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Chapter 22

Insect Influences in the Regulation of Plant Populations and Communities

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This chapter presents an overview and some specific concepts and examples concerning the diverse roles of insects in regulating or influencing plant populations. Also considered are some consequences of these population-centered roles and of other, broader roles of insects that affect plant community composition, functioning, and maintenance. These roles are seen as effects on density, age and quality, patterns of seasonal expression, spatial distribution, and stability of specific populations and, to an extent, the communities of which they are a part (cf. Chapters 2, 12). Both short-term functioning and more distant evolutionary processes are considered. The spectrum of these influences embrace (1) local movement, dynamics, and natural control and (2) larger-scale movement, dynamics, and evolutionary change, all commonly affected by various physical and biotic influences, including their heterogeneity in time and space (cf. Chapters 6–18, 23). Insects can serve such roles as exploiters, allies, or competitors of other species. Their roles as pollinators are presented in Chapter 20, and omitted here. We here emphasize examples where insects are significant in a regulatory sense (Chapter 12). Some populations of plants (as of animals) may be regulated through the reciprocal predator–prey interaction involving insects, and the structure, functioning, and stability of some biotic communities may thus be strongly influenced by insects.

Most terrestrial plants, and also animals and microorganisms, are in some way closely associated with insects. Coevolution of insects and various associated organisms has produced some clearly mutual benefits; and for others roles mainly as food, one for the other. For some, a stable predator–prey (host–parasitoid) relationship at the population interaction level can be seen, despite the violence of individual to individual interaction. Some insects mediate interspecific competition between other organisms, including plants, affecting their dynamics, resource sharing, and succession (Chapters 2, 15). Through their exploitation of epidemic populations and mediating roles, some insects contribute to reestablishing a more natural (primeval) community composition (e.g., through reducing the density of one species of plant where an increased density has been caused by human or other disturbance of balance, or in mediating the species richness of the biotic community). Over long periods of time, it is presumed that individuals' adaptations associated with such activities have undergone a fine tuning, contributing to existing community integrity and relative stability.

Epidemics of herbivores resulting from disturbance may cause destruction of much of certain plant populations. Whether this occurs in patches or more generally will affect the rate of restoration of the plant stand. Rate of restoration will depend upon the type and age distribution of the stand and the characteristics of the individual plant species. For small patches of destruction, compensations (e.g., growth of neighboring surviving plants or branches) may achieve a rapid adjustment; for larger patches, restoration could only be achieved by establishment and maturing of recruit plants. This would be a long time for a redwood forest but much less for vegetation of annual plants.

We first discuss some general roles, processes, and concepts related to influences of insects, in either direct or indirect ways, in the regulation of plant populations and communities. Following this we review the modes of influence and some specific cases wherein insects have been seen to have significant roles in regulating or influencing plant populations, including their roles as vectors of plant diseases. In the last two sections we treat the roles of insects at a broader, more integrating level, embracing not only their influences on specific tree species populations in forests, but whole forest phenomena such as tree species richness and composition, plant succession, and community stability. In this, we deal first with temperate climate forests and lastly with tropical forests.

22.1 ROLES, PROCESSES, AND CONCEPTS RELATING TO INFLUENCES OF INSECTS ON PLANTS

22.1.1 Insects as Mediators of Interspecific Competition (cf. Chapter 15)

Harper (1977) showed the spectacular effect that a small, commonly observed animal may have in mediating the interspecific competition between two plant species. A nematode, *Heterodera avenae*, alters the interspecific competition between oat and barley plants because the barley but not the oat plants are resistant to the nematode (Fig. 22.1). The dotted lines in Fig. 22.1a show the result corresponding to equal competitive coefficients in the two species. In the absence of *Heterodera*, oats were strongly competitive

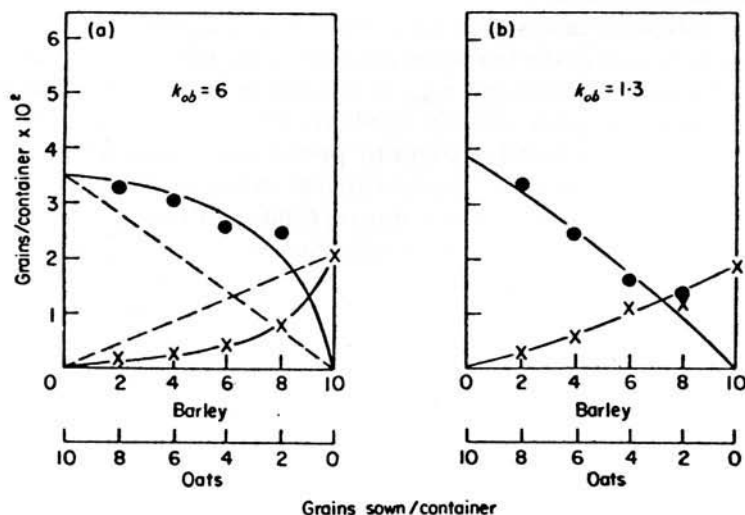


Figure 22.1 The growth of oats and barley in a replacement (competition) series experiment without (left) and with (right) an infestation of the nematode *Heterodera avenae*. x-----x = barley; ●—● = oats. (After Sibma et al. 1964.)

(relative crowding coefficient $k_{ob} = 6$) against barley, not in its presence (coefficient reduced to $k_{ob} = 1.3$). Figure 22.1b shows that the competitive status of the two was then about equal. The biological control achieved by introduction of the thrips *Liothrips urichi* into Fiji for control of the weed *Clidemia hirta* is an example wherein an insect strongly affects plant competition. The plant and insect are native in Trinidad; by the 1920s the plant had invaded Fiji and become known as "Koster's Curse" in grazing lands. Search for enemies of the plant in Trinidad, and testing of their host specificity (for safety to introduce), resulted in introduction of the thrips even though in Trinidad it caused only minor effects on tip growth and did not retard its host populations. In Fiji, however, Simmonds (1933) reported that this herbivore effect was enough to tip the competitive advantage to valuable plant species, with the pest species greatly reduced (i.e., under substantial biological control). Utida (1953) also showed in a laboratory system with two competing bean seed weevil species that the hymenopterous parasite *Neocatolaccus mamezophagus* influenced the outcome of the seed weevil competition. In the absence of the parasite, *Callosobruchus quadrimaculatus* always won over *C. chinensis*, but in its presence they co-existed. Janzen (1970) presented a theoretical model of observed mediation of competition between plant species by insects in certain tropical vegetation, with seed predation being the common route. (cf. Connell 1971)

22.1.2 Single Species of Insects Having a Direct or Suppressive or Regulative Effect

When an insect regulates a plant population's density, it commonly alters that population's competitive status, either through weakening or direct killing of individual plants. In some instances the competitive feature seems relatively minor, as in the biological control* of St. Johnswort in California by *Chrysolina quadrigemina* (or, e.g., of *Opuntia* in Australia by *Cactoblastis*, and the aquatic alligator weed in southern United States by *Agasicles*. St. Johnswort plants are killed outright by prolonged, severe defoliation and consequent retrenchment of the root system which becomes so small that the plants cannot obtain moisture during California's long dry season. In eastern Australia equally severe defoliation leads to much fewer deaths because of more rain in summer. There competition of the weakened plants with other species enters as a more definite feature in the degree of population reduction experienced (Huffaker 1967, cf. Section 22.2.5). The regulating process in a case like *Chrysolina* for St. Johnswort in California or *Cactoblastis* for *Opuntia* in Australia is the same as the regulation of an insect prey or host population by a host-specific enemy insect. There is a reciprocal density-dependent population interaction (cf. Chapters 12, 16).

