advanced state of formal genetics among the Diptera (cf. mosquitoes and *Drosophila*) and the fact that the screwworm program, which led the way, dealt with a medically important dipteran. Some successful programs and investigations have been based on the same sterile insect release technique already proven with *C. hominivorax*, while others use more advanced procedures to be discussed in subsequent sections.

As indicated previously, sterility in the released screwworm flies was induced by gamma-radiation from a cobalt-60 source. At the time the eradication program was begun, irradiation was the only practical way of inducing sexual sterility (Muller, 1927; Bushland and Hopkins, 1951). However, an important requirement of sexually sterilized individuals is that they be fully competitive with wild types, and irradiated insects usually exhibit reduced competitiveness (Proverbs and Newton, 1962; Knippling, 1967; Ducoff, 1972; Snow et al., 1972; Katiyar and



Ramirez, 1972). One way of overcoming this problem is to increase the ratio of sterile wild insects (Rhode et al., 1961). Most recently, however, the emphasis has been on using chemical sterilants to replace irradiation (LaBrecque, 1961; LaBrecque and Smith, 1968; Crystal, 1972; Haniotakis and Galachtiou, 1973; and many others).

Chemosterilants have advantages over radiation because they are less likely to have an adverse effect on longevity and mating competitiveness. In fact, some evidence indicates that chemosterilized insects may be more sexually active than untreated ones (LaBrecque et al., 1962). Chemosterilants are relatively cheap and easy to use when compared to the expensive equipment needed for irradiation (James, 1972). However, in large-scale use it is as yet difficult to attain the uniformity of application characteristic of irradiation. The biggest potential advantage of chemosterilants is the possibility of using them to sterilize wild insects in the field. Knipling (1959) discussed the "bonus effect" this would have compared to insecticide treatment. Not only would insects contacting the chemical be prevented from reproducing (equivalent at the population level to killing them), but they would mate with other remaining unsterilized insects, thus impairing *their* reproductive potential. Should this method become practical, expensive mass rearing of pest insects for sterilization and release might become obsolete. Unfortunately, all but a few known chemosterilants affect humans and other higher animals (or plants) as sterilants, mutagens, carcinogens, and/or toxins (Campion, 1972; McDonald, 1974), so that, at present, their widespread distribution in the environment would be unwise. The proposed solution to this dilemma is the development of attractant-sterilant combinations for use in field application. Then, rather than take the chemical to the pest, the pest would be attracted to the chemical, and environmental contamination would be avoided. Sound, light (Grant et al., 1970), sex attractants (Campion and Outram, 1967), food attractants (Luckman et al., 1967; Pausch, 1969), or oviposition attractants (Bracken and Maw, 1972, 1975), are all possible agents for bringing wild populations into contact with sterilizing chemicals. At present, however, no truly effective sterilant-bait mixtures are available on a large scale, and the use of chemosterilants is limited to laboratory application on mass-produced insects as an alternative to radiation.

In the final analysis, radiation and presently useful chemosterilants are but two different means of attaining the same result: dominant lethal mutations in the genetic material of the treated individuals (i.e. sexual sterility). These two methods are the most extensively investigated ways of applying the sterile insect release technique for insect pest suppression, but they are not the only means of achieving the goal. Two other methods are known which have a different basis, but which theoretically should give the same end result. In one, a strain of insects is genetically constructed in the laboratory such that males of the strain reproduce nothing but male offspring when outcrossed to wild females. If mass produced and released in nature, such males could eventually distort the sex ratio so much that the wild population would face extinction. Such male-producing strains have already been developed in house flies (Wagoner and Johnson, 1974). The second method involves "a kind of prefabricated sterility" called cytoplasmic incompatibility (Laven, 1974). Crosses between geographically isolated (allopatric) populations of the same species (in this case the house mosquito, *C. pipiens* L.) may

produce no offspring. This is caused when the sperm of one strain is blocked for some reason in the eggs of another strain, and therefore the eggs cannot complete development to hatching. Releases of large numbers of male-producing or incompatible males into an area should have the same effect as releases of artificially sterilized males, except that competitiveness, longevity, and vigor is unimpaired in any way.

Several other less studied methods of obtaining sterile insects for release are also known. Denell (1973) has produced a sterilizing mutation in *Drosophila* such that the sperm of males bearing the mutation behaves much as the cytoplasmically incompatible sperm discussed by Laven (1974). Heat treatment of pupae has been shown to be 100% efficient in producing fully competitive sterile male adults of *Heliothis* spp. (Guerra, 1972). Conversely, low temperatures effectively sterilize eggs, larvae, and pupae of the false codling moth, *Argyroplote leucotreta* Meyrick (Myburgh, 1965). High-intensity photoflash equipment sterilized *A. aegypti* (L.) and the parasitic wasp, *D. fuscipennis* (Zetterstedt) (Riordan, 1964, 1966). Another potential way of producing sterile insects for release is through hybrid sterility (Davidson et al., 1970; Davidson, 1974; Proshold and LaChance, 1974; Manglitz and Russell, 1974). This method would only involve the ability to rear large numbers of two related species, and their successful hybridization. In the species pairs under investigation, such matings produce offspring which are partially or completely sterile, yet not reproductively isolated from the parental species, thus eliminating the extra, and often debilitating, sterilization step. In addition, such hybrid insects may exhibit heterosis, or hybrid vigor, and be more aggressive and competitive in nature than the wild, fertile members of their parental species. Another similar proposal by Downes (1959) involves the release of so-called "strong races," of gypsy moth, *P. dispar*, from Asia to mate with "weak" North American races. The resulting females are all intersexual and sterile; the hybrid males are fertile and pass along the impotency to one-half of their female offspring. A recent aspect of the provision of sterile insects for mass release is the demonstration of the reduced drawbacks and increased effectiveness in combinations of the various methods, such as high/low temperatures and chemosterilants (Crystal, 1973), or gamma irradiation and chemosterilants (Guerra, 1975).

#### 4.3.1.3 Additional Sterile-Insect Release Programs

Let us conclude this discussion of insect pest suppression through the use of sterile insects with a few other examples of programs inspired by the success of the screwworm eradication. An early and successful modification was the work of Horber (1963, 1968), in Switzerland, on the cockchafer *M. vulgaris* F. The insect has a long (three year) life cycle and is therefore difficult to mass rear artificially, although diapausing individuals may be accumulated and held at 10° C for more than a year. The biology and distribution of *M. vulgaris* is such that it occurs in relatively isolated local populations, and at certain times the sexes are behaviorally separated in the environment. These characteristics led to a unique application of the autocidal method whereby males were collected from the local targeted population, and then sterilized by irradiation, along with additional males from other so-called beetle "bank" areas. After two releases of sterilized male chafers into the treated area, three years apart, the local insect population was successfully eradicated.

Another successful sterile-insect release program which is unique in concept is the Mexican fruit fly quarantine-barrier program along the USA (California)-Mexico border (Christenson, 1966; Knipling, 1967; Proverbs, 1969). The Mexican fruit fly, *Anastrepha ludens* (Loew), occurs in low numbers in northwestern Mexico and poses a constant threat to adjacent California fruit-growing areas. Until 1963 a barrier was maintained between the two countries with routine insecticidal sprays, but since then the pests have been effectively barred from entry through the release of chemo- or radiosterilized flies. Because of the relatively small native population, only a few million sterile flies are needed every couple of weeks, and the cost of production and release is only a fraction of the spray program replaced.

Several other sterile-insect release programs are more conventional in their adherence to the ideas, procedures, and objectives of the screwworm program, and have shown varying measures of success. The melon fly, *Dacus cucurbitae* Coquillett, was completely eradicated from the Pacific island of Rota through the release of 257 million sterile flies over a period of about 10 months, after the initial population was reduced with insecticide-bait sprays (Steiner et al., 1965). After two typhoons destroyed the host crops and drastically reduced populations of the oriental fruit fly, *D. dorsalis* Hendel, on Guam, the residual population was localized with bait traps, overflooded, and eradicated through the release of 36 million sterilized pupae (Steiner et al., 1970; Chambers et al., 1970). Chemosterilized mosquitoes, *C. pipiens quinquefasciatus* Say, were used in a number of release programs (Davidson, 1974), with incomplete success. In only one small test, on Sea Horse Key in Florida, was total eradication achieved (Patterson et al., 1970). An attempt to eradicate the tobacco hornworm, *M. sexta* (L.), on the Caribbean island of Vieques failed, apparently because radiosterilized male moths suffered a reduced ability to utilize the female sex pheromone in mate location (Cantelo et al., 1973). Irradiation at a later stage of pupal development may reduce the problem. Parallel sterile-insect release projects have been carried out for a number of years in British Columbia (Canada) and Washington State (USA) with the aim of suppressing codling moth, *L. pomonella* (L.), in regional fruit orchards (Proverbs, 1971, 1974; White et al., 1973). In many cases, success has been at least equivalent to that provided by insecticides (Butt et al., 1970). Eschle et al. (1973) were encouraged by the degree of suppression achieved with sterile insect releases in a semiisolated dense population of the horn fly, *H. irritans* (L.), in Texas. Further experiments in a larger nonisolated population area resulted in about 90% population reduction (Kunz et al., 1974).

The preceding are but a small sample of the many and diverse applications of the principles of induced sexual sterility for insect pest suppression now under study. The years ahead look bright indeed for this technique.

### 4.3.2 Genetic Manipulations of Pest Populations

The utilization of induced sexual sterility as discussed in the preceding section is the simplest form of genetic pest suppression. A number of more complicated, intricate, and elegant ways of using an insect's genetic constitution against itself have also been proposed. Some of these are mere extensions of the sterile-male

release principle; others are based on entirely different concepts. Some have been subjected to experimental testing; others are as yet based only upon hypothesis. A few examples will indicate the breadth and potential of this field of study.

#### 4.3.2.1 *Decreasing Genetic Fitness*

The major characteristic which sets the sterile-insect technique apart from other genetic methods of insect pest suppression is the fact that complete sterility cannot be inherited. Other techniques involve the use of various deleterious genes which can be introduced into wild populations, and which will become dispersed throughout the population to reduce its genetic fitness. We have already touched on one such method, the release of a genetic strain which carries a male-producing factor. Although the end result is approximately the same as releasing sterile insects, the male-producing factor is, in fact, transmitted from generation to generation, gradually reducing the practical reproductive capacity of the population as the number of females produced is sequentially reduced.

The release of partially sterile insects is a modification of Knippling's original idea which has recently gained favor, especially for Lepidoptera (Knippling, 1970; Smith and von Borstel, 1972; North, 1975). Enough work on the sterile-insect technique has been done to show the generally adverse effects of high doses of radiation or other sterilizing agents on the behavior and mating competitiveness of many insect species; Lepidoptera appear especially difficult subjects for complete sterility with minimal adversity. Proverbs (1962) seems to have been the first to notice that lower, substerilizing doses of radiation caused the surviving  $F_1$  progeny of treated codling moths to consist largely of sterile males. Such delayed inherited sterility effects have since been noted in other Lepidoptera (Walker and Quintana, 1968; Stimmann, 1971; Cheng and North, 1972; Bariola et al., 1973; North, 1975). Basic observations by Bauer (1967) led others to discover the chromosomal basis for the effect (Walker and Quintana, 1968), and to suggest means of applying the knowledge to insect pest suppression (North and Holt, 1968, 1971). Knippling (1970) reviewed the concept of inherited partial sterility and presented a theoretical appraisal of its effectiveness in use. Lepidoptera are particularly resistant to induced sterility because of the structure of their chromosomes, which lack a distinct centromere. This type of structure is found elsewhere only in Homoptera and Hemiptera, which should prove similarly resistant (North and Holt, 1970). In brief, the effect of radiation of this type of chromosome is to cause rearrangement of the genetic material (translocation) rather than its loss at the next cell division (lethal dominant mutation) as in other insects. Insects bearing the translocations show reduced reproductive abilities. A number of workers have concluded, theoretically and in practical experiments, that the release of insects carrying such inherited sterility would be much more effective for suppression of Lepidoptera than the release of completely sterile insects (North and Holt, 1968, 1971; Knippling, 1970; Proverbs, 1971).

