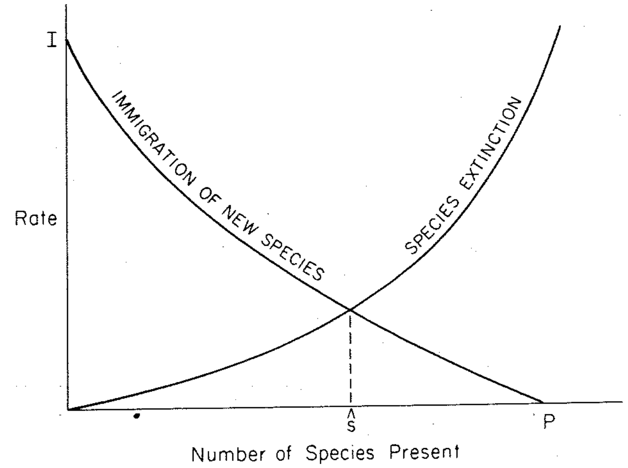

Figure 2.4 The equilibrium model of species on an island. The equilibrium number of species ŝ is at the intersection of the curves of the rates of immigration and the rates of extinction. *I* is the initial rate of immigration and *P* is the total number in the species pool on the mainland. (MacArthur and Wilson (1967). Copyright 1967 by Princeton University Press. Reprinted by permission of Princeton University Press.)

rapid, because the species capable of rapid dispersal are arriving, while the slow dispersers arrive later. These factors combine to produce a concave immigration curve. The extinction curve is also concave, because the more species there are present, the greater the chance of species becoming extinct, simply because there are more species and there is more interactive pressure (principally competition, parasitism, and predation). Thus, we see that the equilibrium number of species ŝ is defined by the point at which immigration and extinction rates balance each other (Fig. 2.4). For the purposes of this discussion extinction refers to both mortality and emigration.

The limits of the immigration curve are set by the total number of species on the mainland that are available as colonists, that is, the species pool *P*, the initial rate of immigration *I*, which depends on *P*, and the distance of the island from the mainland. Immigration to a near island is rapid, because the chances of an individual leaving the mainland and reaching the island are high; immigration to a distant island is slow, because the chances of arrival are greatly reduced. Thus, we can develop a set of immigration curves that differ according to the distance of the island from the mainland (Fig. 2.5).

Extinction rates on islands are also likely to differ, not with the distance of the island from the mainland, but with the size of the island. Naturally, as island size increases, the resource base for species increases, as both species diversity and structural diversity are likely to increase. Thus, extinc-

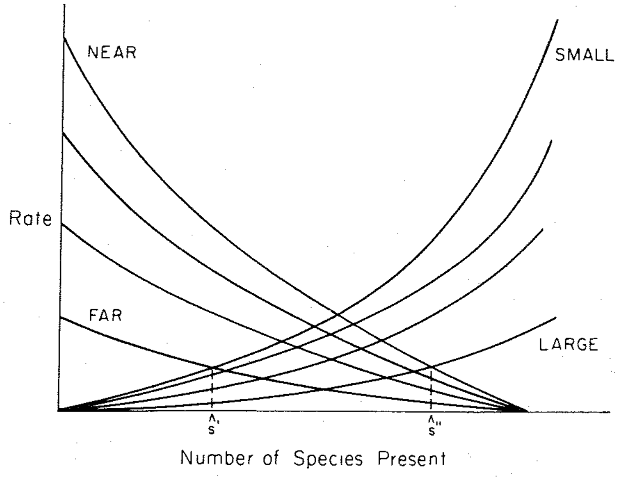

Figure 2.5 A comparison between equilibrium models for near and distant islands and small and large islands using the basic model shown in Fig. 2.4. Note that the equilibrium number of species on near, large islands ŝ ''is much greater than that for distant small islands ŝ'. (From MacArthur and Wilson (1967). Copyright © 1967 by Princeton University Press. Reprinted by permission of Princeton University Press.)

tion rates are likely to be lower on larger islands and can be expressed by a series of curves such as those in Fig. 2.5

Now we can appreciate the full impact of the plant community on the arthropods that are able to exploit it. As the area of the community increases, so its species and physical structure become more complex and, since it is located closer and closer to the source of immigrants, so the equilibrium number of species increases (cf. ŝ'', Fig. 2.5). The opposite reasoning produces an equilibrium number of species for distant small islands (ŝ') far below ŝ''.