*Biological control is the regulation or suppression of a host or prey population by one or more of its natural enemies, at a density lower than would be the case in the absence of the enemy(s)—that is, where they would reduce recruitment.

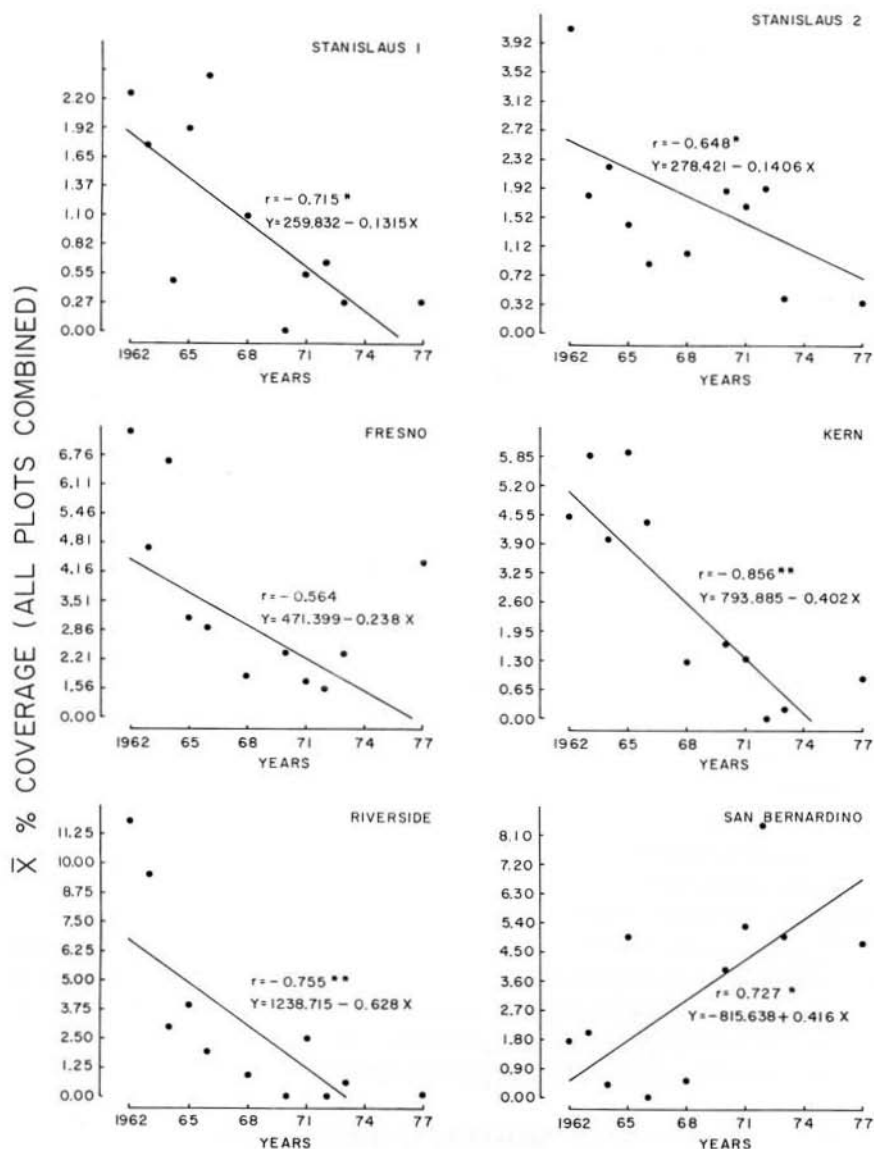


Figure 22.2 Regressions of percentage coverage of ground by puncture vine, *Tribulus terrestris*, at six major areas in California as associated with introduced puncture vine weevils beginning in 1962 and through 1977 (declines in five of the six areas, but an increase in San Bernardino County despite the negative action of the weevils).

Even when *individual plants* (e.g., juveniles) are killed directly by an insect, competition of the *population* with other plant species may be significant because the reduction in individuals (e.g., seeds) lessens the population's competitive impact (Janzen 1970). Thus, while introduced *Microtharus* weevils in California have their main effect on puncture vine (an annual)

through direct seed limitation, the seeds that remain may face intense competition with other plant species and because of their reduced numbers, the weed's competitive potential is lessened. With approximately 46% seed prevention or destruction by *Microgaster*, this pest plant has been substantially reduced over a 20-yr period (Huffaker et al. 1983). (Cf. DeBach 1964, MacArthur & Connell 1956)

22.1.3 Insects Sharing with Other Species or Factors in Complex Regulation

It is clear from the results of introductions of various exotic phytophagous insects for control of specific alien weeds, and from observations on the status of the same weedy plants in their native home areas, that some plant populations may not be subject to regulation or control by a single species of phytophagous insect (or even at all), whereas a complex of such enemies may serve such a role. This is suggested by the fact that the pattern of suppression of *Lantana camara* in Hawaii, beginning in the early years of this century with the first establishment of lantana insects (eight species) from Mexico, has been progressively improved through the accumulated effects from these species and a number of others introduced later, whose combined effects kill more plants at a given site and over a greater range of habitats (Andres & Goeden 1971, Andres et al. 1976). Hazeler (1981) elaborates beyond these basic reasons why a complex of species are required for *Lantana* control in Australia. He notes, too, that *L. camara* exists in Australia in many biotypes that differ in their susceptibility to damage by the various introduced insects (20 in Australia). With increase in the number of species established and with altered pasture management, the pest has gradually decreased in abundance. Other examples include the additive effects from introducing complexes of natural enemies for control of both prickly pear species and St. Johnswort in Australia, North and South America, Africa, and elsewhere (cf. Goeden 1978, Moran 1980) and of other complexes for control of alligator weed in southern United States (Maddox et al. 1971) and of *Tribulus* (e.g., puncture vine) in California (Huffaker et al. 1983) and Hawaii (Andres & Goeden 1971).

22.1.4 Insect Influences as Secondary Predators or Parasites

Exotic enemies of a natural enemy being introduced to control an exotic pest are commonly excluded. The assumption is, and the evidence is suggestive, that secondary enemies interfere with a primary enemy's effectiveness (e.g., DeBach 1974, Rosen 1981, Luck et al. 1981). However, in the native home areas the existing complex of secondary enemies of the primary enemies of insect pests usually do not seem to interfere significantly. Such species as have been introduced into other lands rather commonly appear to be equally effective in their native lands (despite their resident enemies)

and in the new environments (Doutt & DeBach 1964). Yet, obviously, effective prevention of a depressing effect of a phytophagous insect on its plant host's population by a natural enemy of the phytophagous species is action of a secondary enemy, and it is precisely these sorts of enemies that have been so useful in classical biological control of insect pests of crops. Moreover, there are instances of secondary enemies apparently inhibiting effective action of primary weed-feeding enemies introduced for weed control [e.g., native Australian parasites shifted to *Zeuxidiplosis giardi* introduced for St. Johnswort control in parts of Australia (C. B. Huffaker unpubl.)], as may be so for secondary enemies attacking primary enemies of insect pests (Rosen 1981).