A similar system of pest suppression involving chromosome translocations was recognized and suggested as early as 1940 by Serebrovsky. Curtis (1966) rediscovered the idea, and proposed its application for suppression of tsetse flies, *Glossina* spp. The method proposes mass rearing of a strain of insects homozygous for an induced translocation. Translocation homozygotes are generally fully

fertile if they are viable, whereas heterozygotes are frequently semisterile. Release of a large number of translocation homozygotes into a wild population would result in many matings producing semisterile heterozygous offspring, thus reducing the general fertility of the population. For reasons we need not discuss here (Smith and von Borstel, 1972), the minimal population fertility would normally occur when the number of individuals of the homozygous translocation strain is equal to the number of the homozygous wild strain. To retain the equilibrium relationship in a natural population it would be necessary to monitor the gene pool and add the appropriate set of chromosomes as necessary. The presence of multiple chromosomal translocations could reduce the fitness of heterozygotes even more than single translocations, and, in theory, fertility could be reduced to zero (Curtis and Robinson, 1971). The method is now under development for use against a number of insects including the house fly (Wagoner et al., 1969), several mosquito species (Whitten, 1971a; Rai and McDonald, 1971; Laven et al., 1972; Laven, 1974), and the tsetse fly, *Glossina* spp. (Curtis and Hill, 1968, 1971).

Another type of genetic manipulation foreseen by Knipling (1960a) has aroused considerable interest recently. It is the introduction of various conditionally lethal mutations into a wild population. The presence of such a factor allows an individual possessing it to survive in one environment but not in another. Smith and von Borstel (1972) have termed this method "the genetic time bomb." Both dominant and recessive conditionally lethal factors have been recognized and described in various insect species, but the former appear more likely as candidates for use in pest suppression on their own strength. Factors such as heat or cold sensitivity, loss of ability to form a cocoon, or to utilize natural food, may all have potential use. However, most attention has been given to geographic variation in the ability to diapause (Hogan, 1966; Masaki, 1968; Klassen et al., 1970a, b; Wehrhahn and Klassen, 1971). For example, the Australian field cricket, *Teleogryllus commodus* (Walker), passes the cold winter months in the southern part of its range only as diapause eggs (Hogan, 1966). Northern populations, however, produce nondiapause eggs, and if males from the North are mated to southern females the subsequently produced eggs are also nondiapause. Inundation of the southern population with mass-produced males of the northern strain bearing the apparently dominant factor for nondiapause eggs should greatly reduce the fitness of the population in the colder climate, although problems with ecological population isolation mechanisms are still to be overcome (Hogan, 1974). Klassen et al. (1970a, b) present calculations and evidence for similar possibilities in suppressing the boll weevil, *A. grandis*. Here, the effective penetration of the deleterious factor for nondiapause into the wild population may be increased 100-fold if it is genetically linked to a factor for insecticide resistance (Wehrhahn and Klassen, 1971). Thus, far fewer insects would have to be released to obtain effective insect suppression. Selective pressure applied on the wild population through repetitive treatment with insecticide will quickly incorporate the beneficial gene for resistance to that insecticide. Introduction of such a gene closely linked to a gene for nondiapause will distribute both genes rapidly and completely. When cold weather arrives the entire population carrying the dominant conditional lethal for nondiapause will perish.

The rapid incorporation of a conditional lethal by linking it to an otherwise beneficial gene is similar in effect to the phenomenon of meiotic drive as defined

by Sandler and Novitski (1957). The proposed genetic definition describes meiotic drive as "any alteration of the normal process of meiosis with the consequence that a heterozygote for two genetic alternatives produces an effective gametic pool with an excess of one type." Theoretically, only small releases of a deleterious strain would have to be made to overflow the population, although larger releases would speed the process. Several systems have been demonstrated which have a meiotic drive effect in addition to the insecticide-resistance selectivity just described. For instance, Hickey and Craig (1966) describe a sex ratio distorter mutation in *A. aegypti* which results in a high proportion of males (up to 90%) being produced when males bearing the factor are crossed to virtually any female genotype. Such a factor in itself might be useful, particularly in a pest insect where the female is a disease transmitter, by reducing the size of the female population. It might also be used to force deleterious sex-linked mutations on the segregation-distorting chromosome through the population. A recessive female-sterile sex-linked mutation in *A. aegypti* produces bronze body color marker, and in conjunction with the distorter drive system it could be introduced into wild populations to reduce their fitness quickly (Craig and Hickey, 1967). Another useful sex-linked recessive factor renders the bearer refractory to infection by human disease organisms, and could be used to make wild populations incapable of disease transmission (Davidson, 1974).

The mass release of an insect strain homozygous for an induced translocation, as previously discussed in this chapter, might also be used as a sort of carrier mechanism to introduce and distribute conditionally lethal mutations (Curtis, 1968; Whitten, 1971 b). As noted earlier, the greatest effect of the translocation homozygotes in reducing general fertility occurs when they are present in numbers about equal to those of the wild strain in the field population. This equilibrium must be artificially maintained, however, because the translocation heterozygote is semisterile, and therefore less fit than either of the homozygotes. If both homozygotes (i.e. wild or translocation) are equally fit, then the more frequent chromosome type will eventually replace the other in the population (Serebrovsky, 1940; Curtis and Hill, 1968). Although a temporary equilibrium might occur at a frequency of 50%, chance variations in the relative frequencies one way or the other would eventually start a selection process resulting in complete displacement of one homozygote by the other. If we assume that this displacement is in the direction of the introduced translocation homozygote, and if we have associated the translocated chromosome with a conditional lethal previously, then the newly constituted translocation population will completely succumb to the appropriate adverse conditions when they arise. Examples of the potential use for such a mechanism have been devised by Wagoner (1968), Curtis (1968), Whitten (1971 b), and Fitz-Earle et al. (1973). This system makes useful the otherwise unattractive recessive conditional lethals which normally would not penetrate a natural population to any great degree without such a driving mechanism. LaChance and Knipling (1962) and McDonald (1970) discuss several potentially useful recessive conditional lethal mutations. Temperature-sensitive mutations, such as those discovered in *M. domestica* (McDonald and Overland, 1972) or *D. melanogaster* (Suzuki, 1970), might be carried rapidly into a wild population and the genetically unfit population would collapse when the restrictive temperature conditions occur.

#### 4.3.2.2 Increasing Pesticide Susceptibility

Another aspect in the genetic manipulation of pest populations that merits particular and specific mention is the concept of increasing pest susceptibility to pesticides. The major proponent of this idea has been Whitten (1970, 1971 b) in his work with the Australian sheep blow fly, *Lucilia cuprina* Weidemann. Most likely the system would be applicable to other species as well.

Whitten advocates genetic manipulation of the natural population of *L. cuprina* to reduce the frequency of the gene for resistance to insecticide. For instance, dieldrin suppressed the fly effectively until 1956 when a single gene arose which conferred very high resistance to the insecticide (Shanahan, 1961). The frequency of the gene rose rapidly from near zero to nearly 100%, and although the use of dieldrin was discontinued, the gene still persists at a high enough level in nature to preclude the use of this pesticide again. Although the wisdom of the widespread use of a highly toxic persistent chemical such as dieldrin is questionable in the first place, the fact remains that elsewhere other safer pesticides have suffered similar fates. Rather than increasing the dosage or frequency of application to unreasonable extremes just to maintain the same level of suppression, or shelving the pesticide in favor of a new, expensive to develop, and perhaps more toxic chemical, why not make a resistant population once again susceptible?

As we have seen, methods for doing this are available. Whitten (1970, 1971 b) advocates the use of single or even multiple strains bearing induced chromosome translocations for rapidly displacing the wild gene for resistance with one for susceptibility. Any of the other manipulations displaying characteristics of meiotic drive might also have potential use in this regard. The possibility may exist not only for making insects again susceptible to chemicals for which they have gained resistance, but also for induction of susceptibility to simple chemicals never before usable as pesticides.

#### 4.3.3 Competitive Displacement

The ecological concept known as competitive displacement refers to the phenomenon of one species of insect (or other organism) displacing or eradicating another species in nature over a substantial area through competition. Although the process does not always involve a deliberate genetic manipulation by man, it is nevertheless basically dependent upon genetic differences between the two species, be they natural or induced. The concept of competitive displacement is closely allied with the principle known as Gause's Law, which states that different species occupying identical ecological niches (i.e. ecological homologues) cannot coexist indefinitely in the same habitat (Gause, 1934). Ecological niche does not refer simply to the physical habitat alone, but instead implies all the things that the organism does or requires for survival and reproduction in the habitat. Combat or predation are not necessarily involved in competition between ecological homologues. In fact, the two species need not ever come into direct contact. What is required is that some critical resource(s), for example food, be subject to the exact same sort of utilization by both species, and that one species have some *intrinsic* (genetic) advantage over the other in using the resource.

Several good reviews are available on the whole concept of competitive displacement (DeBach and Sundby, 1963; DeBach, 1964c, 1966; National Academy of Sciences, 1969a), but for the present we are concerned with how the idea might be applied to insect pest suppression. In a very broad sense, most of the examples already cited in this chapter have as their basis a kind of intraspecific competitive displacement, in which a mass-produced genetic strain of an insect pest is released into the natural population with the aim of overflowing and displacing the wild strain. This is why researchers are always concerned about the competitive ability of their released insects. In many of our examples, the competition between strains occurs at the reproductive or genetic level, and overall fitness in the ecological niche is frequently determined by reproductive proficiency. We may especially recall the instances utilizing meiotic drive phenomena in this regard. For instance, boll weevils carrying a gene or genes for insecticide resistance quickly spread that ability throughout a natural population subjected to heavy selective pressure from use of the insecticide (Wehrhahn and Klassen, 1971). Thus, the introduced resistant genetic strain is more fit than the wild strain to the existing ecological niche, and displacement occurs. Now, if the released weevils also carry a dominant conditionally lethal genetic factor for nondiapause, then the coin is flipped when cold weather arrives, and the entire population is suddenly unfit and collapses. Also consider the work of Whitten (1970, 1971b) with increasing pesticide susceptibility, or similar suggestions by Curtis (1968) or Davidson (1974) to replace mosquito strains capable of vectoring diseases with other refractory strains. In other experiments, Foster and Gallun (1972) demonstrated that the Great Plains race of the Hessian fly, *M. destructor*, carrying dominant genes for avirulence, could be effectively used to overflow and displace the eastern races normally infecting wheat varieties grown in Indiana. Smith and von Borstel (1972) suggest selecting a strain of phytophagous pest in the laboratory which, instead of feeding upon the normal crop plant host, prefers only to feed upon a pest plant or weed. Displacement of the wild population through mass release of this new strain could turn a pest into a beneficial insect.