Now that we have looked at some characteristics of the island habitats, we must look at the qualities of the colonizing species. Of course, efficient colonizers must have two vital characteristics: large numbers of progeny, because colonization is hazardous, and a high dispersability of progeny so that vacant sites for colonization can be reached. We are already familiar with good colonizers among plants, since they are the weeds that grow on disturbed land, that is, vacant sites, be they produced by gardening, farming, or construction work. One need only think of the common dandelion, *Taraxacum officinale* W., and its large production of small seeds, each seed with a pappus or parachute, which provides an efficient means of dispersal. The dandelion is always an early colonizer, because the chances of its small airborne seeds reaching a vacant site are very high. In contrast, we can think of oak trees, which produce large seeds too heavy to be dispersed by wind, seeds that drop to the ground and may be dispersed over short distances by small mammals. Thus, it may be several decades before an acorn reaches a vacant site. We see that the strategy of the oak is not to avoid competition by reaching a vacant spot before any other plant, but to arrive much later and to succeed in an already established community by virtue of its competitive ability; hence the large energy store that the parent plant invests in each acorn.

Thus, we see two extremes on a continuum of reproductive strategy in plants: the production of many small seeds of high dispersability and low competitive ability, and the production of relatively small numbers of large seeds with low dispersability and high competitive ability (see Fig. 2.13). In the parlance of evolutionary ecologists, these are spoken of as *r* strategies and *K* strategies, respectively; it is believed that they evolved in response to *r* and *K* selection (see MacArthur and Wilson, 1967; Pianka, 1970, 1972; Price, 1984). Each type is adapted for exploiting very different ecological conditions, as we shall see when we consider community succession.

Just as plants can be divided into good colonizers (*r* strategists) and good competitors (*K* strategists), so can insects. As we should expect, many pests of crops are *r* strategists. They are small and can be dispersed great distances by wind, and are often present in crops very soon after germination of the host plant. Aphids, thrips, cicadellids, and many flies are a few examples of some of the most effective early colonizers, and numbered among them are some of our worst pests.

In contrast to the herbivores, their predators and parasitoids are slower in colonizing vacant sites. There is no selective pressure for them to colonize early, as they would encounter a shortage of food. This difference in colonizing ability, coupled with differences in reproductive rates, frequently leads to pest outbreaks early in the season or after the application of insecticides, which kill both the herbivores and their predators and parasites.

We should also remember that early colonists must be adapted to harsh, unsheltered sites where physical conditions may be extreme. Thus, the mortality of colonizers usually results from factors associated with severe weather conditions. Such factors are termed density independent, because their operation does not depend on the population density of the organism involved. The best way to adapt to such factors is to produce many offspring, that is, to be an *r* strategist. In contrast, after establishment of a community the microclimate is ameliorated and the severest threat to survival may become predation and competition from other species, often density-dependent factors that increase in severity with the increasing population density of the affected organism. The best way to adapt to this situation is to invest a lot of energy in improving the competitive ability of progeny and in defending them against predation, that is, to be a *K* strategist.