22.1.5 The Role of a Natural Enemy—Use of Manipulation

One can learn if a plant (or animal) population is being strongly limited (even regulated) by an exploiter species by use of manipulative methods: (1) by augmentation of the exploited population and (2) by exclusion, removal, or strong inhibition of an exploiter species suspected of having such an effect (DeBach & Bartlett 1964, DeBach et al. 1976, Harper 1977, and Chapter 12). The latter, but not the former, has been widely used in applied biological control. Little use was made of either method in field communities until recently, except for use of fences to exclude large ungulate grazers and rabbits in seminatural grazing lands and Connell's (1961) use in marine habitats. Procedures to inhibit or exclude the much more selective grazers among the insects have received little attention (Huffaker 1957, 1959, Harper 1977), but there are exceptions. Foster (1964) applied a complex of pesticides to quadrats in permanent grassland and reported that *Bellis perennis*, a constituent species, increased markedly. C. B. Huffaker and C. E. Kennett (unpub.) applied DDT to quadrats in a St. Johnswort-infested range under heavy attack by *C. quadrigemina* (cf. Section 22.2.5) and found that only in the treated quadrats did the wort survive beyond that summer, except as "trace" and depauperate individuals; other plant constituents flourished (cf. Huffaker & Kennett 1959, 1969). Cantlon (1969) applied insecticide to the ground in a Michigan woodland, and a rapid increase in the herb *Melampyrum* occurred. The cause was traced to the suppression of a polyphagous orthopteran which preferred *Melampyrum*.

22.1.6 Some Influences of Evolution

Evolution can modify characters associated in the regulation of a population. Genetic feedback may rather "permanently" alter properties (long-term evolution); this is seen in the deeply set characters of higher taxa and may be reflected in the density at which a population is regulated by density responsive factors. Or it may alter properties irregularly and during short periods of time and be reflected in altered population dynamics and reg-

ulation (cf. Nicholson 1957, 1960 and Chapters 9, 12). Such changes may result in response to any selective factor. In the interspecific competition experiments of Pimental and Al-Hafidh (1965), for example, shifts in competitive superiority of housefly and blowfly populations seemed to occur alternately, fostering coexistence of the two species.

A herbivore that has closely coevolved with a particular host species in some instances may be a more detrimental consumer to a relative of its natural host than to the natural host itself. This was true for the scales *Carulaspis visci* and *Lepidosaphes newsteadi* that invaded Bermuda. There they caused severe damage to *Juniperus bermudiana* which is much less resistant to these insects than their native hosts in the Orient (Thompson 1954). A spectacular case, not involving an insect, occurred with arrival in the United States of the fungus *Endothia parasitica*, to which its natural hosts were resistant. It quickly devastated our susceptible American chestnut. However, this type of occurrence is not typical of biological control of insects. Classical cases of highly effective biological control of insect pests have involved alien species which had colonized new areas of the world without their coevolved natural enemies being present (e.g., DeBach 1974, Wilson & Huffaker 1976). Usually, in the native home each species was relatively scarce and not a pest, suggesting possible effective biological control. Upon introduction of one or more effective enemies, the exotic pest population was then greatly reduced and so maintained subsequently [30–90 yr now for various cases (Huffaker & Messenger 1976)].

22.2 CASES OF INSECTS REGULATING OR INFLUENCING PLANT POPULATIONS

In Section 22.1 and in Chapters 2, 11, 12, 15, and 16, some general concepts concerning the roles of insects in the regulation of various populations were considered. In this section we detail specific instances of various influences of insects on plant populations, and in Sections 22.3 and 22.4, the roles that some insects may have in community structure and succession.

22.2.1 Modes by Which Insects May Affect Plant Population Regulation

Insects can affect plants by their feeding. The obvious and direct adverse effects can lead to a variety of significant indirect consequences. Certain species induce gall formations in their hosts. Feeding on foliage, for example, reduces photosynthesis and growth of the whole plant. It may alter moisture demand (e.g., mite and thrips feeding can increase moisture loss by the plant, thereby increasing the requirement) and affect flowering and seed production during the same or a subsequent year, and may lead to death of roots or other tissues, or the whole plant. Reduction in size or function of root systems reduces uptake of both water [sometimes beneficial

(Harper 1977) but lethal if a full root system is needed] and minerals. Extensive cambium destruction is often lethal. Borers in internal nonvital plant parts may introduce pathogens that destroy the plant or perhaps its mechanical support system. Beneficial influences of insects as pollinators are dealt with in Chapter 20, and in other ways in Chapter 18.

22.2.2 Seed and Flower Feeders

Direct flower feeding is often of less significance than feeding on seeds, juveniles, or adult plants. This is because there is a greater chance that such "deaths" of flowers may be dispensable rather than indispensable. Thus, flower feeding may indeed prevent seeds from developing, but the plants may compensate, to a degree, for the loss of flowers or young fruits, by producing replacements (e.g., Adkisson et al. 1964, Lloyd et al. 1962). For lack of space to consider both flower and seed feeders, we here emphasize the seed feeders.

Here we are interested in (1) the roles of insects as density-responsive regulators of the population densities and dynamics of the plants preyed upon and (2) their influences on the pattern of plant species occurrence and abundance in natural mixed communities. These two considerations involve not only the adaptive capabilities of individual plants and plant species populations to exist and compete with their siblings and other species in the absence of seed predation, but more importantly, the roles that seed predation and flower feeding (preempting seeding) might have in mediating such competition and its consequences for any of the aforestated considerations.

Seeds of many species may suffer heavy destruction by insects and sometimes insects transport and/or bury seeds, producing effects on patterns of growth and occurrence (e.g., Janzen 1971, 1977, 1980, Tevis 1958, Petal 1978, Carroll & Janzen 1973, Carroll & Risch 1981). Janzen (1971) reviewed the question of seed predation by animals, among which insects have some importance. The pattern of seed predation is highly structured and has involved evolutionary and coevolutionary relationships of chemical, morphological, and physiological nature. Pulliam and Brand (1975), for example, found that plants in an Arizona grassland appear to have adapted their seed morphology and reproductive phenology to minimize seed predation. A consequence is also an interclass (especially ants vs. sparrows) competition for seeds. Seeds produced after the winter rains are too smooth for ants to carry easily, and although these seeds are a type more readily eaten by sparrows, at this time sparrows are shifting their diet to insects. Seeds produced after the summer rains (ripening as cold weather arrives) have conspicuous awns and bristles and require husking, for which the sparrows' bills are poorly adapted, and although these seeds are readily carried by ants, this is a period when cold weather makes the ants inactive.

