complex behavioral sequence that allows it to arrive at the source of the odorous plume. Studies on the effect of various neurotransmitters and neuromodulators have shown that odor perception and response periodicity is greatly influenced by several biogenic amines. Further studies on the effect of agonists (a chemical substance capable of combining with a nervous receptor and initiating a reaction), antagonists (a chemical that acts within the body to block its nervous receptor), and related pharmacological agents on the action of these biogenic amines could lead to a new way of “jamming the receiver” and, thus, a new approach to the mating disruption technique.

The manipulation of a communication system that is as basic to the insect’s survival as the sex pheromones requires an in-depth knowledge of the whole communication system, from whole-body behavior to the molecular level.

Keeping Ahead of the Wolf: Pest Resistance to Agricultural Pesticides

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The Resistance Problem

Only after decades of pest control remedies and problems has an appreciation grown of the threat posed by pesticide-resistant pests to world and U.S. food production. Since the first case of resistance to lime sulfur in 1908 in San Jose scale (an insect that sucks plant fluids), 428 species of arthropods (insects, mites, and ticks) have become resistant to one or more pesticides worldwide. Of that number, 268 are agricultural pests; the rest are medical or nuisance pests. Resistance has arisen in 150 plant pathogens (fungi, bacteria) and about 50 weeds to herbicides. Only 10 rodents or plant-attacking nematodes have developed resistant populations.

Multiple and Cross-Resistance

Multiple- and cross-resistance to pesticides among pests are becoming more common, too. Cross-resistance is when a pest develops resistance to one compound, but also shows resistance to another, usually related, compound. Multiple-resistant pests tolerate pesticides from many classes of compounds with diverse modes of action.
Certain aphids have become resistant to some pesticides (magnified 200 times).
An example is with the kdr-factor involved in DDT resistant which also confers resistance to the recently introduced synthetic pyrethroid (SP) insecticides. Resistance of several pests to SP's has been reported even though their use has been limited.

Many pests now have multiple-resistance factors in their genetic makeup. Among insects, half of the 428 species are resistant to 2 or more of the 5 major insecticide groups, and at least 17 have adapted to all 5. The housefly, green peach aphid, beet armyworm, diamondback moth, and twospotted spider mite are examples of these “super” resistant bugs. Most recently, strains of pests resistant to even their own growth hormones and natural pathogens have been found.

One recent, dramatic case of multiple resistance is with the Colorado potato beetle in Long Island, NY where resistances to every compound registered for use on potato has developed. Up to 10 sprays per year of aldicarb and oxamyl were used to control the beetle until recently. Use of these compounds contaminated ground water, and some desperate farmers, unable to use any conventional insecticide, returned to standby pesticides used decades ago. Cases like this raise the question—is the human race winning the battle against these adaptive competitors?

Research on Resistance Management

Back when resistances first became common, researchers sought to understand the genetics and biochemistry of resistance in pests to circumvent or diminish their impact on agricultural crops.

After many failed attempts, a certain inevitability syndrome set in—given time, resistance would eventually develop with intense selection. Many believed that resistance was irreversible and compounds were lost forever.

More recently, and in association with development of the integrated pest management (IPM) approach to pest control which has gained acceptance worldwide, better understanding of resistance and factors influencing its development have been gained. Also, new measures to reduce the occurrence of resistance have been researched and are being implemented.

Basic research to identify the biological, ecological, and operational (those under the control of pest managers) factors influencing resistance development has been done through both experimental and modeling studies. This work has improved understanding of how the complex of variables influencing resistance interact in a resistance episode.

There is now a more wide-ranging perspective from the genetics and biochemistry of resistance at the cellular level to the population genetic or ecological levels. For example, awareness has grown of how the ecological setting of a particular agricultural site (e.g. the type of surrounding habitat and sources of colonization by genetically susceptible organisms) influences the extent or course of resistance development. Improved understanding of resistance has helped identify new methods and better integrated use of old and new methods which conserve pesticides as finite, valuable resources.

Resistance management tactics fall into three categories: new or altered pesticide products, changing pesticide use patterns, and ecological tactics.

New or Altered Pesticide Products. Mixtures or multiple-site compounds attacking several target sites simultaneously are usually more difficult to develop resistance to by pests than are single genetic target-site compounds. In responding to fungicide resistance, chemical
companies often use mixtures of chemicals. Synergists applied with pesticides may reduce resistance development by interfering with the detoxifying enzymes that allow the pest to survive pesticides.

Researchers have identified many new chemical agents with novel modes of action and properties that lessen the likelihood of resistance. Pesticides persisting in the environment for short times and tending to act on only limited portions of a pest’s generation and specific stages, may slow resistance. By limiting exposure, the pest’s full array of potential to develop resistance never comes into play.

Other innovative compounds may be used at low doses that selectively kill plant-feeding pests rather than biological control agents. These place less pressure on pests to develop resistance. Similarly, slow-acting toxicants, which allow host-plant resistance and other factors to take their toll on pests, reduce selection for resistance.

Behavior-modifying chemicals that reduce a pest’s ability to locate and attack host plants are additional examples of insecticides that combine selectivity and a broad-spectrum pest activity to aid in resistance management.

**Changing Pesticide-Use Patterns.** Often, when dosages of pesticides are reduced, fewer pests die, so the pressure to develop resistance is less. Occasionally, increases in dosages also may hinder resistance buildup, but this tactic does not work unless resistance is detected at low levels and knowledge of the immigration of susceptible organisms is available.