We can see this trend from *r* to *K* strategies if we look at closely related insects in a relatively unpredictable, harsh temperate climate and in a predictable, equable, tropical climate. For example, the large milkweed bug, *Oncopeltus fasciatus* (Dallas), occurs in temperate North America, and its close

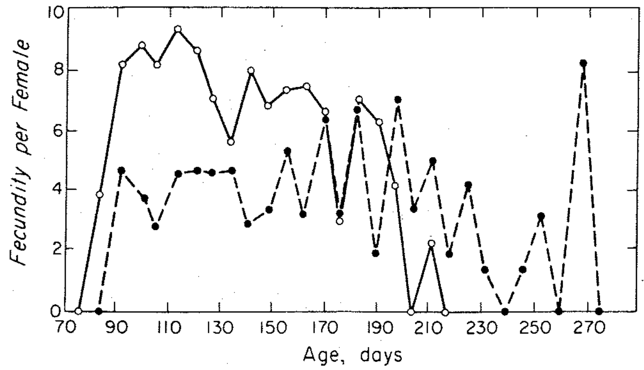

Figure 2.6 The number of eggs laid per week by milkweed bugs, the temperate *Oncopeltus fasciatus* (solid line) and the tropical *Oncopeltus unifasciatellus* (dashed line). Note the earlier start and higher rate of egg laying in the temperate species. (After Landahl and Root (1969). Copyright 1969 by the Ecological Society of America. Reprinted with permission of Duke University Press.)

relative *Oncopeltus unifasciatellus* Slater is found in tropical South America. When egg production is compared, we see that *O. fasciatus* females start to oviposit much sooner after reaching maturity than do their relatives; egg production per day is much higher in their early life, and they produce more eggs, 556 versus 324 eggs per female (Fig. 2.6) (Landahl and Root, 1969). The result is that the population growth rate of the temperate species is much more rapid than that of the tropical species, supporting the assertion that species in harsh environments are likely to be relatively more *r* selected than those in equable environments. Even within one species individuals in northern populations may lay more eggs than those in southern populations (e.g., the Klamath beetle, *Chrysolina quadrigemina* (Suffr.); Peschken, 1972).

During the colonization process, once the species equilibrium has been reached, we are likely to see a rapid shift from the dominance of *r* strategists in the community to the dominance of *K* strategists. Thus, two phases in colonization can be recognized (Wilson, 1969). The *noninteractive phase* occurs during colonization before equilibrium is established and may often lead to overshooting the equilibrium number. This is seen in the defaunation studies on the nearer islands, *E*2, *E*3, and *ST*2 (Fig. 2.3). Later, as competition increases because of increasing population densities, and as more species of predators and parasitoids arrive, biotic interactions in the community assume a more important role. This *interactive phase* brings the number of species to equilibrium. When wheat was first grown on the Siberian steppes, recolonization of the cultivated land by predators played an important role in the establishment of stability in pest populations (Grigoryeva, 1970).

It has been postulated that, given longer periods of time, there is an *assortative phase* in the community, essentially a reshuffling of *K* strategists, resulting in the selection of those species that can coexist most efficiently. This may allow the species equilibrium number to increase slowly (Wilson, 1969).

Finally, given even longer time spans, we can conceive of an *evolutionary phase* in community development in which species not only are sorted but undergo genetic change as a result of selection during coexistence, so that species become mutually adapted for living together (Wilson, 1969). We mentioned earlier in this section the increase in the number of herbivores per plant species with evolutionary time. Evidence for this phenomenon is seen clearly in the comparison of insect faunas on different species of trees in Great Britain (Southwood, 1961). The longer the tree has been resident on that island, and the more abundant—estimated by an analysis of all Quaternary records of plant remains—the more insect species it has associated with it (Fig. 2.7).