Seeds, flowers, and juvenile plants occupy a special role: supplying re-

cruits for plant population maintenance and/or increase. The dispersal role of animals (mainly mammals, birds, and ants) is often closely associated with these animals' roles as predators (killing by eating), since even true seed predators drop viable seeds incidental to their feeding. This transport can generate a variable "seed shadow" pattern, with more spread and variation from birds and mammals than from ants. While some of the birds and mammals serve primarily as dispersers, others serve both roles; and the positive dispersal feedback can offset, or more than offset, the negative feedback from seed predation. The attributes of coevolved seed predators and their associated plant species have resulted from a mix of these classes of feedback (Gadgil & Bossert 1970). As Janzen (1971) noted, "The game is played by mobile predators in search of sessile prey plants; escape is through a single dispersal move, seed chemistry, parental morphology and evolutionary change." Janzen emphasized the ecological and evolutionary distinction between feeding on parent plant tissues (fruits) and killing of seeds and juveniles (recruits).

Predispersal seed predation may be light or heavy (1–100%). Such predation by prey-specific seed predators has a high potential of serving a direct density-dependent role in causing an adult plant population density to be lower in a mixed stand than would be the case if such seed predators were absent and interspecific competition were the only challenge. Thus, a biological control impact (by insects or other organisms, especially rodents, on seeds or other plant tissues) has been postulated to have a role in mediating and/or maintaining the high degree of plant species richness that exists in much of the tropics (e.g., Ridley 1930, Janzen 1970, Huffaker 1974; but cf. Johnson & Raven 1970); and to a degree, through removal of a strongly dominant plant species or more subtle effects on succession, in certain temperate forests (cf. Section 22.3, and, e.g., Moore 1942, Graham 1956, Smith 1970, Sartwell & Stevens 1975, Smith 1976) and in seminatural rangelands (e.g., Bond 1945, Dodd 1940, Huffaker 1957, 1959, 1974, Tevis 1958, Sharp & Barr 1960).

Postdispersal seed predation effects differ from those of predispersal predation effects in several ways. The pattern of the seed shadow (its heterogeneity, etc.) influences both the number of successful progeny and their placement positions. The character of the specific dispersers and of the propagules dispersed and influences of wind and streams produce in total a very complex aggregate seed shadow (Janzen 1970, 1971, Smythe 1970). Postdispersal seed predation also ranges from very light to very heavy for certain species and for the community as a whole (Janzen 1971, and references cited therein). Degree of litter or soil cover may be significant, including seed burying. The analysis of postdispersal predation has been difficult; assessment work is currently being intensified.

The chemical defenses of plants against herbivore feeding, including that on seeds and flowers, has become an extensive subject. Various workers (e.g., Janzen 1969, 1971, Jones 1966, Whittaker & Feeny 1971) consider

that the abundance and diversity of "secondary compounds" in seeds that are toxic to seed predators are not likely to be waste products. It is suggested that seed chemistry has coevolved with the host specificity of the density-responsive seed predators, with the latter naturally influenced strongly by fluctuations in seed availability (cf. Janzen 1971). Interestingly, Janzen (1971) remarked that although insect predators of temperate zone seed crops characteristically support large secondary exploiter (parasite) populations as, for example, do bruchids of some common tropical hosts, there is "almost no evidence of entomophagous parasites of tropical *host-specific* seed predators." Janzen considers the latter to be due to the fact that these predators are serving, in the species-rich tropical vegetation, the role of secondary predators (parasitoids) superimposed on the lower trophic level, regulating predator-prey interaction, which he assumed to exclude the hyperparasites (parasites of the host-specific seed predators). He notes that even in the much less diverse northern temperate forests, parasites of seed crop predators usually attack an array of host species.

22.2.2.1 Satiation of Seed Predators and the "Mast Year" Phenomenon. The question of satiation of predator requirements is important in the predator-prey ecology of both carnivores and herbivores. An extreme carnivore case is illustrated by the now extinct passenger pigeon. This bird nested in concentrations of hundreds of thousands, even millions, in a large primeval nesting habitat. It is reported that although enormous numbers of both avian and mammalian predators congregated at these locations and satiated themselves daily, they took but a small portion of the total recruitment. This bird's extinction in later years by humans, both as devastating predators and as destroyers of the prime breeding habitats, is of course not the point being made here. For plants the synchronous presence during a fruiting season of the seed crops of one tree species, and even of a group of species, may enable the seeds of a given plant or a whole species to escape predation through satiation (Janzen 1971, 1972). Seeds of one species may also be protected beyond the satiation effect by the greater predation on seeds of more preferred species. And, through selection, the timing of respective seed crops may be related to this potential of many predators to utilize several different species' seeds (Hurlbert 1970, Janzen 1969, 1970, Smith 1970).

The seed predator satiation effect has been significantly interrelated in the evolution in plants of the phenomenon known as "mast years," that is, years of heavy seed crops followed by one or more years without seeding. Thus, at the population and community level several workers (Lauckhart 1957, Smith 1970, Svardson 1957, Janzen 1971) consider that predator satiation is responsible for the spectacular coevolutionary and rather cyclical fluctuations in seed predators and their own enemies in northern forests of North America and Europe. It is conjectured that a weather event at some time resulted in failure of a seed crop one year, and due to the

conserved nutrient reserves, a larger seed crop could be produced the next year, with satiation of seed predators resulting in more seed escapes. There is then a selection of plants hyper- or hyposensitive to the weather event and also for a physiology more responsive, in terms of greater seed production, the longer the plant has gone without producing a crop. For a tree species, there may have been a lengthening of this period without seed crops to 2–10 yr. This lengthening, however, is constrained by the competitive disadvantage of not putting seeds into the habitat, the costs of storing nutrients, and the probability of the tree suffering severe damage before it produces the delayed seed crop. Predators following a peak seed year are apt to be numerous and put heavy pressure on any seeds developed outside of the synchronized mast year pattern; hence predation generates selection against out-of-phase fruiting.

Janzen (1971) noted further, "The seed predator is confronted with the problem of waiting out the time between crops. A variable fraction of the insect population generally goes into diapause for 1 to 5 years, a behavior strongly reinforced by severe competition among the insects for the off years' seeds. Where diapause is highly synchronized with the plant population, percent seed predation by such predators, even in the peak years may, in fact, be higher than during the off years" (cf. Lyons 1957, Kraft 1968, Dalke 1953). Janzen (1971) also noted that in tropical communities with high species richness a shortage of dramatic weather-synchronizing cues, and so forth, such synchronization of extensive populations or whole communities as occurs in northern temperate zones is unlikely but does occur in one forest type that is dominated by Dipterocarpaceae in Malaysia.

22.2.3 Fruit Feeders

Animals that feed on fruits may have several distinct roles: namely, as seed dispersers or seed predators (previous section), as consumers of other parts of fruits, and as parasites or gall formers which often produce distinct malformations and may interfere with seed development (e.g., Varley 1937, Mellini 1952, Zwölfer 1967). Coevolution of attractively colored, tasty, and nutritious fruits and their specialist vertebrate consumers that coincidentally serve as dispersers has been commonplace (see Harper 1977). Insects, however, have had their main mutualistic coevolutionary role with plants at the pollinating (Chapter 20), rather than the seed dispersal level. But insect destruction of fruits (or seeds) reduces dispersal and thereby can change the species composition of communities.