Such examples of intraspecific competitive displacement perhaps stretch the concept far beyond its usual meaning. Most observations of the phenomenon and suggestions for its application in pest suppression involve interspecific competition. In general, four basic procedures are recognized for this purpose. In one, the harmless species (or group of species) of a pair of sympatric ecological homologues would be directly encouraged to displace the harmful species by the release of large numbers of mass-reared individuals. Secondly, habitat manipulation could be used to indirectly encourage displacement of a pest by a sympatric nonpest when the two are ecological homologues except for some limiting environmental feature which is amenable to change. A case of this type has been recognized by Aitken and Trapido (1961) in Sardinia. The malarial vector mosquito, *Anopheles labranchiae* Falleroni, was the subject of classical eradication procedures for several years, resulting in its replacement by a nonvector mosquito species, *Anopheles hispaniola* (Theobald). *A. labranchiae* became scarce while *A. hispaniola* flourished. The newly dominant *A. hispaniola* apparently moved in to fill the niche from which *A. labranchiae* was forcefully ejected, because of slightly different habits of both larval and adult stages which favored its



survival under the imposed eradicated conditions. A similar displacement between malarial vector and nonvector *Anopheles* spp. was also observed in East Africa (Gillies and Smith, 1960).

The third, and most commonly considered procedure for pest suppression through competitive displacement, is by the importation and establishment of allopatric nonpest competitors. A frequently cited example of this procedure is the experimental work of Furman et al. (1959), who found that *Hermetia illucens* (L.), a stratiomyid fly of low nuisance value, was able to eliminate *M. domestica* in limited field trials, apparently through larval competition for food. Tingle et al. (1975) recently described a naturally occurring case of such competitive activity. Other coprophagous insects may be considered beneficial as well, and, in fact, may show that useful ecological homologues need not be in the same genus, as in the *Anopheles* mosquitoes, or even in the same order, as in the aforementioned flies. Several species of large harmless coprid beetles (Scarabaeidae) are being imported from Africa to Australia for aid in disposal of huge accumulations of cattle dung which persist in the vast Australian grazing lands (Waterhouse, 1974). The native species of dung beetles were adapted to the droppings of native marsupials and were unable to utilize those of the introduced European grazing animals. This resulted in greatly increased problems from the bush fly, *Musca vetustissima* Walker, and the buffalo fly, *H. irritans exigua* (De Meijere), which were able to breed extensively in the accumulating dung. Initial indications are that the introduced coprids are extremely successful competitors, reducing fly emergence by 80–100%/cow pat in some tests (Bornemissza, 1970), and also limiting the reproductive cycle of pat-inhabiting intestinal helminth parasites of cattle which occur in the pats. Merritt (1975) found that another scarab, *Aphodius fimetarius* (L.), reduced the production of horn fly and face fly, *Musca autumnalis* DeGeer, from cattle dung in California.

Another group of insect pests which should be particularly susceptible to species replacement are the various biting flies, gnats, and mosquitoes, whose immature stages are aquatic or soil-inhabiting. In these insects the adult is the stage which causes discomfort, injury, or carries disease; we would not care to add competition at this stage of the life cycle. However, the larval stages are usually innocuous, and if ecological homologues could be found which compete during this time, then useful replacements might be instigated. For example, homophilic biting flies might be displaced by species which do not attack humans, but which compete successfully in the shared larval habitat (Beirne, 1960). Pestiferous *Hippelates* eye gnats might be similarly displaced by other species from the Caribbean area which are not attracted to humans (Legner, 1970). Gubler (1970) has suggested that *A. polynesiensis* Marks, the major vector of aperiodic bancroftian filariasis in the South Pacific, might be displaced in nature by a more "vigorous" allopatric nonvector mosquito, *A. albopictus* Skuse. Additional studies by Rozeboom (1971), Gubler (1971), and Lowrie (1973) have strengthened the case in favor of the proposal.

The final proposed approach to pest suppression by competitive displacement is the most controversial. It involves the importation of a potential pest species for the purpose of displacing another established pest species which is its ecological homologue. Such an approach would find use in only very specific situations

(DeBach, 1964c). For example, an introduced species which could displace the established pest but was unable to survive a local harsh cold or dry season might be useful. The imported species would die out after it had accomplished its purpose and colonization was discontinued. A more elegant variation on this idea is to replace a pest for which no adequate control measures are available with an ecological homologue that is known to be subject elsewhere to eradication or biological suppression. For instance, the Florida red scale, *C. aonidum* (L.), has been suppressed everywhere that its parasitoid, *A. holoxanthus* DeBach, is colonized (National Academy of Sciences, 1969b). *C. aonidum*, imported into a new country might successfully displace another scale, such as *Chrysomphalus dictyospermi* (Morgan), and subsequently be suppressed itself by introduction of *A. holoxanthus*. Another possibility would be the replacement of a species of fruit fly by a homologous species which is subject to eradication by the sterile insect approach.

The controversial nature of the utilization of the competitive displacement principle is immediately apparent. The problem arises as to whether the introduced ecological homologue might become a more serious problem than the original pest it displaced. It is obvious that great care must be exercised in selecting the limited number of subjects and situations to which the method will be applicable. Extensive ecological information, laboratory, and controlled pilot tests must be available before field applications are made, much in the manner of the precautions required for importation of phytophagous insects for biological weed suppression (Harris, 1971).

Whether we decide to actively use competitive displacement for pest eradication or not, it would be wise to consider the principle and its ramifications. The successful manipulation of the genetic material of pest insects is now a proven viable means of virtual population eradication, and, as a result, nondirected species replacement has become a distinct possibility. In other words, what will happen to the ecological niche left vacant when we eliminate the species which occupies it? Will it remain unoccupied? Will its resources be divided and appropriated among collateral inhabitants of the environment? Or will a new and perhaps more noxious pest move in to replace the one eradicated? A fourth possibility is that the pest will be replaced in its niche by another, relatively innocuous species, either as a matter of natural course (see Aitken and Trapido, 1961) or through the directed efforts of man. This is why we must consider the phenomenon of species replacement, so that if the necessity arises, we can assure that the species which occupies a vacant ecological niche is one with which we can live. Other ecological aspects of insect eradication are considered in a paper by DeBach (1964c) to which the reader is referred.

#### 4.3.4 Genetic Improvement of Beneficial Organisms

The genetic improvement of beneficial organisms can be approached from two different aspects, (1) increasing genetic diversity, and (2) artificial selective breeding.

The importance of the former method was first recognized by Clausen (1936), who pointed out that beneficial organisms are not necessarily constant in their abilities and adaptations throughout their natural range of occurrence. Therefore, he suggested, it is best to make use of these available differences by importing the chosen beneficial organisms from many different regions, assuring the best chance of obtaining an effective strain well-adapted to the new environment. This may be even more important if the spatial distribution of the target pest in the new environment covers a diverse range of conditions. Simmonds (1963) further expanded upon the idea and took issue with the support given by DeBach (1958b) to the alternative method of improvement through selective breeding. The subject of introducing genetic diversity into populations of beneficial organisms, and whether and how it should be done, has become controversial, as we have seen (2.3.3.3; DeBach, 1965; Wilson, 1965; Force, 1967; Remington, 1968; Levins, 1969; Whitten, 1970). Nevertheless, one consideration on which everyone seems to agree is that, in the past, biological control work has been too empirical and has paid too little regard to the genetic constitution of the beneficial organisms utilized. In the future, greater attention to the principles of genetics would be most advantageous to achieve maximal benefit from colonization attempts, both successful and unsuccessful. A recent example of such concern may be found in the work of Tauber and Tauber (1975), who presented criteria for selecting biotypes of the green lacewing, *C. carnea*, that are most suitable for use in biological pest suppression.

The second method of improving beneficial organisms for use in biological insect pest suppression involves the process of artificial selective breeding for increased fitness to the conditions of the new environment. The entire subject still remains largely conjectural even though the idea was suggested at least 60 years ago (Mally, 1916). The premise behind the suggestion is that, in light of the great successes achieved by selective breeding in improving varieties of domestic plants and animals, it should be possible to improve parasitoids, predators, and insect disease organisms in the same manner. Whereas, in the method of genetic improvement suggested above, a diverse gene pool is presented to the environment in hopes of a postcolonization natural selection of a well-adapted strain, in the second method, discerned weaknesses in adaptation are improved upon in the laboratory by artificial selection before colonization. Simmonds (1963) and Messenger and van den Bosch (1971) have pointed out several disadvantages and difficulties in carrying out the laboratory selections. For example, because of the inherent complexity of the natural environment, the exact factors to which a beneficial organism may be maladapted are frequently impossible to determine *ex situ*, and therefore cannot be dealt with in the laboratory. Lack of knowledge concerning the genetic basis for inheritance of desirable characteristics in beneficial organisms make intelligent selective breeding a difficult and lengthy proposition. It is necessary to obtain a sufficiently broad genetic diversity to assure the availability of suitable characters on which to base selections. Consideration must also be given to the possible accumulation of detrimental qualities selected unintentionally in association with the desirable characteristics. Finally, after a suitable strain has been developed and released, will it breed true under natural conditions, or will reversion to the wild type occur, or natural selection act to

produce the best adapted strain despite any amount of effort expended (uselessly?) in the laboratory before colonization?

A number of workers have carried out selective breeding procedures on beneficial organisms with some degree of success. However, most of the genetic improvements obtained have proven significantly important for purposes of laboratory production, whereas little demonstrable gain has been made in terms of improved biological field application and pest suppression. In the classical study of this kind, Wilkes (1942) was able to influence the temperature preference of certain strains of the eulophid parasitoid, *D. fuscipennis*, for oviposition; one strain selected 9° C and another 25° C. Later, Wilkes (1947) was able to improve his laboratory strain of *D. fuscipennis* by doubling the mean number of progeny per female, decreasing the number of sterile males produced from 35 to 2%, and reducing the variability in development, oviposition, and adult life span. Simmonds (1947) achieved similar success by selecting out a strain of the ichneumonid, *Mastrus* (= *Aenoplex*) *carpocapsae* (Cushman), which produced a high proportion of female progeny. Urquijo (1951) selected a strain of *T. minutum* (Riley) with superior host-finding ability, whereas Allen (1954, 1958) elegantly broadened the host preference range of an ichneumonid, *Diadegma* (= *Horogenes*) *molestae* (Uchida), beyond the normal host, *Grapholitha molesta* (Busck), to include a more easily reared laboratory host, the potato tuberworm, *P. operculella* (Zeller), for improved mass production. The resulting strain of *D. molestae* was 24 times as efficient on *P. operculella* as the initial stock.