Thus, a crop grown for the first time in an area away from closely related species may be occupied by a relatively depauperate herbivore fauna. Soybeans in Illinois are an example. With time, however, we may expect more species of herbivores to adapt to soybeans, thereby increasing the potential for pest problems. However, when a crop is grown close to wild relatives, there is the probability that many herbivores will transfer and that pest problems will immediately be critical. In other words, in the latter situation there is a nearby source of many herbivores preadapted for exploiting the

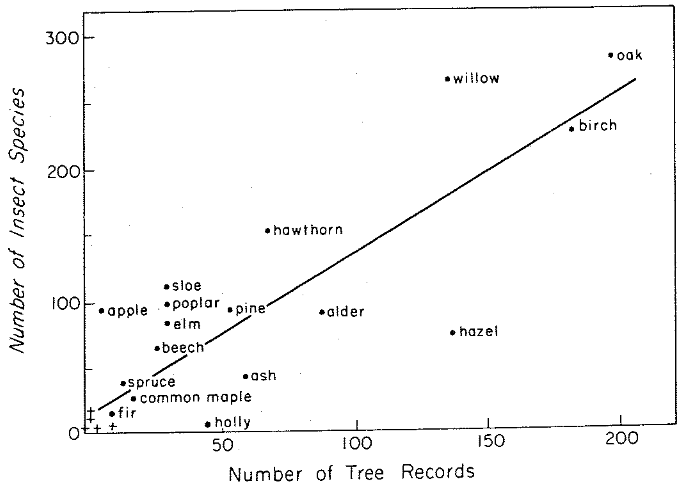

Figure 2.7 Relationship between the number of records of trees, based on their relative abundance and geological time over which they were resident in Great Britain, and the number of insect species that have adapted to exploiting these tree species. The trees that have been established longest, for example, oak, birch, and willow, have the largest insect faunas. Note that naturally colonized trees (●) support many more species than recently introduced trees (+). (After Southwood (1961).)

crop. The most dramatic example is the transfer of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), from its native hosts, wild species of *Solanum,* to the potato, *Solanum tuberosum* (L.), when this crop was first cultivated on the eastern slopes of the Rocky Mountains. Other examples are provided by Strong et al. (1984).

Of course, the plant species will respond in evolutionary time to colonization by insects. Through natural selection induced by heavy herbivore pressures, a plant population may show an increase in the production of toxic substances (secondary metabolic products). This may limit to a few species those insects that can exploit the plant, but with time more herbivorous species will adapt as they evolve mechanisms that enable them to tolerate or detoxify the chemical defenses of the plant. Thus, in plant–herbivore relationships we are dealing with a coevolutionary process (see Ehrlich and Raven, 1964, 1967; Thompson, 1982; Futuyma and Slatkin, 1983; Spencer, 1988). The plant evolves in response to the herbivore, and the herbivore evolves in response to the plant. In this way many herbivorous insects have become highly specific to groups of plants that contain similar defensive chemicals and are toxic to the majority of other organisms. For example, the flea beetles, *Phyllotreta cruciferae* (Goeze) and *Phyllotreta striolata* (Fabricius), are restricted in their food selection to plants in the families Caparidaceae, Cruciferae, Tropaeolaceae, and Limnanthaceae (Feeny et al., 1970). The common quality of these families is that all species contain mustard oils, potent antibiotics that are toxic to most animals but not to the flea beetles. Thorsteinson (1953) demonstrated a feeding response to mustard oil glucosides by the imported cabbage worm, *Pieris rapae* (L.), and the diamondback moth, *Plutella xylostella* (L.).

Again we see that if we plant crops closely related to indigenous plants, we are likely to witness the rapid adoption of the crop by the coevolved fauna because of a lack of chemical barriers and the presence of the correct chemical cues to initiate feeding. The chemically mediated relationships between plants and herbivores is an aspect of the rapidly developing field of *chemical ecology.* Any student of insect pest management should be familiar with this field because it involves many aspects of insect pest ecology (Chapter 7). These include behavior; plant defenses; insect learning; three-trophic-level interactions between plants, herbivores, and carnivores; feeding specialization; population dynamics; and effects of stress and feeding on plant–insect interactions; but this is by no means a complete list. Major reference works on the chemical ecology of plant and insect herbivore interactions should be consulted (Barbosa and Letourneau, 1988; Heinrichs, 1988; Spencer, 1988; Bernays, 1989–1992; Price et al., 1991; Rosenthal and Berenbaum, 1991, 1992; Tallamy and Raupp, 1991; Fritz and Simms, 1992; Metcalf and Metcalf, 1992; Roitberg and Isman, 1992; Papaj and Lewis, 1993).