There are innumerable insect feeders on fruits, and because of their economic importance, they have received extensive agricultural and silvicultural attention. The impact of *their* natural enemies on *them* has also been studied extensively. Bennett et al. (1976) summarized some of these relationships for tropical fruits and nuts, as did MacPhee et al. (1976) for

temperate climate fruits and nuts. Many of these kinds of pests attack the rind or fleshy parts and only incidentally damage seeds. They are in effect, ordinary herbivores. Hence, Janzen's (1971) reference to the reasons for scarcity of host-specific parasites of seed predators in natural tropical vegetation would not apply. In fact, the insect pests of tropical, as well as temperate, fruits are frequently attacked by relatively host-specific, as well as more generalized parasitoid and predatory insects. Thus, introduction of exotic natural enemies of economically important fruit flies has had a prolonged history, with quite checkered results. In a few cases successes have been reported (Bennett et al. 1976), a major one being the biological control of *Dacus dorsalis* in Hawaii by a complex of *Opius* spp. (Chapter 15) and another that of *Dacus passiflorae* in Fiji, mainly by *Opius oophilus*. Rather little is known about the biological control of native fruit flies by native enemies.

22.2.4 Root and Stem Feeders

Root- and stem-feeding insects such as wireworms, rootworms, maggots, white grubs, wood borers, cambium feeders, bud feeders, gall formers, and so on, are often serious pests of crop plants, and as such have received much attention (cf. texts in economic and forest entomology).

The periodical cicadas in eastern United States are notorious for their great abundance and strictly synchronized periodicity. While we are not well informed as to their impact on host plants, the coevolution of the three species with their two life cycles is an intriguing subject. There are three species, *Magicicada septendecim*, *M. cassini*, and *M. septendecula*, and each appears as adults in natural woodlands and orchards after 13- or 17-yr periods of feeding on root xylem (White & Strehl 1978). The results of years of work on them have produced some hypotheses concerning competition, coexistence, predation, disease, and predator satiation as factors in cicada regulation, brood displacement, or synchronization of cycles (e.g., Lloyd & Dybas 1966a,b, Lloyd & White 1980, Dybas & Lloyd 1974, White 1980, White & Lloyd 1975). The three species occur together and are perfectly synchronized (linked) with one another over the 17-yr period in mid and northern areas (and 13 yr in valley and southern areas). The story and hypotheses are still evolving, but predator satiation on adults is thought to be the factor firmly linking the three species together; yet competition occurs and is thought to be a factor during larval development. The species have different preferences for the various tree species and specific sites in a general locality, and this contributes to their continued coexistence (e.g., White 1980). There is some evidence that the three species of 13-yr cicadas have been extending northward and driving out the three species of 17-yr cicadas, although 13- and 17-yr cicadas will hybridize every 221 yr, which

slows down the process of displacement (Lloyd et al. 1983). Other stem and root feeders are dealt with below.

22.2.4.1 Regulation of a Shrubby Tree by a Stem Borer. Species of prickly pears, *Opuntia*, became serious weeds in many dry areas of the world. By the early 1920s, some 60 million acres of range, timber, and arable lands in Queensland, Australia, were so heavily infested that the land could not be used. Some 50 species of insects were introduced to control it, many from southeastern United States where *Opuntia stricta*, a main pest in Australia is native. In the end, however, it was a phyticid moth, *Cactoblastis cactorum*, a native exploiter of cacti related to *O. stricta* in Argentina that proved effective. This illustrates that natural enemies used for biological control, though usually ones coevolved with the pest species in its native environment, need not necessarily have so coevolved (cf. Section 22.1.6). Within 3 yr of the moth's introduction the cactus had been reduced spectacularly (Fig. 22.3) (Dodd 1940). The pear now exists as a very sparsely scattered population; the insects are correspondingly scarce. Studies by Monro (1967) (cf. Birch 1971) reveal that *C. cactorum* clusters its eggs on *Opuntia* plants in such a way that while some plants are entirely destroyed others escape and this, it is argued, tends to maintain both *Opuntia* and *Cactoblastis* at rather constant, if low, levels over quite small areas. This testifies to its significance as a regulating biological control agent (cf. Laing & Hamai 1976, Goeden 1978). Haseler (1981) notes that for the *O. stricta*-*O. inermis* complex in Australia, completely satisfactory control is maintained by *Cactoblastis*, supplemented by *Dactylopius opuntiae*, over most of the infested environments, exceptions being in central and southern New South Wales and coastal areas of Queensland. This is a fine example of how host-specific herbivory can reduce a dominant, and therefore open up space for other species.

Interestingly, Moran (1980) studied the whole complex of *Opuntia* insects and concluded that "the co-evolution of *Opuntia*-feeding insects and their hosts has culminated in a community of specialist insects to the exclusion of nearly all generalist(s)"—with the immature stages possessing special adaptations that reduce the risk of attack by natural enemies. This Moran considers to be the consequence of the lack of hiding places on this structurally simple plant type.

22.2.4.2 Influences of Two Stem Feeders on Aquatic Weeds. Two successes of note have been achieved in attempts to control aquatic weeds with insects. The case of partial success in control of alligatorweed, *Alternanthera philoxeroides*, by an introduced stem-feeding flea beetle, *Agasicles* sp. (cf. Maddox et al. 1971, Coulson 1977), stimulated much interest in the role of insects (and other natural enemies) on various other serious weeds in aquatic habitats throughout the world. One such weed is the fern *Salvinia molesta*.



Figure 22.3 Destruction of prickly pears (the *Opuntia stricta*/*O. inermis* complex) at a site in Queensland, Australia, within 3 yr from the introduction of the moth borer *Cactoblastis cactorum*. (After A. P. Dodd 1940 and DeBach et al. 1976.)

It develops dense floating mats on lakes and rivers. It and other *Salvinia* species have spread across Africa, India, and Australia, where it is reported as clogging pumps and irrigation channels. It also causes a depletion of other life. Herbicides are prohibitively expensive in some of these situations. Australian entomologists (see Room et al. 1981) obtained a bud-feeding beetle, *Cyrtobagous singularis*, in Brazil in the late 1970s. It multiplied so rapidly when released in Australia's Lake Moondara that a dense stand in 1978 was reduced to a placid scene of blue water in 1981 (Fig. 22.4). These authors suggested also that failures in other regions of the world may have been because of taxonomic misfits between the *Salvinia* present and the insect(s) introduced.