The successful utilization of beneficial organisms for pest suppression within the currently popular framework of resource management implies, in many cases, that the biotic agents be compatible with chemical pesticides. This goal is most often achieved through the use of temporally or actually selective chemical treatment. However, an alternative approach is the development of insecticide-resistant strains of parasitoids and predators. There is little evidence to indicate that beneficial insects are physiologically less likely capable of developing such resistance than pests (Ferguson, 1969). Yet Croft and Brown (1975) were able to cite evidence for insecticide resistance in 224 pests but in less than 10 natural enemies. The development of a strain of parasitoid resistant to insecticides, for release in the field, should have great practical value, and was first attempted by Pielou and Glasser (1951) with *Macrocentrus ancylivorus* Rohwer. By the F<sub>19</sub> generation of selection, a maximum resistance ratio of 12 times the normal was attained, but this declined gradually in succeeding generations, and resistance disappeared altogether when the selective pressure of DDT treatment was discontinued (Robertson, 1957). A more recent attempt to develop pesticide-resistant strains in a boll weevil parasitoid, *B. mellitor* Say, was even less successful (Adams and Cross, 1967). The best known and, thus far, only successful field application of the principle of using pesticide-resistant biotic agents involves two species of phytoseiid mites, *Typhlodromus occidentalis* Nesbitt and *Amblyseius fallacis* (Garman), both of which are specialized predators of tetranychid spider mites on deciduous fruit trees (Croft and Brown, 1975). In these species, resistance arose through natural selection in the field, but both have been moved about and recolonized widely (Croft and Barnes, 1972; Meyer, 1975; Croft and Brown, 1975). An interesting complication in the utilization of resistant beneficial organisms is the prob-

lem demonstrated by Ferguson (1969) with mosquito fish, *G. affinis*. Endrin-resistant *Gambusia* tolerated massive body burdens of the insecticide without adverse effect to themselves, but susceptible fish in the same water with them died within two days, and various larger vertebrates which might potentially utilize *Gambusia* as prey, died within 24 h after forced ingestion of the endrin-laden fish.

Recently, White et al. (1970) have directed the genetic adaptation of the scale parasitoid, *A. lingnanensis* Compere, to various temperature extremes, as well as coincidental improvement in genetic hardiness as measured by adult longevity. Strains of *A. lingnanensis* were developed with improved tolerance to high temperatures, low temperatures, and alternating extremes of high and low temperatures.

Beneficial microorganisms have also been the subject of investigations for genetic improvement. Briggs (1963) discussed commercial production of insect pathogens and the importance of selecting not only strains which are adaptable to mass production techniques, but also those which show beneficial characteristics, such as rapid development in the host or increased virulence. Aizawa and Fujiyoshi (1968) pointed out the difficulty in using *B. thuringiensis* in sericultural countries because of its pathogenicity to the silkworm. They attempted to select and breed a strain of *B. thuringiensis* which would have low toxicity to the silkworm but retain its virulence to injurious pests. At least partial success was achieved by producing variants of the bacterium with ultraviolet radiation and possible bacteriophage conversion. Other bacterial mutants showing increased virulence to their normal hosts have been produced and isolated through similar means by several other workers (Aizawa, 1971). Serotypes of *B. thuringiensis* are now so numerous and diversified that products can be virtually "tailored" specifically to any susceptible pest species as the need arises (Heimpel, 1972). Evlakhova and Chvetzova (1964) and a number of other Russian workers (see Aizawa, 1971) exposed entomogenous fungi to insecticides, irradiation, and chemical mutagens, and then selected strains with the increased virulence thus produced. Roberts (1968) advocated the use of genetic manipulation (including genetic recombination) for production of fungal strains better suited to use for microbial pest suppression. He suggested that the important pathogenic characteristics of the fungi be determined, and then in vitro tests for these characteristics be devised. For example, by this method, mutants could be selected which would germinate either at lower relative humidity, or at temperatures different from the wild type. Strains might be selected also for increased toxin production or superior cuticle penetration. The resulting beneficial traits might finally be incorporated into a single strain by genetic recombination. Very little success or effort is documented for the improvement of insect viruses through mutation and selection (Smith, 1967). Virus strains of different virulence are available in natural insect populations for selection as promising biological agents, but the characteristics of virus strains in the laboratory appear particularly implastic (Aizawa, 1971). A strain of the nuclear polyhedrosis virus of the jack pine sawfly, *N. swaini* Middleton, was developed for increased virulence by selecting only from the first larvae to die after inoculation in each generation (Smirnof, 1961). Some investigators have found that more virulent virus strains could be selected on the basis of the shape of the polyhedral bodies (Hukuhara, 1968). Smirnof (1963b) reported that the

host range of the nuclear polyhedrosis virus from the sawfly, *Trichiocampus viminalis* (Fallén), could be broadened to include *Trichiocampus irregularis* (Dyar), and that virulence increased as adaptation took place over three generations. Smirnof (1968) was also able to adapt the microsporidan pathogen, *Thelohania pristiphorae* Smirnof, to infect both its natural host, the larch sawfly, *P. erichsonii* (Hartig), and the tent caterpillars, *Malacosoma disstria* Hübner and *Malacosoma americanum* (F.).

Until now, we have discussed breeding improvements made by selecting from single species populations; however, a number of workers have advocated interspecific crosses for increasing germ plasm diversity and adding useful characters not available intraspecifically. Handschin (1932) successfully crossed two species of parasitic wasps, *Spalangia orientalis* Graham and *Spalangia sundaica* Graham, to produce a fecund, long-lived, fertile hybrid which was better adapted to the environment of North Australia than either parent. Box (1956) improved the host-preference behavior of the tachinid parasitoid, *Paratheresia claripalpis* (Wulp), by hybridizing two geographically isolated strains of the species which would not normally interbreed in nature. Hodek (1973) cites a Russian study in which increased viability (heterosis) was gained through intraspecific crossbreeding of coccinellid beetles from different climatic regions. Hoy (1975) hybridized various geographic strains of *Apanteles melanoscelus* (Ratzeburg) to improve diapause response. White et al. (1970) tried irradiation as another means of increasing genetic diversity in their breeding stock of *Aphytis*, but no benefit was evident.

One final point to consider in regard to the genetics of laboratory or insectary reared beneficial organisms, is the possibility of deterioration of the desirable qualities originally displayed by the initial strain or those qualities selectively bred into it. For example, arrhenotokous stocks of *Trichogramma* egg parasitoids were unaffected by continuous laboratory rearing, but a deuterotokous stock, similarly reared, deteriorated significantly in host finding efficiency over a period of 4 years (Ashley et al., 1973). Constant monitoring is necessary to maintain and preserve the virulence of pathogenic microorganisms, as well, especially those produced on artificial substrates (Briggs, 1963; Aizawa, 1971). Three processes seem most important in causing decay of laboratory strains of entomophagous insects (Mackauer, 1972): (1) The founder effect results from the fact that the initial laboratory stock is rarely a representative sample of the genetic variability of the parent population as a whole. Therefore, changes in gene frequencies within the laboratory strain resulting from normal random processes may cause the loss of some alleles and the fixation of others, due to the small size of the breeding population. This loss of genotypes through sampling error severely limits the capacity of the laboratory population to respond to environmental stress by evolving a new type, and the chance of subsequent extinction is great. (2) Inbreeding is a second process which may decrease the viability of small isolated populations. Inbreeding in randomly mating populations leads to a reduction of the heterozygous genotype according to genetic population theory, and the resulting increase in the homozygosity of the strain frequently decreases such qualities as viability, fecundity, longevity, sex ratio, size, weight, and overall fitness. (3) Finally, the selective pressures applied to a laboratory stock are completely different from those occurring in nature, and may result in the inadvertent

selection of a phenotype which is tolerant of constant temperature and humidity, crowding, unnatural photoperiods, and artificial diets. Most such qualities contribute little to fitness under field conditions, and the selection of such a laboratory "ecotype" may render the strain essentially useless for field colonization.

## 4.4 Natural Determinants of Growth, Metamorphosis, and Behavior

In this chapter we will discuss a diverse spectrum of naturally occurring chemicals which have recently been embraced by many entomologists and the public as among the most promising new tools for combating insect pests. The compounds under consideration function as chemical messengers at either the intra- or inter-organismic level. The very fact that insects in general are so successful in their adaptations to life in most earthly environments is in large part related to their dependence upon such chemical cues. Only in the last 15–20 years have entomologists come to realize the possibilities for using these age-old and vital communication mechanisms against the insects, and devised various schemes (some quite elegant) for doing so. Concurrently, the capabilities of natural products chemists to isolate, characterize, identify, and synthesize the chemicals involved have grown remarkably. The combined efforts of the two disciplines have yielded a great deal of valuable and hitherto undreamed of information, which is at the same time bewildering in its extent and diversity, and exciting in its potential usefulness. With the accelerating expansion in research efforts in this field has come the need for a specialized journal. Thus the *Journal of Chemical Ecology* was begun in 1974 to complement previously established journals such as *Entomophaga* and the *Journal of Invertebrate Pathology* by publishing papers of interest to biological control workers.

The complexity of the chemical relationships between insects and their internal and external environments, and with others of their own kind can be inferred from the proliferation of terms which has accompanied their elucidation (e.g. Wright, 1964 b). A recent and reasonably complete classification of these relationships recognizes three possible functional levels for a chemical messenger: intraorganismic, intraspecific, or interspecific (Chambers, 1974). These categories are not necessarily mutually exclusive as illustrated, for example, by Lüscher (1972) who suggests that the pheromone responsible for caste determination in some termites may, in fact, also be their juvenile hormone. A termite trail-following pheromone is chemically identical to a termite attractant present in fungus-decayed wood (Matsumura et al., 1969). The pheromones of some species may also act interspecifically to attract their predators (Brown et al., 1970). In the following pages we will examine a representative group of chemicals from each of the three levels to assess its potential for use in biological insect pest suppression. Except where the chemical compound used is a biological analogue of the naturally occurring compound showing similar activity, we shall not concern ourselves with synthetic chemicals, in order to remain within the bounds of our overall definition of biological insect pest suppression.

### 4.4.1 Hormones

The internal (intraorganismic) environment of the insect pest is regulated by hormones just as it is in plants and other animals. The early pioneering work of Wigglesworth (1935, 1939) was instrumental in demonstrating the presence and activity of several insect hormones. Then, with the extraction of the first insect hormone, came the suggestion of its use as an insecticide (Williams, 1956): "In addition to the theoretical interest of the juvenile hormone, it seems likely that the hormone, when identified and synthesized, will prove to be an effective insecticide ... insects can scarcely evolve a resistance to their own hormone." This, because topical application of a crude extract of natural hormone to the abdomen of a pupal silk moth, subsequently produced an imago which retained some pupal characteristics, was inviable, and effectively nonreproductive.

Williams (1967) later proposed the term "third-generation pesticides" for the juvenile hormone (JH), several other insect hormones, and natural and synthetic chemicals from other sources which displayed similar effects. By this he meant that the crude inorganic pesticides used before World War II could be considered a first generation, DDT and all of its subsequent synthetic chemical relatives constituted a second, more advanced generation of materials, and the various insect hormones might well be developed for use as a highly sophisticated third generation of chemical pesticides displaying a completely new and different mode of action.