In summarizing this section, we can say that the number of arthropod species in a community is closely correlated with five major factors:

1. Plant species diversity
2. Plant structural diversity
3. Distance of community from source of colonists
4. Length of contemporary time available for colonization
5. Evolutionary time available for coevolution between herbivores and their host plants.

IV. CROP ISLANDS IN AGRICULTURAL ECOSYSTEMS

During the early settlement of North America by European colonists, agricultural crops were grown in small patches surrounded by large tracts of uncultivated land. Crops were like small islands in a matrix of natural vegetation. As agriculture developed, this matrix dwindled until, at first sight, it may now seem to be an insignificant component of agricultural ecosystems. It is obvious that this is a misconception if we remember two things about insects: their ability to fly long distances and their need for protected sites in which to pass inclement seasons.

Protected sites are found in uncultivated areas, and these may provide cover and insulation from the cold in winter, moisture and milder temperatures during very hot, dry periods of the summer, and food when crops are not available. Adult insects must frequently live through such periods, and the majority do so in uncultivated areas around crops, necessitating emigration from the crop and recolonization. These areas therefore constitute a vital part of the ecological niche of many pest and beneficial insects.

Overwintering sites include under the bark of trees, under fallen leaves, logs, and other litter, under stones, and at the bases of various plants. For example, boll weevils, *Anthonomus grandis* Boheman, and bean leaf beetles, *Cerotoma trifurcata* (Forster), winter under ground litter in the woods; chinch bugs, *Blissus leucopterus* (Say), in bunch grasses; and squash bugs, *Anasa tristis* (De Geer), under rocks and other large objects. During the hot periods of summer many species leave lowland crops to aestivate, and later to hibernate, in nearby mountain areas, returning in spring to the lowland breeding areas. Many cutworms, other noctuid moths, and coccinellids make such migrations (Johnson, 1969). One well-known example is the massive aggregations of the ladybird beetle, *Hippodamia convergens* G. M., in mountainous areas of the western United States. The beet leafhopper, *Circulifer tenellus* (Baker), overwinters on wild annual plants; as these die in April and May, the insects migrate to sugar beets in the San Joaquin Valley, California. Hedges and windbreaks harbor a much more diverse fauna than neighboring crops, even during summer weather, because of the shelter and food provided by the wild plants (Lewis, 1965, 1969a,b).

At this point we must note that by no means do all insects associated with crops retreat to uncultivated areas during unfavorable seasons. For example, the European corn borer, *Ostrinia nubilalis* (Hübner), winters in corn stalks; the Hessian fly, *Mayetiola destructor* (Say), behind the leaf sheaths of wheat; the northern and western corn rootworms, *Diabrotica barberi* (Smith & Lawrence) and *D. virgifera* LeC., as eggs in the soil in the crop field; and the codling moth, *Laspeyresia pomonella* (L.), under the bark of apple trees.

Of course, uncultivated areas offer resources other than just protection. For example, parasitoids have been found to be much more effective in areas where there are abundant wildflowers that provide nectar and pollen (Leius, 1967); northern corn rootworms, although highly host-specific as larvae, as adults feed on the flowers of a wide array of plants, including many Compositae.

In many cases it is clear that the theory of island biogeography is applicable to the recolonization of crops after hibernation or aestivation by insect pests. For example, the incidence of sugar beet mild yellows virus declined rapidly with increasing distance from storage pits for beets in which the aphid vectors *Myzus persicae* (Sulzer) and *Rhopalosiphoninus staphyleae* (Koch) overwintered and contracted the virus (Fig. 2.8) (Heathcote and Cockbain, 1966). Other examples are given by Wolfenbarger (1940, 1946, 1959). This indicates the important role that distance from the source plays in colonization.