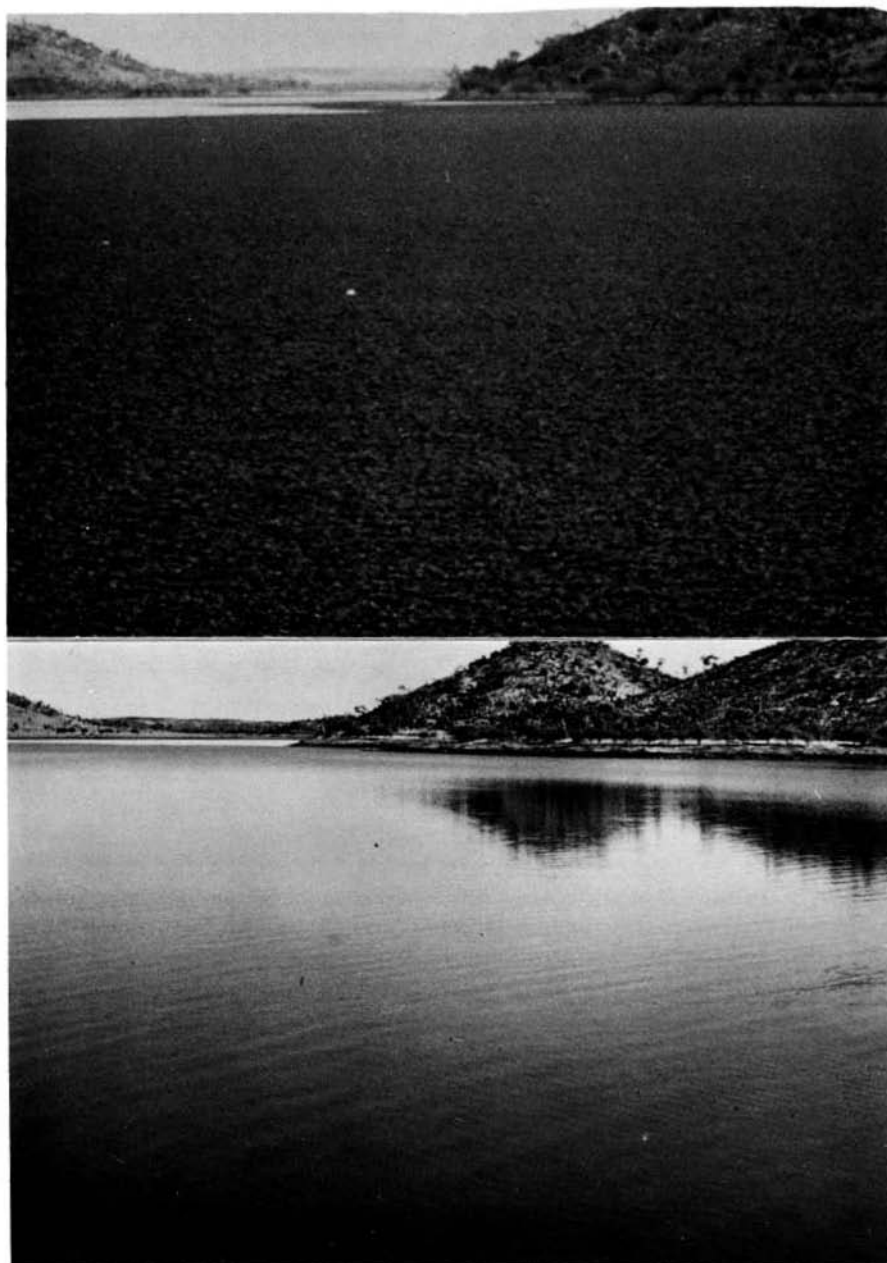


Figure 22.4 The clearing of Lake Moondara in Australia of the aquatic fern, *Salvinia molesta*, by introduction of a bud-feeding beetle, *Cyrtobagous singularis*. (After Room et al. 1981.)

22.2.5 Leaf Feeders

Leaf feeders produce the most obvious damage to vegetation. Apparently because of this and because the vegetation of the world remains "green," Hairston et al. (1960) proposed the proposition that plants are thus not limited by the herbivores that feed on them. They thus discerned a relative lack of foliage (or other debilitating) exploitation by herbivores. Their second conclusion was, therefore, that the natural enemies of these herbivores must be exerting a powerful depressing effect on the phytophagous species. Slobodkin et al. (1967) modified this concept to emphasize the "dominant components of the vegetation." Huffaker (1962) had pointed to the incompatibility of the view with respect to lower rank species of plants which may be under biological control by host-specific phytophagous insects. Ehrlich and Birch (1967) objected on this and other grounds. While being overstatements, these ideas do suggest the potential importance of leaf-feeding and other phytophagous insects as regulators of their plant hosts' populations, that is, if their own enemies were absent! Massive, contemporary defoliation (or killing) of their plant hosts over large areas of natural vegetation by insects is occasionally seen in temperate climate forests, mainly during insect outbreaks. In subtropical and tropical areas intense defoliation occurs on a much smaller spatial scale, primarily because the individual species of plants do not occur so *en masse* but are more spaced-out in the tropics, and this latter appears to be due in large part to effective regulating action by their own herbivorous seed predators.

One of the best documented cases of the role of a leaf-feeding insect in suppressing and regulating its host plant's populations in seminatural lands is that of the biological control of St. Johnswort, *Hypericum perforatum*. It is widespread in both natural and agricultural situations. Harper (1977) referred to the biological control of this plant (also known as Klamath weed) as "... perhaps the most exciting experiment in the whole of the science of plant-animal [population] relationships." The "experiment" has involved different species and ecological relationships in different parts of the world, and correspondingly different consequences. The plant was introduced into Australia in 1880 by a nostalgic German immigrant and inadvertently invaded California ca. 1900. Because it develops dense swards on favorable sites, crowds out grazing species, and causes skin phytosensitization and other toxic effects in livestock, the weed became a prime target for biological control attempts. In both Australia and California four principal insects were introduced: two leaf feeders, *Chrysolina quadrigemina* and *C. hyperici*, a root borer, *Agilus hyperici*, and a leaf gall former, *Zeuxidiplosis giardi*.

Huffaker (1967) summarized the main factors accounting for the lesser degree of suppression in Australia, in contrast to California. He later observed in 1970-71 that the 1963 conditions (reported in 1967) were unusually favorable for biological control by the leaf feeder *C. quadrigemina* in eastern Australia, where in both 1970 and 1971 this beetle was scarce

and therefore much less effective than in 1963. Many weed stands that were much reduced in 1963 had returned to their approximate densities prior to 1963. Thus, the contrast between this beetle's effectiveness in eastern Australia and California are even more pronounced than Huffaker (1967) contemplated; the reasons he gave for the differences existing in 1963 were even more relevant. In California a single complete defoliation continuing through the spring causes death in about 99.9% of the plants, with virtually no regeneration. Similar complete defoliation in eastern Australia in 1963 caused approximately 46% mortality of the plants, with extensive vegetative regeneration. In California *C. quadrigemina* is well adapted to the climate and is synchronized with the growth phases of the plant. It quickly builds up high populations and so reduces the foliage (and indirectly the root system) that this high mortality occurs because of and during the long rainless summers. In contrast, in eastern Australia the existence of some summer rain may seriously disrupt the cycle of the beetle and provides for recovery of fully defoliated plants. Western Australia, on the contrary, has a rainfall pattern like California and effectiveness of the beetle there is also comparable. Huffaker (1974) found that the action of *C. quadrigemina* converted northern California rangelands from a condition of very high dominance of *H. perforatum*, with few associated plant species of minor individual size and total mass, to a condition of considerably more species of much increased individual sizes and total biomass (Fig. 22.5, Table 22.1).

Table 22.1. Numbers of plant species dominant in microplot positions before removal of *St. Johnswort* by beetles (1952 at Loftus^a; 1948, other sites^a) and subsequently^a

Year	Loftus	Loomis	Blocksburg	Ft. Seward
1946	—	20	24	28
1948	—	23 ^a	29 ^a	34 ^a
1949	—	—	—	—
1950	—	23	37	41
1951	19	22	28	31
1952	24 ^a	—	—	—
1953	28	30	36	37
1954	32	—	—	—
1955	33	26	34	30
1956	27	—	—	—
1957	29	25	32	34
\bar{x} of post control years	29.8	25.2	33.4	34.6

^aYear the beetles removed the weed; not yet sufficient time for much effect. After Huffaker (1971a).