Insect endocrinology has captured the imagination of many researchers since the 1950s, and a number of extensive reviews of the subject have appeared (e.g. Novák, 1966; Wigglesworth, 1970; Sláma et al., 1974). The so-called juvenile hormone (and its relatives) have generated the most interest (Menn and Beroza, 1972; Staal, 1975), but ecdysone (molting hormone) and its relatives have also been suggested as potentially useful chemicals (Robbins et al., 1970, 1971). Although the chemical identities of both juvenile hormone (Röller et al., 1967) and ecdysone (Karlson et al., 1963) have been determined, the complex structure of the latter, which is a steroid, has made the prospects for its large scale production look remote due to difficulty and expense in synthesis. Shortly after the isolation and identification of ecdysone from the silkworm, two independent groups of investigators surprisingly isolated compounds of similar chemical structure and high biological activity from certain plants (Galbraith and Horn, 1966; Nakanishi et al., 1966). The term ecdysoids has subsequently been used to denote chemicals of plant and/or animal origin exhibiting biological activity similar to the true molting hormone, and many have been found (Sláma, 1969; Sláma et al., 1974). Although these new sources greatly increase the availability of ecdysoids, the practical use of these compounds is still thwarted by their instability in field applications and comparative lack of biological activity at low topical dosages.

#### 4.4.1.1 *Characteristics of Insect Hormones*

In recent years, insect physiologists have shown that the remarkable diversity of developmental and metamorphological changes which occur in virtually all insects examined are regulated very precisely by the same three hormones, collec-



tively known as developmental hormones. The first, the brain hormone, is secreted by neurosecretory cells in the brain, and is also known as the activation hormone (Sláma et al., 1974), because of its superior role in stimulating secretory activity of other endocrine glands. Little has been accomplished in adapting the brain hormone to use against insect pests.

The second hormone is the ecdysoid produced by the prothoracic glands. Ecdysone production is stimulated after each molt in immature insects or at the termination of diapause, and its increased titer in turn stimulates growth and development of various somatic tissues and other physiological and morphological changes required for the continued repetition of the molting cycle. Prothoracic glands and ecdysone are absent in adult insects, except the Apterygota which continue to molt after reaching the sexually mature adult stage. In contrast to the juvenoids (see following), there are no effective direct methods for topical application of ecdysoids. In fact, current research indicates that during normal insect development it is difficult to find a stage that is highly sensitive to ecdysoids via any applicative route (Sláma et al., 1974). For this reason, and the others previously cited, the potential for practical use of these compounds remains to be proven. The most interesting result of research in this area involves the discovery of steroid compounds, structurally related to molting hormones, which inhibit sclerotization of the cuticle in the hemipteran, *Pyrhhorcoris apterus* L. (Hora et al., 1966). In addition, many of these same compounds showed strong chemosterilizing activity against house flies (Řežábová et al., 1968), but both effects were demonstrable only through injection. Compounds of this type showing topical activity might have practical value should they become available.

The third hormone important for normal growth and development throughout the Insecta, is the juvenile hormone. Since Williams' extraction of the famed "golden oil" from the abdomens of male *Hyalophora cecropia* L. moths in 1956, a number of other sources have been found for natural chemicals showing similar JH activity. Surprisingly, the glandular site of secretion of JH, the corpora allata, is a comparatively poor source for obtaining the compound in quantity (Williams, 1963; Williams and Law, 1965). The other sources are as diverse as extracts of various human tissues, heavy cream (Williams et al., 1959), most invertebrate and vertebrate groups, microorganisms, and plants (Schneiderman et al., 1958, 1960), and the so-called "paper-factor", or juvabione, accidentally discovered by Sláma and Williams (1966). After the identification of farnesol as the juvenile hormone-active substance in the excrement of *Tenebrio molitor* L. (Schmialek, 1961), the whole field of synthetic juvenile hormone analogs was opened to terpenoid chemists (Sláma, 1971; Pallos and Menn, 1972; Sláma et al., 1974). The proliferation in the number of natural and synthetic compounds exhibiting juvenile hormone activity has resulted in a corresponding proliferation in new terms. In a manner similar to that described previously for ecdysoids, any compound from any source having biological activity similar to authentic juvenile hormone has come to be called a juvenoid or juvenile hormone analog (JHA) (Sláma et al., 1974). A broader term, insect growth regulator (IGR), has been proposed to include the juvenoids and several other compounds with a different mode of action, e.g. those which interfere with JH activity (Walker and Svoboda, 1973; Staal, 1975), or other physiological processes (Granett and Dunbar, 1975).

In contrast to the brain hormone and ecdysoids, juvenoids are well studied in terms of their chemistry and biological activity. Physiological studies aimed at understanding the metabolism of juvenoids in both target and nontarget organisms are well underway as necessary prerequisites to predicting the impact of distributing these compounds in the environment as third-generation pesticides (Menn and Beroza, 1972; Sláma et al., 1974; Pickens and Miller, 1975; Norland and Mulla, 1975). Juvenile hormones work in concert with ecdysones to assure the proper course of insect growth and development. A commonly held misconception is that the two hormones work antagonistically. In actuality, the major function of the ecdysoids is to predispose the insect to molt at periodic intervals, whereas the juvenoids primarily determine the type of molt which will occur, according to their concentration in the blood. Thus, a high JH titer produces another larval (nymphal) instar, but low titer or complete absence of JH causes the pupal or imaginal molt to occur. The Achilles heel of insect pests (as Williams has called it) is that period in their development when low JH activity is required. Effective treatment of the pests with juvenoid at such times should result in fatal disruption of the normal life cycle (Figs. 43 and 44). In addition to morphogenic disturbances, juvenoids are known to cause sterility, diapause disturbance, and to have ovicidal effects.

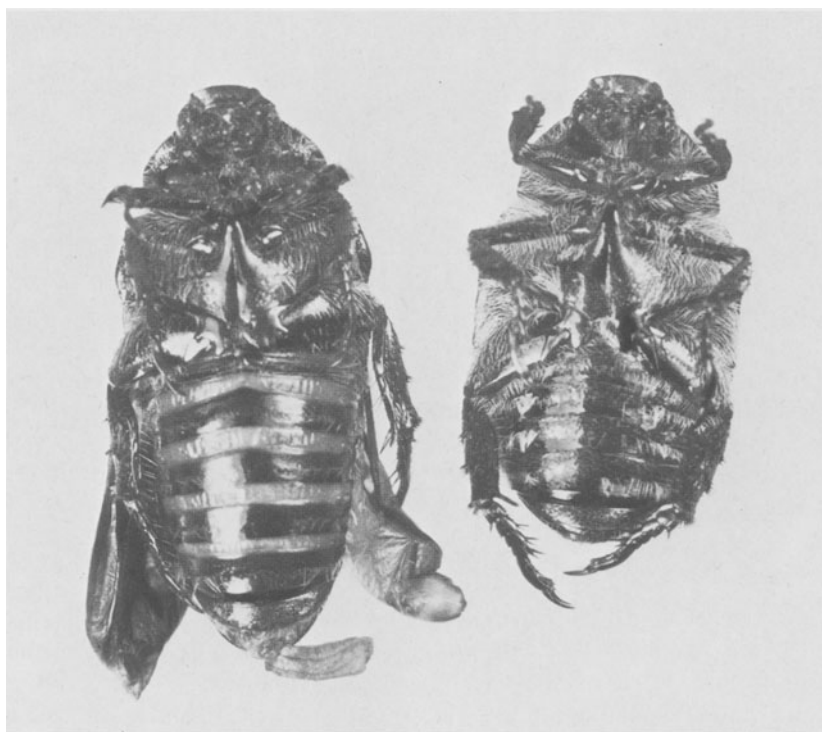


Fig. 43. Adult Japanese beetles, *Popillia japonica* Newman, (ventral view) produced from JHA-treated (*left*) and untreated normal (*right*) pupae. Note the uncontracted abdominal segmentation, protruding saclike wings and elytra, and everted adult hindgut in the treated insect. (Courtesy USDA, Japanese Beetle Laboratory)

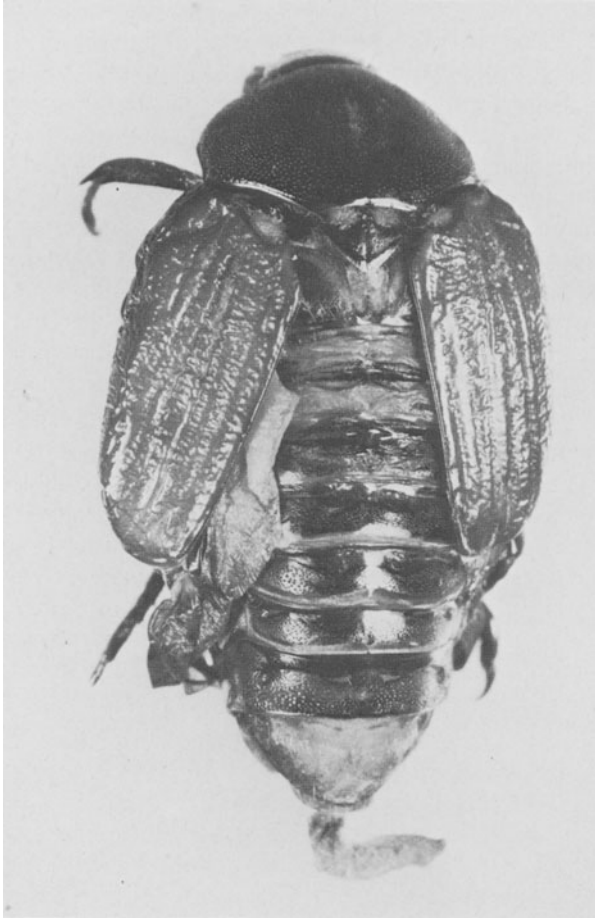


Fig.44. Dorsal view of a JHA-treated Japanese beetle as in Fig.41. (Courtesy USDA, Japanese Beetle Laboratory)

A vast literature on the theoretical and experimental aspects of juvenoid research is available, much of it cited in the works of Menn and Beroza (1972), Sláma et al. (1974), and Staal (1975). We shall conclude our discussion here, however, by briefly examining several attempts at practically applying juvenoids for insect pest suppression.

#### 4.4.1.2 Potential for Use of Hormones

Use of JH-active chemicals as “insecticides” was first proposed by Williams (1956), but it was not until the mid-1960s that the possible effectiveness of the method was demonstrated on the bug, *P. apterus* (Sláma and Williams, 1966; Williams and Sláma, 1966). Research, development of materials, and methods for their use have grown at an accelerating pace ever since, thanks to interest and support from governmental, academic, and industrial sources. Among the latter institutions we find several of the established chemical companies long associated with the production of agricultural chemicals and insecticides, and new organizations, such as Zoecon Corporation of Palo Alto, California, which are vigorously

pursuing the development of juvenoids as alternatives to the old chemical toxicants (Diekman, 1972).