Defining the source pool for colonists is not always so easy, as will be seen later in the discussion on sources of colonists. Crop fields are commonly invaded by a variety of arthropods that come from varying distances and may be true colonists or only transients. Price (1976) found many more species arriving at the margin of a soybean field than at its middle. However, many of the insects that arrived at the edge of the field could not survive on soybean and soon went elsewhere or died. Rey and McCoy (1979) argued that taking into account such transients makes the concept of the source pool meaningless and that one should concentrate on the suite of economically important insects—the pests and their enemies.

Nevertheless, we can profitably consider a crop field an island in a matrix composed of a mosaic of land types—uncultivated land, fallow fields, and land planted in other crops. It is time that we fully realized the importance of this matrix, particularly uncultivated land or semipermanent crops like alfalfa, in the dynamics of both the destructive and the beneficial insects associated with crops (see Lewis, 1965; Van Emden, 1965; Bunce, 1990). Its impact on the development of the whole insect community cannot be overrated, and we should keep in mind the possibilities available to us for manipulation of this matrix for the improvement of insect pest-management practices. One enlightened use of wild plants was suggested by Doutt and Nakata (1973), who found that wild blackberries, *Rubus* spp., support the rubus leafhopper and its egg parasitoid. When grape leafhoppers become abundant, the egg parasitoid invades vineyards and plays a major role in limiting pest numbers.

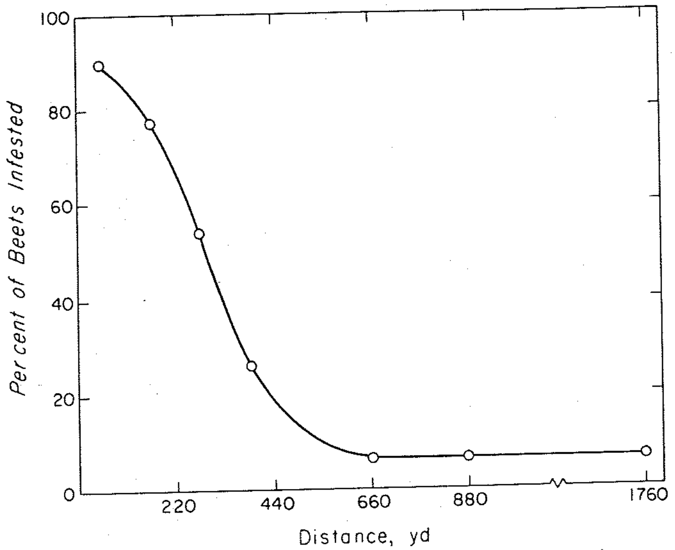

Figure 2.8 The percentage of beets infested by sugar beet mild yellows virus with distance from storage sites for beets in uncultivated areas, indicating the distance traveled by the disease vectors *Myzus persicae* (Sulzer) and *Rhopalosiphoninus staphyleae* (Koch). (Data from Heathcote and Cockbain (1966).)

Next we consider the nature of the crop islands in the matrix. In view of the determinants of the number of species in a community listed in Section III, it is clear that there are major differences among crops of short duration (e.g., 1-year fields of corn, wheat, soybeans, or cotton), moderate duration (e.g., alfalfa or pasture), and long duration (e.g., orchards or forests). The most influential differences among these systems result largely from differences in their longevity and these are (1) plant species diversity, (2) plant structural diversity, and (3) the length of time available for colonization.

Plant species diversity is likely to increase as crop duration increases. Only annual crops receive such intensive care through their duration that weedy species are kept at a minimum, thus keeping the plant community in a very simple state. In crops that last for 2 or 3 years little can be done to exclude the invasion of other species with time, and the plant community is likely to become progressively more diverse. With orchards and forests often no attempt is made to exclude all other plant species, so initial diversity is high and may continue to increase with time.