Figure 22.5 Removal of Klamath weed, *Hypericum perforatum*, by the introduced leaf beetle, *Chrysolina quadrigemina*, at Blocksburg, California. (A) 1948: Foreground shows weed in heavy flower while the rest of the field has just been killed. (B) 1950: Same location when the entire field had come under control and a heavy grass cover had developed. (After Huffaker and Kennett 1969 and DeBach et al. 1976.)

22.2.6 Insects as Vectors of Plant Diseases

Insects may also damage plants and suppress their populations through their vectoring of plant pathogens. The importance of pathogens in the dynamics of their plant hosts is related to the severity of the diseases caused and to their rates of spread. A number of factors influence the severity of disease expression. These include the host and pathogen genotypes, the age and physiological condition of the host, and the environmental conditions. Similarly, a number of factors influence the rate and pattern of a pathogen's spread through a plant population by an insect vector. These include the abundance and spatial and temporal activity patterns of the vector, the behavior of the vector, efficiency of pathogen transmission by the vector, abundance of inoculum and its location relative to other susceptible plants, and the abundance and spatial and temporal patterns of susceptible plants (cf. Chapter 21, and Carter 1973, Harris & Maramorosch 1977, Kennedy 1976, Maramorosch 1969, Harper 1977).

The effects of insect-borne plant pathogens on plant populations have been most studied in agroecosystems. In many cases effects have been devastating. Beet western yellow virus transmitted by at least nine aphids has reduced seed yields in lettuce by 44% in California (Ryder & Duffus 1966). Yield losses up to 95% were reported for rice infected with hoja blanca virus spread by the plant hoppers *Sogatodes oryzicola* and *S. cubanus* (Everett & Lamey 1969). In more natural ecosystems insect and other arthropod-borne plant pathogens can also have significant effects. Oak wilt, caused by *Ceratocystis fagacearum*, affects a number of oaks. The pathogenic fungus is spread by both insect vectors and natural root grafts. Long-distance spread is by insect vectors, the most important being nitidulids and scolytids (Rexrode & Jones 1971). From 1943 to 1965 it had spread to 20 states, causing much mortality of oaks (Carter 1973). In parts of Iowa up to 25% of the oaks were lost (True et al. 1960). Based on rates of spread from 1956 to 1965, it was estimated by Merrill (1967) that about 1% of the oaks in Pennsylvania would be infected 50 yr later, while in West Virginia 1% and 50% infection would occur about 25 and 40 yr later, respectively.

Dutch elm disease, caused by the fungus *Ceratocystis ulmi*, has caused extensive mortality of elms in Europe, where it is spread by several *Scolytus* beetles, and in North America, where it is spread primarily by *Scolytus multistriatus* and *Hylurgopinus rufipes*. By 1976 mortality of elms in southern England, following appearance of an aggressive fungus strain in the 1960's, reached 39% (Gibbs 1978). The pathogen was found in New York City in the 1920s and by 1940 had spread over 5500 mi². It has since spread to and widely killed elms in much of the United States. Species of elm differ in susceptibility, and thus the species composition of mixed stands of *Ulmus* are being changed by the disease. From 1951 to 1965, at one location in Illinois, 98% of the *U. americana* and 86% of the *U. rubra* died, while five other species, or hybrids, were virtually unaffected (Gibbs 1978).

In a diverse community with its plant hosts well separated, an insect-transmitted pathogen is spread rapidly and reliably only by a vector which has a good ability to search for its hosts over a wide area. Where the pathogen or vector characteristics are such that the probability of long-distance spread is low, while that for short-distance spread is high, healthy individuals are likely to persist in a plant population if they are widely separated. In Basutoland, Africa, where a number of potato viruses and their vector aphid, *Myzus persicae*, are common, "local" potato varieties planted in gardens quickly succumb to virus. Where volunteers grow as widely separated plants in fields or along roadsides, the disease is rare (Van der Plank 1948). In general, epidemic disease is rarely seen in natural vegetation except after major disturbance. Disease most often occurs where either the pathogen or the host has been introduced into a new area and coevolution has not occurred. A case in point concerns rough dwarf maize virus, which is endemic in Israel where it does not cause damage to its endemic weed hosts. Yet, it severely infects introduced maize, and is transmitted by leafhoppers (Harpaz 1972). It is possible that many natural invasions into new areas by plants have failed, at least in part, because of pathogens in the new area to which the plants were not preadapted (Harper 1977).

22.3 INSECT INFLUENCES ON PLANT POPULATIONS AND COMMUNITIES IN TEMPERATE CLIMATE FORESTS

Due in large part to their need of wood for shelter and warmth, humans have long been aware that insects damage trees and may influence forest composition. Continuing to present time, this need has dominated both attitudes towards, and research on, insects in forests. Thus, the principal attitude toward insects by forest managers and researchers has emphasized their negative effects, and research support has been mainly for work on those single species that do the most obvious damage to the most valuable tree species, and only at times of outbreaks (epidemics). Thus, our knowledge of the influences of insects on the less economically important species, and the longer term effects of these insects (and also those that cause epidemics) on the whole forest community has been accumulated very slowly. This applies not only to the insects that damage trees, but also to the large complex of natural enemies (parasites, predators, and pathogens) that prevent such damage and the varied complex of soil organisms in the forests. Thus, pest outbreaks were and still are treated as single pest phenomena, whereas in many cases a complex of pests, including plant pathogens, are actually involved. Most of the available information deals with the types of damage caused rather than the eventual effects at harvest and subsequently. Of course there has been a long-term interest, in that cost-benefit estimates must include the time from seedling establishment to

harvest (30–100 yr) for a given stand. Over such a long period, the costs of extended chemical insect control, plus other costs, could easily exceed expected returns.

The major effects of pests in a forest stand are on stocking density and species and age composition. These features, in turn, affect both productivity and succession of the plant community as a whole. The broader and longer term effects are just beginning to be understood and for relatively few forest types. We emphasize in this section the specific influences of insects in these respects. Beginning largely with the works of Graham (cf. Graham 1956, Knight & Heikkinen 1980) there has been some emphasis on the need of a fuller understanding of the conditions that favor the various phytophagous insect populations and their longer term effects on forest dynamics. Two main concerns are the insects' effects on productivity of a stand and influences on succession, each of these being both ecologically and economically significant. We focus mainly on the ecological significance. Sacrifice of stands to save the forest has been used very little in forest management. Yet such an option could have great ecological as well as economic potential. Insects that have catastrophic effects on current productivity (e.g., bark beetles) produce different ecological (and economic) effects than those which cause growth losses, as with some defoliators, sucking insects, and shoot or tip insects. The latter can also have effects on final productivity as well as on tree species competition, and hence on species composition and succession.

Graham (1956) theorized that stands of mixed species and mixed ages, and ones not overstocked, are least subject to damage or heavy feeding by insects and other organisms. He considered stands low in species and age composition and/or overstocked to be unstable and conducive to outbreaks. In such stands the insects and other pests, by their thinning, in time alter the situation. This thinning can increase growth rates and productivity and foster or hinder succession. Thus, Graham considered that the *law of natural compensation* serves to return the forest toward a stable condition. Basically, this "law" states that in a natural biotic community compensating forces tend to keep each species in its coevolved proportion to others. Temperate forest ecosystems and their herbivores and carnivores have coevolved for thousands of years. Thus, Mattson and Addy (1975) argue that some low degree of insect feeding in forests is normal every year and that regardless of the low level, it should not be ignored, as has largely been the case. On the other hand, epidemic species like the spruce budworm (*Choristoneura fumiferana*), Douglas-fir tussock moth (*Orgyia pseudotsugata*), gypsy moth (*Lymantria dispar*), and several bark beetles (*Dendroctonus* spp.), among others, may not only cause drastic tree mortality but drastic changes in the plant community as well.