The basic principle involved in using juvenoids for pest suppression is the fact that the application of an appropriate material at the appropriate time causes developmental disturbances in the pest insects, leading eventually to mortality or prevention of reproduction. The qualifications, corollaries, and ramifications of this simple principle are several. Juvenoids have little or no direct toxicity to insect pests, but instead display the foregoing indirect delayed effects. Therefore, they are not useful for short-term elimination of an outbreak situation. Also, unlike the well-known insecticides, they are not effective on almost any developmental stage, but must instead be synchronized in their application to precisely determined sensitive periods in the life cycle of the target insect. This, in turn, means that a certain degree of stability or environmental persistence is desirable in juvenoid formulations for practical use, because most potential target pest populations have a heterogeneous age distribution under natural conditions. Currently popular conventional insecticides, such as carbaryl, kill a variety of life stages upon application and then quickly break down; juvenoids, acting only on a particular susceptible stage, must persist in, on, or near the target insects until all have attained that stage of development before breaking down. Intimate knowledge of the developmental status of the pest population is obviously most critical for effective use of juvenoids. Finally, selecting the appropriate juvenoid for use against the target insect may present difficulties. Fortunately, almost all information published to date indicates that juvenoids as a group are nontoxic (acutely and chronically) to vertebrates, other nontarget organisms, beneficial parasitoids and predators, or other components of the environment. For the most part, they break down rapidly as well, and are not implicated in any pharmacological side effects. However, there is no "universal" juvenoid, much as that is to be desired by the commercial chemical industry for ease in registration and production procedures. To be sure, a number of juvenoids exhibit moderate activity against many unrelated species, in fact equalling or surpassing the effectiveness of most insecticides. But the really potent materials of the more than 500 juvenoids now recognized are much more selective in the species which they affect. This should be advantageous once proper identification is made. Difficulties arise first in attempting to screen all of the potential chemicals for the most effective, and secondly because juvenoids with the highest activity in the laboratory are not always the best under field conditions (e.g. lack of sufficient stability).

Despite the prediction by Williams (1956) that "insects can scarcely evolve a resistance to their own hormone," recent literature (Staal, 1975) has suggested a more complex situation, in which insect strains resistant to certain insecticides are also cross-resistant to juvenile hormone analogs. However, the actual selection for resistance to hormones, per se, has yet to be demonstrated. A number of the preceding considerations will be amplified in the following examples.

#### *4.4.1.3 Pest Suppression Tests Using Hormones*

Based on the preceding discussion of some characteristics of juvenoids for pest suppression and a general knowledge of insect biology, one might almost predict which insects would be promising candidates for the approach. For example,

insects which are only pests as adults should be particularly suitable because prevention of the imaginal molt is a primary result of juvenoid treatment of the larval stage. For this reason, mosquitoes were early selected as prime targets to pursue. In addition, the close synchrony of development in a mosquito population (especially floodwater species) somewhat alleviates the requirement for environmental stability of the juvenoid. Demands created by environmental awareness and almost complete insecticide resistance in some mosquito species further encourage the use of insect growth regulators for the purpose. Since Lewallen (1964) first noted the mortality caused by treating *Culex* larvae with 1 ppm of farnesol, hormonal suppression of mosquitoes has come a long way. One juvenoid, methoprene, has an experimental registration for use against floodwater mosquitoes in the United States (Marx, 1973; Staal, 1975). Tests thus far indicate it has no effect on nontarget aquatic organisms or on vertebrates, and that it is one of the safest materials ever used for pest suppression (Zoecon Technical Bulletin, 1974). Methoprene (Altosid SR-10) in microencapsulated or slow release polymer form appears to have nearly all the qualities necessary for safe practical use (Diekman, 1972; Dunn and Strong, 1973; Schaefer and Wilder, 1973). Methoprene is relatively stable to begin with, but in these formulations it remains in the environment long enough to have given "complete control" of the insecticide-resistant California floodwater mosquito, *A. nigromaculus* (Ludlow), in field trials at as little as 27 g/ha (Schaefer and Wilder, 1973). Treatment is most effective in the last larval instar, and either prevents adult emergence or produces unthrifty adults. As might be expected, methoprene varies in its effectiveness against different species, even among the mosquitoes; however, for *A. nigromaculus* it is not only the best material available, it is the *only* material worthy of consideration. It is sufficiently potent, stable, economic, and non-toxic for practical use right now. Researchers have noted that Altosid is also effective against problem midges (Chironomidae) (Marx, 1973; Mulla et al., 1974), and black flies (Simuliidae) (Dove and McKague, 1975).

Another group of insects which have proven susceptible to growth regulator treatment are the muscoid flies associated with cattle and poultry manure, feedlot wastes, and beach debris. Wright (1972) first demonstrated this possibility when he found two juvenoids active against stable flies, *S. calcitrans*, when the larval growth medium was sprayed with 1% emulsions in simulated field tests. Later, in small plot tests, Wright et al. (1973) used JHAs to inhibit adult *S. calcitrans* emergence by 64–91% in Nebraska feedlot wastes, and 95–99% in Florida beach debris. Harris et al. (1973) and Miller and Uebel (1974) achieved even better success by feeding cattle directly with the IGRs, thus assuring even distribution of the materials in the feces. Such treatment was especially effective against the face fly, *M. autumnalis* DeGeer, the horn fly, *H. irritans*, and the stable fly, in which 100% inhibition of adult development was achieved. Methoprene was effective in manure passed up to 10 days after oral treatment was discontinued. Neither research group found the IGRs particularly useful against house flies.

One of the first attempts to suppress a forest insect with a juvenoid under field conditions was reported by Retnakaran et al. (1974). They also used methoprene, applying it in aqueous emulsion from a helicopter against the eastern hemlock looper, *Lambdina fiscellaria fiscellaria* (Guenée). The results indicated that "the

desired reduction in population was obtained," although the project well illustrated the fact that foliage protection from treatment with IGR occurs in the succeeding year, not immediately. The authors emphasized the importance of accurately timing the juvenoid application to coincide with the sensitive stage of the target insect, in this case, the last larval instar. In addition, they presented evidence corroborating the safety of the method to birds, mammals, fish, and other invertebrates, and found that the chemical formulation used was sufficiently stable for practical purposes, resisting weathering, ultraviolet, and water spray treatments. For further information on the use of juvenoids against insect pests in the field see Bagley and Bauernfeind (1972) and Staal (1975).

#### 4.4.2 Pheromones

The intraspecific level of organization in the chemical environment of insects is represented by the pheromones. The term was used by Karlson and Butenandt (1959), and despite etymological criticism and several proposed alternatives, "pheromone" is now the accepted term for the general class of chemical messengers produced by an organism exogenously to influence the behavior or physiology of other members of the same species. The definition encompasses exocrine products with a number of specific functions amongst the insects. Social forms use pheromones for communication, caste determination, and other types of social integration. They share with nonsocial forms territorial, aggregation, and trail-marking substances; alarm and defense chemicals; and, of course, the best known of all, the sex pheromones. At present, the sex pheromones appear to hold the most promise for early practical use in pest suppression, although some of the other pheromones, notably trail-marking chemicals (Tai et al., 1971; Esenther and Beal, 1974), may prove valuable in specific cases. In light of the emphasis currently placed on sex pheromone research, we will center our discussion around the projected use of these substances.

##### 4.4.2.1 *Characteristics of Insect Pheromones*

Pheromone researchers have found that the more deeply they delve into their discipline the more complex it becomes. Hypotheses which once seemed simple, obvious, and straightforward have become burdened and confused with exceptions and controversy. Nevertheless, at the risk of being overly general we can make several statements about sex pheromones which are applicable to our discussion and which are representative of a majority of research findings to date. Sex pheromones have evolved as an efficient method of bringing both sexes of a species together for the purposes of reproduction, and their existence has been surmised since the 1800s (Jacobson, 1972). They are biologically active in minute quantities. In general, substances produced by females serve as attractants, whereas those produced by males function as aphrodisiacs. Female sex pheromones appear to have the most potential for use by man because of their effectiveness over greater distances than that of male pheromones. Female attractants are usually produced by ectodermal glands located in the abdomen, and male recep-

tors are commonly found on their sexually dimorphic antennae. There is considerable species specificity in pheromonal communication, probably as an evolutionary mechanism for preventing hybridization. Specificity may be chemical (i.e. different compounds, different mixtures of the same group of compounds, or even different isomers of the same compound), temporal (i.e. pheromone release or response with specific diel or seasonal periodicity), or spatial. Typically, only virgin adults produce sex pheromones, particularly in those species which mate but once. Conversely, the male is capable of repeated responses, as long as periods of low pheromone concentration allow for respite from constant sexual excitation. Initial responses of males to their pheromone include positive anemotaxis and a decreased incidence of turning, which may be followed by courtship and copulatory behavior as the distance to the pheromone source becomes very short.

Many of the preceding generalizations may be applied to other types of potentially useful pheromones, i.e. aggregation pheromones, trail-marking substances. Aggregation pheromones have been found, to date, only in Coleoptera, throughout the family Scolytidae (Borden, 1974), and also in the cotton boll weevil, *A. grandis* (Hardee, 1970). Apparently the location of a suitable host site initiates such pheromone production, and both sexes respond and assemble to feed and mate. Trail substances are used mostly by social insects for defense recruitment or as an aid in foraging, and are only active over relatively short distances. A postovipositional fruit-marking pheromone produced by the black cherry fruit fly, *Rhagoletis fausta* (Osten Sacken), has potential for use by cherry growers in deterring damage from this pest (Prokopy, 1975).

Identification of the chemical nature of a pheromone was, at one time, considered a monumental and culminating achievement in itself; it is now but a beginning. The purpose of identification is to make available larger quantities of synthetic pheromones for studying and understanding their effects on the biology and behavior of the species producing them naturally. From there the ultimate objective is to find ways and means of using the materials to the detriment of pest insects. Even before the chemical identity of the first insect sex pheromone was established [which, incidentally, was that of the nonpest silkworm moth, *B. mori* L. (Butenandt et al., 1959)], entomologists were contemplating and experimenting with methods for pheromone exploitation using living insects as pheromone sources (Kunike, 1930; Lemarie, 1933; Götz, 1939, 1951). Techniques for analysis of natural products such as pheromones have advanced remarkably in sophistication since the identification of the *B. mori* sex pheromone. As a result, the number of chemically known natural pheromones has quickly grown to more than 150, many of which have been produced synthetically (Mayer and McLaughlin, 1975). In fact, several small companies have been organized with the purpose of producing and supplying such chemicals on a commercial basis (e.g. Chem Samp Co., Columbus, Ohio). Likewise, with increased availability of known active materials the techniques for their utilization have been tested, refined, and improved. The popularity of controlling insect behavior through the use of pheromones is currently so great that numerous reviews of various aspects of the theory and practice are readily available (Wright 1964a; Jacobson, 1965, 1972; Knipling and McGuire, 1966; National Academy of Sciences, 1969a, 1972; Beroza, 1970; Wood et al., 1970; Young and Silverstein, 1974; Birch, 1974). We shall not attempt

another such lengthy review here, but instead we will briefly indicate the several ways in which sex pheromones could be and are being used in insect pest suppression, and then examine some recent projects which illustrate the methods described.

#### 4.4.2.2 *Potential for Use of Sex Pheromones*

Uses for sex pheromones fall naturally into two categories: pest survey and pest suppression. The former application has become practical more rapidly than the latter, and eventually may prove the most valuable use for most insect pests. An important function of insect pest survey is the detection of pest populations early in their development, before large and damaging numbers are present. Few, if any, survey methods can match pheromone monitoring for determining the presence and relative numbers of insect pests in low density populations. Already the use of pheromones for survey and detection has spread throughout the world, and frequently the information they provide has become the basis of highly effective integrated pest suppression programs (Riedl and Croft, 1974). Precise and dynamic knowledge of the progress of pest populations in the field allows wise decisions to be made on whether suppressive measures are required to protect against economic pest damage, and, if so, on the type and extent of action necessary. Perhaps a cultural or other biological manipulation is all that is necessary to sufficiently reduce pest numbers. If an emergency situation is forecast, then suitable insecticide applications can be made at the right time, only in those areas where necessary, and only for as long as the pest is a threat, based upon data gathered with sex pheromone monitoring. Utilizing sex pheromones for pest survey requires the development of suitable technology in trap design and deployment, plus sufficient understanding of the pest to relate trap catches to actual population density. Determining the quantitative relationships between pheromone survey results and economic thresholds remains a major research problem area for future emphasis. The use of pheromones in pest suppression requires something more than their use in survey. Newly identified pheromone chemicals may frequently find practical use in survey almost immediately, and certainly within a year or two of field evaluation. Substantially more information on biology, behavior, and population dynamics of the target pest is required for use in suppression, however (Tette, 1974). Also, in the United States and other developed countries, federal registration regulations on the safety and effectiveness in practical use of pheromones for pest control must be satisfied just as they must be by new insecticides (Birch et al., 1974; Djerassi et al., 1974). Such restrictions do not apply to materials used in survey applications.