There is likely to be a concomitant increase in structural diversity with age, because each new plant species added to the community is likely to differ structurally from those already present. This increase will be particularly striking if trees are added. The result is, of course, that the resources of the plant community can be divded so as to yield a greater number of niches for insects.

Finally, the length of time available for colonization is very different among the three crop types. We saw in the defaunation studies that the arthropod community on an island only 2 m from the mainland took almost 300 days to reach dynamic equilibrium. This is a period of time far longer than the growing season for many crops, so we must wonder whether equilibrium is ever reached in annual crops. Price (1976) thought that an equilibrium may eventually have been reached in his soybean field but that it came too late to be of predictive value. The failure of the community to develop an equilibrium certainly reduces the predictability of the community in terms of the number of species present and the stability of populations, since in the colonization phase competition and predation have little regulating influence. Nevertheless, an understanding of how changing conditions in the field affect colonizing arthropods does make the system more predictable. Mayse and Price (1978) found that colonizers in soybean did not reach an equilibrium, but that after the fifth week colonization by both herbivores and parasites and predators correlated closely with the increase in habitat space as the plants grew. Price (1976) found an early rapid colonization of soybeans by herbivores, but little colonization by the more mobile parasites and predators until the canopy closed and ameliorated the harsh conditions on the bare soil between the plants. Similarly, Mayse and Price (1978) showed that planting soybeans in more closely spaced rows caused the canopy to close sooner and that this almost always led to an earlier buildup of predators. The application of island biogeography theory promises to be a fruitful approach even with annual crops; however, it is not, as pointed out by Rey and McCoy (1979), a substitute for the careful study of the natural history of the system in question.

In longer-lived crop communities such as alfalfa and pasture, equilibrium is probably reached, since many species are capable of overwintering in situ, so that each spring the insect community becomes reestablished more rapidly than in the first year. In orchard and forest communities most arthropods are likely to be resident. Thus, equilibrium should be established and some predictability should be evident both in the number of species present, dictated by the equilibrium, and the kinds of species as determined during the interactive phase.

Colonizing arthropods may be conveniently classified according to their origin immediately before reaching the crop. They may be present in the crop field at the time of planting, may invade from nearby communities in the matrix, or may migrate from distant areas. We refer principally to annual crops, but the parallels in perennial crops of either short or long duration can readily be seen.

Resident species, in other words, species present in the field when the crop is planted, may have a head start on those that must invade the crop and may preempt resources so that another species cannot become established.

Colonization of the crop is almost immediate, and the population density in any part of the field is probably independent of its distance from the crop perimeter. However, population density is profoundly influenced by the success of the insect in a particular field the previous year. Examples include species that originally become established when the land is in another crop, such as white grubs and wireworms, which may attack corn planted on land previously in sod. There are also species that are particularly successful when land is continuously planted to the same crop, such as northern and western corn rootworms. In rare instances insects may be introduced by humans when the crop is planted. Gladiolus thrips, *Taeniothrips simplex* (Morison), for example, may winter on corms stored indoors and become active after the corms are planted.

In contrast, insects that must invade from the surrounding matrix probably colonize gradually, and there is likely to be a gradient in population density from perimeter to center, particularly leeward of overwintering or aestivation sites and when small insects that are likely to be windblown are involved, such as aphids, cicadellids, or flea bettles. Population densities are much less likely to depend on breeding success at the same site the previous year. Insects may move to the crop from wintering quarters, as do the Mexican bean beetle, *Epilachna varivestis* Mulsant, the bean leaf beetle, and the European corn borer. These movements may be synchronous but are usually relatively gradual and may extend over a fairly long period of time. Movement may be from other crops, for example, chinch bugs from small grains to corn, or grasshoppers and armyworms, *Pseudaletia unipuncta* (Haworth), to corn from small grains or weedy patches. These are likely to be synchronized mass movements that may have a dramatic impact on the colonized crop. They may be triggered by a natural event, as when chinch bugs respond to the ripening of small grains, or by cropping procedures, as when potato leafhoppers, *Empoasca fabae* (Harris), are driven to nearby soybean fields when alfalfa is cut. Such movements are most likely to have an important impact when related or complementary crops are grown in close proximity.