Rotation of compounds with different modes of action in sequence may limit resistance to pesticides by permitting pests to revert to susceptibility while alternate chemicals are being used. A variation of this approach involves alternating “negatively correlated cross-resistant pesticides,” where resistance to one chemical is associated with decreased resistance to another chemical, and vice versa.

The timing and placement of pesticides also affect resistance. Applying pesticides over limited areas reduces the proportion of the pest population exposed and thus limits resistance by keeping in the population more genes that confer susceptibility. Treating alternating generations of pests allows for more reversion to susceptibility, because of reshuffling of genes and immigration of nonresistant pests between generations.

**Ecological Tactics.** While these methods of managing resistance have received limited study, ecological factors are major determinants of whether resistance will occur and how severe it will become.

Recent study has centered on the effects of immigration on the evolution of resistance. Under most conditions, high rates of immigration of susceptible individuals from untreated areas (refugia) mean that genes conferring resistance in treated populations are flooded out. Susceptible immigrants can be attracted into an area or released into the environment in nondamaging stages. Also, resident populations in treated areas can be limited by applying pesticides intensively before periods of immigration. If such immigration of pests can be tolerated, these may be effective approaches.

Any resistance-management measure may stem resistance by itself. But multiple, integrated measures as part of IPM are usually needed for best results. Regular and frequent monitoring also is essential to effective management. In the early stages of resistance development, the key is to detect resistance at low levels while
the trend can still be reversed. Later, monitoring allows users to switch tactics in response to observed resistance levels, especially where cross-resistance or multiple resistance is a problem.

**Cases of Resistance Management**

Several recent cases of resistance management show progress in limiting resistance and conserving pesticide resources.

In Australia, resistance to synthetic compounds (pyrethroids) by the cotton pest, *Heliotis armígera* was detected in the early 1980’s. By careful monitoring and areawide coordination of limited SP use, resistance has been held in check and effective pest control obtained with chemical products including SP’s. Similar programs on cotton in the United States are recommended on a preventative basis to minimize the possibility for resistance in closely related species.

Pear psylla, a serious pest in the United States, has developed resistance to many insecticides of all classes. When the SP, fenvalerate, was proposed for use in the Pacific Northwest throughout the growing seasons, preliminary tests showed that the insect developed resistance in less than 3 years. But where the pyrethroid was used only in early season and an alternative compound (amitraz) was used for summer control, the pest has been effectively controlled for at least 10 years.

In the same region, use of natural enemies to help control spider mites on apples has appreciably slowed resistance buildup to organotin acaricides. Resistance to these chemicals developed in pears and strawberries in the absence of effective biological controls, and additional or substitute compounds were required on these crops for effective mite control. In contrast, in Washington State, integrated control of mites is widely practiced on apples, using predators and limited chemical application (averaging one-half to one annual spray per orchard). There, cyhexatin has remained effective for the 15 years that

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**Biological and operational factors which influence resistance development to insecticides in arthropod pests.**

<table>
<thead>
<tr>
<th>Biological</th>
<th>Operational</th>
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<tbody>
<tr>
<td>Genetic</td>
<td>Avoid cross-resistance</td>
</tr>
<tr>
<td>Frequency of R-gene(s)</td>
<td>Persistence of residues</td>
</tr>
<tr>
<td>Number of R-gene(s)</td>
<td>Dosage applied-selection level</td>
</tr>
<tr>
<td>Dominance of R-gene(s)</td>
<td>Life stage selected</td>
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<tr>
<td>Fitness of R-gene(s)</td>
<td>Treatment threshold</td>
</tr>
<tr>
<td><strong>Biotic</strong></td>
<td><strong>Alternation of generations selected</strong></td>
</tr>
<tr>
<td>Generation time</td>
<td><strong>Space limited selection</strong></td>
</tr>
<tr>
<td>Offspring/generation</td>
<td><strong>Rotation of different compounds</strong></td>
</tr>
<tr>
<td>Mode of reproduction</td>
<td><strong>Mixtures of compounds</strong></td>
</tr>
<tr>
<td><strong>Ecological</strong></td>
<td><strong>IPM</strong></td>
</tr>
<tr>
<td>Dispersal capabilities-mobility</td>
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<tr>
<td>Host specificity</td>
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<td>Refugia within treatment area</td>
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the chemical has been marketed.

In Japan, study of biochemical changes in resistant insects led scientists to develop a method for restoring the effectiveness of carbamate insecticides against green rice hopper. The key was discovering a detoxifying enzyme in the insect, which was overcome by adding a synergist. In addition, by using the organophosphate fungicide Kitazin P to control the disease rice blast, Japanese workers also suppressed organophosphate resistance in the same insect because the fungicide inhibited another enzyme.

Houseflies on Danish farms have become resistant to virtually every new insecticide since the 1950's. Now, through strict regulation and monitoring, prevention of widespread resistance to pyrethroids has occurred. In 1978 and 1979, surveys indicated that resistance was occurring, and would reach high levels since many flies were carrying resistance genes. A decision was made against registering residual pyrethroids for this use.

Continued monitoring indicates that relatively nonpersistent pyrethroids plus a synergist can be used for several seasons if applications are not too frequent.

**Need for More Research**

While these selected cases of resistance management are encouraging, they are only limited victories in the fight against pesticide resistance. As pointed out in a recent U.S. National Academy of Sciences study on pesticide resistance, additional research on factors influencing resistance, tactics of resistance management, better monitoring methods, improved resistance risk assessment and changes in policy governing pesticide use are needed to stem the tide of pest control failures and keep ahead of the raging wolf of pesticide resistance.