Proposals to suppress pest populations through manipulation of their pheromonal communication systems have two things in common (Tette, 1972); first, they are preventative measures, i.e. males are stopped from reaching females (or vice versa); secondly, they hold promise for use only in low density populations. There are two main approaches to the problem: (1) mass trapping of adults to remove a large portion of the breeding population, and (2) disruption of the intersexual communication system to prevent normal courtship and mating behavior. Both of these procedures have been suggested as being sufficiently power-



ful tools in and of themselves to suppress or eradicate pest populations. However, pheromones may find their greatest successes when used in conjunction with other methods of pest suppression which first reduce the population density to the low levels at which pheromones are most efficacious. Nevertheless, despite almost 15 years of intensive investigation and considerable creative thinking on pheromone exploitation, no practical system of pest suppression based on pheromones has yet been developed to the point of complete success (Birch et al., 1974). Before we discuss the attempts which have been made, let us examine the two proposed approaches as they relate to the general characteristics of pheromones previously stated.

The use of attractants for trapping insects predates recorded history according to Chambers (1974), who describes an invaginated glass fly trap from ancient China. The earliest attempts at using sex pheromones (living females) as bait in traps for pest control may well be those involving the gypsy moth, *P. dispar*, in the early 1890s (Jacobson, 1972). The principles behind the practice are simple. If the sex pheromone is the only or major method by which the sexes of a pest species get together, then it should be possible to attract the respondent sex to a trap which simulates the odor of the opposite sex. Only small quantities of synthetic pheromone per trap should be sufficient to outcompete wild females because of the high biological potency of these materials. Males can respond to sex pheromone (and frequently can mate) many times, so their chances of being captured are great, although it is preferable to remove them before they respond to a virgin female and fertilize her. The use of pheromones for pest suppression is very much dependent on insect biology despite the simplicity of the underlying principles. For example, not all pheromones which are identified may be suitable for practical use in traps, because the respondent insect may depend on visual or auditory cues in addition to simple olfactory signals; or, if only sex pheromones are used, there is always the possibility of "resistance" developing (Beroza, 1960). That is, a trapping program provides strong selective advantage to individual insects which can locate each other and reproduce without the use of the pheromonal communication system.

Finally, many ways of deploying pheromones for mass trapping have been proposed, and theoretical models for predicting their effectiveness have been developed (Knipling and McGuire, 1966; Mertins et al., 1975). Pheromones themselves, of course, are not significantly toxic, but serve only as the bait to lure the target insect to its death by other means. Pheromones may be used with a sticky-surfaced trap (Fig.45; Coppel et al., 1960; Trammel et al., 1974), aquatic trap (Dickerson and Hoffman, 1975), a simple physical restraint design (Klein et al., 1973), or with an electric grid (Hienton, 1974), pathogen or insecticide (Ostaff and Gray, 1975; Barak and Burkholder, 1976), chemosterilant (Campion, 1967), or physical removal of aggregated insects (Knopf and Pitman, 1972; Dyar, 1975). Pheromone effectiveness may be increased by adding chemical (Roelofs and Co-meau, 1971) or physical (Chalfant et al., 1974) synergists, stabilizers or "keepers" (Fitzgerald et al., 1973; Bull et al., 1973), or perhaps even food odors (Pearce et al., 1975). The common goal is to remove most, or all, of the target insects from the local breeding population. Traps might be effectively used as a barrier zone in preventing minor infestations in new areas, as eradication devices in spot infesta-

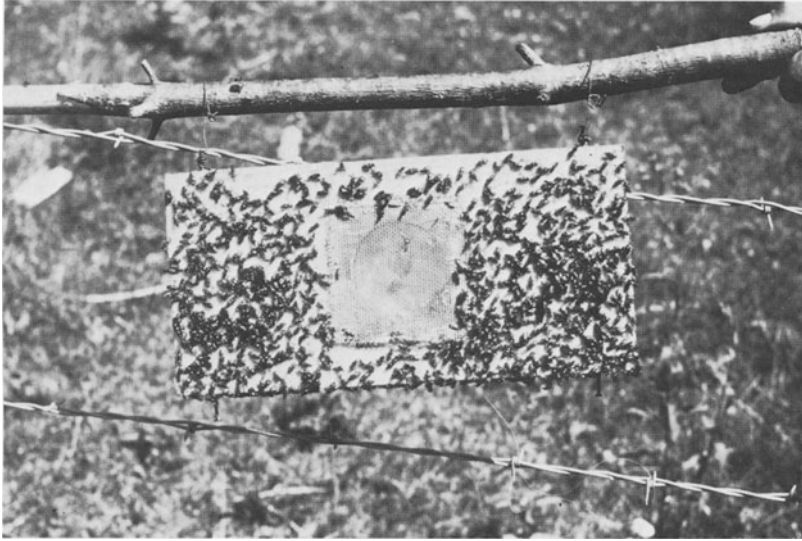


Fig. 45. A sticky-board trap baited with a single virgin female introduced pine sawfly *Diprion similis* (Hartig), showing some of the more than 11000 male sawflies attracted to her sex pheromone and captured by the trap

tions outside a generally infested area, as a means of reducing the area or severity of general infestation, or as the final eradication blow to a population previously reduced by other methods (Cameron, 1973).

The second general approach to the problem of using sex pheromones in pest suppression is through disruption of the intersexual communication which normally leads to successful reproduction. The approach has also been called the "confusant method," although the term disruption of communication is preferable. The method involves broadcasting a high concentration of the sex pheromone of the pest into its environment, thus permeating the atmosphere with enough of the chemical to inhibit the normal response behavior of males to available virgin females. Exactly how this works is still uncertain, although it appears most likely that a complete habituation of the sensory receptors on the male antennae occurs with continuous exposure to sex pheromone concentrations above a certain minimum level (Bartell and Lawrence, 1973). Thus the male is no longer stimulated by the pheromone to seek a mate. An alternative explanation gives rise to the term confusant in that the background levels of pheromone are thought to be so high that the responding male is incapable of orienting to the comparatively small extra increment of pheromone produced by a receptive female. Another kind of disruption of communication is also possible utilizing certain other chemicals which are not attractive to respondent insects, but which have been found incidentally to mask, inhibit, or block reception of the pheromonal signal (Roelofs and Comeau, 1968; Carde et al., 1973). Saturation of the environment with such agents should also be effective in preventing mate location (Arn et al., 1974).

Deployment of pheromones for disruptive purposes requires extensive biological and behavioral information and technical innovation just as does their use in mass trapping. Information is required on the emergence patterns and dispersal capabilities of both males and females, mated and unmated. Mating behavior must be well-known to determine whether other factors beside pheromonal cues are involved, and to discover how often both sexes mate. It is also desirable to know whether the pheromone is used by beneficial insects in some manner (e.g. Brown et al., 1970), and what effect its broadcast in the environment might have on them. The method and extent of dispersal in the pest's habitat may also be important. Wright (1965) speculated on the concentration of pheromone necessary to saturate the receptors of male insects and inhibit mating, suggesting it might be  $10^5$  molecules/cm<sup>3</sup> higher than the threshold for behavioral response. Pheromones applied as sprays may well disperse or break down too rapidly when they come in contact with foliage. Therefore, various carriers, dispensers, or slow release formulations have been devised for this specialized purpose (Cameron, 1973; Fitzgerald et al., 1973; Shorey et al., 1974). We should know also whether the pheromone must be dispersed uniformly throughout the environment both horizontally and vertically, or if a number of strategically placed point sources are sufficient. Finally, consideration must be given the potential danger to the biosphere in wholesale dispersal of a potent organic chemical. So far, the pheromones tested are among the safest and least toxic pest control chemicals known, but from past experiences with widespread agricultural uses of organic chemicals we have learned to be very cautious in this regard. In the United States and elsewhere, pheromones are defined as pesticides and must pass rigid safety tests before use.

As previously stated, no insect pest population has thus far been suppressed with pheromones on a practical economic basis. However, the progress of our knowledge and development of our technology is at the point where the first successes are imminent. A few examples of progressive research projects which are nearing the goal of fruition will illustrate the point.

#### 4.4.2.3 *Pest Suppression Tests Using Pheromones*

The use of the synthetic boll weevil pheromone, grandlure, in traps, is one of the most promising methods for suppression of this species (Birch et al., 1974). Grandlure thus far has shown effectiveness in a number of integrated schemes of suppressing boll weevil populations, the most extensive of which is the Pilot Boll Weevil Eradication Experiment in southern Mississippi, Louisiana, and Alabama. In addition to various cultural and chemical methods, grandlure baited traps are being used to (1) physically capture weevils as they emerge from hibernation in the spring and thereby further reduce an already low population, or (2) draw the early weevils to a trap crop area of early-planted, early-fruiting cotton, which is treated with insecticide (Lloyd et al., 1972; Scott et al., 1974).

A second area in which mass pheromone trapping has shown particular promise is in orchard pest suppression, especially for tortricid moths (Birch et al., 1974). Of the 10 or more important tortricid pests of apple, mass trapping has been effective against the redbanded leafroller, *Argyrotaenia velutinana* (Walker), in

New York (Trammel et al., 1974). In two experimental apple orchards, collapsible paper traps were used at approximately one/tree, each trap emitting synergized pheromone equivalent to about 10 virgin females. Analysis of resulting harvests indicated subeconomic injury levels in the treated orchards from *A. velutinana*. The success attributed to the trapping program is all the more impressive when one considers the abundance of nearby wild hosts for the insect, always providing a significant reservoir for moth infestation in the orchards. In this regard, information is still lacking on the flight range of adult leafrollers, and the minimal number of traps necessary to adequately protect each particular orchard ecosystem from damaging attack.

Mass trapping of *A. velutinana* has proven less effective in vineyards, where traps have been able to hold high populations stable but not to reduce them to subeconomic levels (Taschenberg et al., 1974). Disruption of communication between the sexes has been more successful than mass trapping with both *A. velutinana* and the grape berry moth, *Paralobesia viteana* (Clemens). Although populations of both species were too high for suppression by mass trapping in the vineyards tested, the application of sufficient synthetic pheromones to inhibit mating provided a viable alternative method, and almost total disruption was achieved.