The above discussion emphasizes the point that the planning of the spatial relationships of crops and uncultivated land should be done at the ecosystem level, in anticipation of insect movements over a period of years in relation to their densities in crops, prevailing winds, and cultural practices. In this way large colonizing populations may be avoided, or at least predicted, as explained in Fig. 2.9.

Next we must consider insects that colonize from a considerable distance and may be loosely termed migrants (c.f. Rainey, 1976; Rabb and Kennedy, 1979; Berryman and Safranyik, 1980). In the United States many pest species overwinter in the Gulf states and migrate with the prevailing winds into northern states. Some of these migrants are small and can be dispersed rapidly over long distances by wind, for example, the leafhoppers *Empoasca fabae* and *Macrosteles fascifrons* (Stål), grain aphids (Johnson, 1969), and some species of thrips. Other species are larger and migrate more slowly,

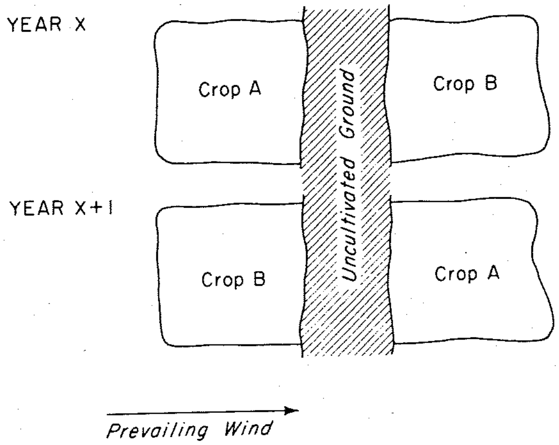

Figure 2.9 In year *x* uncultivated ground provides overwintering sites for adults of pest species on crop A. Thus, in year $x + 1$, with crops arranged as shown, conditions are ideal for the pest to colonize crop A from its overwintering quarter if the prevailing wind is as indicated. This provides a very simple example of the type of planning that should be conducted on a very extensive basis.

for example, the large milkweed bug, *Oncopeltus fasciatus* (Dallas) (Dingle, 1972). The adaptive features of this migration make some species exceedingly important pests. Overwintering may be very successful in a mild climate, and reproduction may continue during the winter. Mass migration may occur under favorable conditions, arrival times and places may be unpredictable, and relatively high densities may be established suddenly. All these characteristics mitigate against the early establishment of predator and parasitoid populations large enough to contribute effectively to population regulation. In fact, a sweeping generalization that may nevertheless be worth considering is that the greater the distance from which an insect colonizes, the more likely it is to become a serious pest if it can become established at all.

From time to time species invade areas in which they did not previously occur, usually because they are accidentally transported by humans. A quick look at a few such invaders should convince us of their potency as pests: the alfalfa weevil, *Hypera postica* (Gyllenhal); the Japanese beetle, *Popillia japonica* Newman; the European spruce sawfly, *Diprion hercyniae* (Hartig); the European corn borer, *Ostrinia nubilalis* (Hübner); the cottony cushion scale, *Icerya purchasi* Maskell; and the gypsy moth, *Porthetria dispar* (L.). Of course, it is most unlikely that the appropriate parasites, parasitoids, and predators will be accidentally introduced at the same time or that endemic species are well adapted to prey on or parasitize the introduced species. Furthermore, the colonists may be preadapted for exploiting a vacant niche and may thus avoid severe competition from indigenous species.

The extent of the inadvertent movement of insects by humans is enormous (e.g., Drake et al., 1989). One example is particularly informative. If the distribution of carabid beetles in North America is examined, we see that many species also exist in Europe (Fig. 2.10) (Lindroth, 1957). The most