Similar programs are showing successes with other lepidopteran pests, and some on a much larger scale. A synthetic sex pheromone, looplure, was used in disruption experiments against the cabbage looper, *T. ni* (Hübner), in California (Shorey et al., 1967, 1972). The chemical was released at various rates from evaporators placed at various intervals in the test plots. Effectiveness was assessed with virgin female baited traps placed in the fields, and by the mating success of tethered females. The tests were successful in several different climatic areas and disruption seemed independent of the population density of *T. ni* in the plot. Pheromone release rates of as little as 0.1 mg/ha/night caused disruptions of more than 80% in mating success. In five of the experimental plots with higher release rates, mating disruptions of 98–100% were indicated. The authors suggested that the spacing of evaporators or method of pheromone distribution did not appear as important to successful disruption as was the total amount of pheromone released in a given land area per night. Subsequent experiments utilizing looplure as a disruptant for nine other pest lepidopteran species, in addition to *T. ni*, indicated that perhaps effective disruptive chemicals wouldn't have to be very specific (Kaae et al., 1972). Communication was disrupted in seven of the ten species studied by at least 84%, including 100% effectiveness against *T. ni*, the alfalfa looper, *Autographa californica* (Speyer), and the soybean looper, *Pseudoplusia includens* (Walker), species which probably share the same pheromone. More recent disruption tests against *T. ni* with ten pheromone-like chemicals, including looplure, cast some doubt on the hope for a broad-spectrum "confusant" (Kaae et al., 1974). Although several of the chemicals showed some activity in disruption, none approached looplure in effectiveness, and it now appears likely that the species-specific pheromone, or a very close chemical relative, will be necessary to achieve levels of disruption high enough for significant population suppression.

Similar experiments with the pink bollworm, *P. gossypiella* (Saunders), in California cotton fields, have utilized a synthetic attractant, hexalure, known not to be

the true sex pheromone of this species (McLaughlin et al., 1972; Kaae et al., 1972, 1974; Shorey et al., 1974). Initial small field plot experiments indicated that at release rates of at least 20 mg of hexalure/ha each night males could be almost completely prevented from locating virgin females in traps within the plots. Larger scale season-long experiments conducted subsequently used hundreds of thousands of small evaporator substrates made of knotted cotton string to disperse the hexalure. Later, smaller numbers of larger aluminum foil and nylon mesh evaporators proved more practical and just as effective. The hexalure, evaporating continuously into the cotton fields over the whole growing season, proved so effective that examination of cotton bolls near the end of the experiment indicated *P.gossypiella* infestation rates comparable to fields subjected to recommended insecticidal treatment programs, and far lower than infestation rates in untreated check plots.

The most extensive application of the principle of disruption of pheromone communication is the gypsy moth program in the northeastern United States (Beroza and Knipling, 1972; Cameron et al., 1974; Beroza et al., 1974). In fact, Beroza (1960) probably had the gypsy moth in mind when he first suggested the "confusion" technique. Once the sex pheromone of *P.dispar* had been correctly determined, and its synthetic counterpart, disparlure, was available in large quantities, field tests were begun. Early experiments were conducted with released males either before or after the normal flight season of *P.dispar*, and also in areas having no naturally occurring populations (Stevens and Beroza, 1972; Beroza et al., 1973). Various formulations for dispersing the disparlure were used, including mineral oil-xylene spray, impregnated hydrophobic paper squares, and granular cork. Encouraging results from these experiments resulted in field tests in natural infestations during the flight season. These were less than successful in disrupting mating perhaps because the population levels exceeded the upper level at which the technique is applicable. Also it became apparent that there was a need for a longer-lasting pheromone formulation and considerably more knowledge of the biology and behavior of adult gypsy moths.

A long-lasting microencapsulated formulation of disparlure was first used by Cameron (1973) and Beroza et al. (1973), and it has subsequently been the focus of most mating disruption experiments with *P.dispar*. The formulation was aerially applied, and through the incorporation of a sticker, a vertical stratification of pheromone throughout the forest profile was obtained. A single application of the microcapsules effectively disrupted mating among released laboratory-reared gypsy moths up to six weeks. The first successful application of the disruption technique against wild gypsy moths established in an artificial population occurred in 1973 (Cameron et al., 1974; Schwalbe et al., 1974). Results indicated that application of 15.0 g/ha of microencapsulated disparlure would effectively disrupt mating activity of gypsy moths for at least six weeks and at densities up to 32 pairs of pupae per hectare. Many of the plots showed at least the 90% infertility rate believed necessary for population reduction. The authors made note again of a continuing concern with behavioral differences manifested between laboratory-reared and wild gypsy moths (Richerson and Cameron, 1974), and emphasized that final definitive tests of the disruption principle must be made on wild populations.

Such a test was carried out successfully by Beroza et al. (1974) in a naturally infested forested area in Massachusetts. A large plot, 60 km<sup>2</sup>, was aerially treated with 5.0 g/ha of microencapsulated disparlure. The resulting population suppression was substantial when compared to similar untreated control plots. When compared to an insecticide-treated plot on a large scale, the method appeared economically feasible. Later tests indicate the need for higher concentrations of disparlure, and that disruption of the gypsy moth pheromone communication can best be accomplished in low level populations, such as in incipient infestations, or as a follow-up to insecticidal treatment of early larval instars (Beroza et al., 1975). Disruption techniques become more effective as the population density drops, similar to the sterile insect release technique (Beroza and Knipling, 1972). The next step suggested by Beroza et al. (1974) is an island experiment of three years duration to demonstrate the possibility of gypsy moth eradication using the mating disruption technique. The first year insecticide treatment would reduce larval populations to low levels, and those surviving to adulthood would be treated with microencapsulated disparlure. Treatment in the second year would consist only of pheromone. In the third year, a large number of highly potent traps would exert further suppressive pressure if necessary, pinpointing small areas needing extra treatment, or perhaps show the complete absence of remaining moths.

#### 4.4.3 Antifeedants

From the standpoint of practical use in pest suppression, the most promising of the chemical signals which function interspecifically are in a group which have been referred to collectively as feeding deterrents (Dethier et al., 1960; Dethier, 1963), feeding suppressants (Beck, 1965), feeding inhibitors (Benjamin and All, 1973), or antifeedants (Wright, 1963; Munakata, 1970). As products of living organisms (mostly plants) with potentially beneficial use by man, antifeedants can be legitimately considered biological control agents. Feeding inhibitors are representative of a larger group of interspecifically active chemicals known as allomones (Brown et al., 1970), whose roles favor the organism releasing them. Also included in this group are such things as defensive repellents and venoms, gall-inducing substances, and attractants for prey or pollinators (Chambers, 1974). A complementary group of chemicals, known as kairomones, includes such things as food, oviposition, and shelter attractants which are normally beneficial to the receiving organism, but which might also be used for pest suppression (e.g. Steiner et al., 1961; Jones et al., 1971).

##### 4.4.3.1 *Characteristics and Potential of Antifeedants*

Antifeedants function differently from most other agents of pest suppression because they eliminate the damage caused by the pest rather than the pest itself. Of course, a powerful antifeedant could also kill the pest indirectly by eventual starvation, especially in monophagous or oligophagous species. When insects are given a choice between untreated host plants and those treated with an antifee-



Fig.46. A sprig of "old" jack pine foliage, showing the differential feeding activity of *Neodiprion* sawfly larvae (note: accumulated frass) between one end (*right*), treated with a natural antifeedant extract from "new" foliage of the current growing season, and the other, untreated end (*left*). (Courtesy J. N. All and D. M. Benjamin, Univ. Wisconsin)

dant, there is little difference in their initial attraction to the plants. The significant difference lies in the initiation of feeding activity, and especially in its continuation (Fig.46). Insects on treated plants may continue to sample small bites at various points, or to investigate the plant surface with their taste receptors and then move on to another spot, but those on untreated plants begin feeding at one location and continue to do so without abnormal interruption. Antifeedants can act either by inhibiting the stimulation of gustatory receptors which normally recognize the plant as acceptable food material, or by stimulating receptors which elicit a negative reaction to deterrent chemicals (Jermy, 1966). The relationship of such behavior to plant resistance and to insect attack (Chap.4.1), especially of the non-preference type, should be obvious. And, in fact, one basis for resistance in a number of plants has been demonstrated as an extractable, identifiable chemical feeding deterrent (Matsumoto, 1962; Maxwell et al., 1965; Gilbert and Norris, 1968; McMillian et al., 1969; Munakata, 1970; All and Benjamin, 1975).

#### 4.4.3.2 Utilization of Antifeedants

The use of antifeedants in protecting our health, food, and fiber has not progressed beyond the stage of basic research and experimentation for most naturally occurring compounds, although several synthetic compounds have shown promise for practical use (Moncrieff, 1950; Wright, 1967). Of the botanical extracts, only pyrethrum has progressed to the point of practical development (Bry and Lang, 1974). The natural pyrethrins are organic esters extracted from dried flowers of a daisy-like plant, *Chrysanthemum cinerariaefolium* (Treviranus) Boccone,

grown mostly in Africa. They are best known for their insecticidal qualities (Casida, 1973), but they also exhibit definite antifeedant characteristics as well. For example, Dethier (1947) noted that biting flies, *Glossina* and *Culicoides*, would settle on residues of pyrethrins but not bite, and that codling moth larvae, *L. pomonella*, were also deterred from feeding by their use. Synthetic antifeedant chemicals were first used as mothproofing agents for clothing and stored products, but most were never really accepted in competition with repellent mothproofing agents such as PDB (Moncrieff, 1950). On the other hand, synergized pyrethrins have found wide use by the U.S. government, and particularly the Armed Forces, in protecting flour and other cereal products destined for long-term storage or overseas shipment in multilayered paper bags (Gillenwater and Burden, 1973). Recently, Bry and Lang (1974) have recommended that, because of their effectiveness and low mammalian toxicity, pyrethrins should be considered as a suitable substitute for hard pesticides in protecting woolen fabrics during short-term storage by the homeowner. Their tests showed that pyrethrins were effective by action other than toxicity (i.e. antifeedant) against the black carpet beetle, *Attagenus megatoma* (F.), in protecting woolen cloth from attack.

In his evaluation of the antifeedant concept, Wright (1967) pointed out the advantages and disadvantages of utilizing these compounds. The most important advantage is the perfect suitability of antifeedants to integration with the use of beneficial insects. Parasitoids, predators, and pollinators are not harmed by antifeedants because such compounds generally have low toxicity, and only affect the behavior of the insect pests which actually attack the protected crop. In fact, the pests are not necessarily harmed directly either. Instead, since they remain wandering and exposed on the host plants or on weedy alternate plants, beneficial organisms can find and utilize them (Benjamin and All, 1973). Additionally, feeding deterrents generally limit damage to the protected substrate more effectively than conventional insecticides because of the time lag before a toxicant can act. With complete coverage, antifeedants act immediately to halt feeding activity which might continue for a significant period with an insecticide. Unfortunately, to date, feeding inhibitors are active only against surface-feeding chewing insects, and seem to provide a protective halo of short duration around the treated host. Those insects which feed beneath the surface (e.g. leafminers, borers), or sucking insects (e.g. aphids, plant bugs, leafhoppers) are generally unaffected. The answer to this problem might be a systemic antifeedant as opposed to the surfactants now available (Jermy and Matolcsy, 1967). Such a material would also combat the other major drawback of antifeedants for protecting plants, the need for complete coverage. Plants are growing organisms and, even with efficient application techniques, they will soon produce new growth that is not protected by antifeedants applied earlier to the outside. Because the target insects are not killed by antifeedant activity, they are free to move on the plants to unprotected areas.