Major holocausts in forests (devastating winds, snow and ice storms, and fire) tend to favor single species forests. Outbreaks of insects, though they may cause heavy, intensive mortality, are somewhat different because insect

feeding (and the resulting mortality) is more selective in terms of tree species and takes place over a longer period of time. In either case plant succession is influenced, but rather differently. A recycling of the whole successional process can occur with a major holocaust such as fire. In some cases it appears that insects tend to act like fire; in other cases they may only hasten or slow the on-going successional processes. With outbreaks, productivity may be reduced initially but increased in the long run.

Basically, there are two situations where insect outbreaks occur. In the first case the insects appear to be acting as scavengers and attack weakened trees. They may then build up large populations capable of successfully attacking healthy trees. These situations occur on poor sites (the species are not adapted to the site), or where the trees are crowded (overstocked) and/or declining in vigor from competition, or where they are simply overmature. The second situation is a density-related one in which vast amounts of favorable food, favorable conditions, and stand type (e.g., monocultures) are present. In some forests trees of the same species and age often occur together either naturally or by planting. At some point in development they rather uniformly become susceptible to a pest.

Examples of the influences of insects in specific temperate climate forests that illustrate these relationships include the following.

In eastern United States large areas of mixed white pine and hardwood forests were cleared for agriculture in the 1700s and 1800s. Many sites were later abandoned and were colonized by abnormally pure and commonly even-aged stands of eastern white pine, *Pinus strobus*. Thousands of acres of such stands developed in the early 1900s, presenting an ideal condition for the outbreaks of the white pine weevil, *Pissodes strobi*, which then occurred. This insect not only kills the tips (resulting in crooked stems) but eventually provides entrance courts for pathogens (Smith 1976). There are related situations from abandoned sites in southeastern United States involving loblolly pine forests (*Pinus taeda*). These sites, too, had formerly contained mixed hardwoods and pines. *Dendroctonus frontalis*, a tree-killing bark beetle, developed high and destructive populations, with the consequence of shifting these sites back toward the former condition. In Michigan pure aspen stands have resulted from early logging and repeated burning (Graham 1956). In 1910 these young aspen stands were abundant in areas that were once pine-aspen-birch forests. However, a complex of insects and pathogenic organisms were active at each growth stage of these stands, reducing the aspen and hastening a corrective succession. In some areas conifers are returning and in others a mixture of hardwoods.

The gypsy moth, *Lymantria dispar*, a defoliator, became established in eastern United States in the mid-1800s. The larvae feed on many species of trees but prefer oaks, particularly white oak and chestnut oak. The long-term effect of defoliation by gypsy moth has been to alter the species composition of some eastern hardwoods stands through their selective killing (Campbell & Sloan 1977). As a result, subsequent gypsy moth outbreaks

have been less damaging on those sites—with the most severe damage being on weaker trees in the lower crown classes. It has also been reported that this insect is associated with disturbed and poor sites (Bess et al. 1947, Houston 1979). Disturbances due to fire and logging activity have hampered development toward more mixed hardwoods, thus favoring the oaks preferred by gypsy moths. The recent major outbreaks in New England have occurred in stands with low moisture availability, as on dry ridges or drained sandy soils. Trees on these sites are often the preferred hosts. Stands on moist sites are fast-growing and have more nonpreferred hosts in the mixtures. The straight-trunk trees on these sites also provide fewer refuges for the insect than those on poor sites. Houston (1979) considers that the gypsy moth generally hastens succession toward mixed hardwoods with fewer of the trees preferred by gypsy moths.

A close relative of the gypsy moth, the Douglas-fir tussock moth, *Orgyia pseudotsugata*, occurs in western United States and Canada. The larvae are defoliators of Douglas-fir, *Pseudotsuga menziesii*, and true firs, *Abies* spp., depending on location. In California the larvae feed almost exclusively on white fir, *Abies concolor*, except at high populations when they feed on almost any plant. Outbreaks occur every 9 to 10 yr. In northern Idaho, defoliation of grand fir, *Abies grandis*, was greatest on upper slopes and ridgetops and in the older stands of grand fir and Douglas-fir (Stoszek et al. 1981). The grand fir in the stand was also important, as was the stocking level. The higher the site occupancy, or stocking, the greater the damage. There appears to be a density-dependent relationship between the insect and grand fir in northern Idaho. Tussock moth activity would lead to changes in stocking level, species composition, and age composition on these sites. In California the results of another study were similar except that the greatest damage was in relatively open-grown white fir stands (Williams et al. 1979). Although the stocking levels were low, these stands were predominantly white fir. In another study it was found that white fir growth rate of the stand actually increased 10 yr following an outbreak (Wickman 1980).

The spruce budworm is probably the most important forest insect in North America. It periodically defoliates millions of acres of spruce-fir forests in eastern North America. The ecological implications are indeed interesting since it appears that the budworm is important in maintenance of the mixed spruce-fir type and perpetuation of balsam fir, *Abies balsamea*, even though mature fir is preferred over spruce. Those stands with a high content of mature balsam fir are most susceptible to budworm (cf. Chapters 24, 25 for details).

Bark beetles' (scolytids) relationships to trees or stands have been studied extensively. Most species are essentially secondary exploiters and act as decomposers or recyclers of nutrients in the community. Only a few tropical ambrosia beetles are considered primary exploiters; that is, they attack standing, healthy trees (Rudinsky 1962). Some of the most interesting bark

beetles (e.g., *Dendroctonus*, *Ips*, *Scolytus*, and *Pseudohylesinus*) are intermediate, but basically secondaries that attack weakened and predisposed trees that are standing and still green. As a result, tree hazard rating systems have been developed to identify trees susceptible to attack (e.g., Salman & Bongberg 1942, Ferrell 1980, Schmid & Freye 1976). These insects can have a tremendous impact on forest communities in terms of stocking levels, species composition, age composition, and harvestable timber. Even on a longer term basis, insects may increase the species composition and stability of the forest. Since the beetles are dependent upon, and respond to, weakened or dying host trees, their population densities are closely related to availability of such host material. However, if the beetles have built up high populations (e.g., on slash), they can attack and kill apparently healthy green trees. And so, their epidemics have often been of great economic concern.

The effect of several bark beetle species that only attack following severe damage from messy logging, windstorms, or snow breakage is that of assisting breakdown of waste, recycling of nutrients, and renewal or revitalization of the forest (e.g., Nilsson 1976). Other bark beetles attack trees that have been predisposed by such factors as drought, flooding, root diseases, smog injury, crowding or competition, and so on. These beetles often act mainly as thinning agents by removing or killing badly weakened trees, hastening deaths that would occur anyway due to the predisposing condition or other factors (insect or disease).

Spruce beetle, *Dendroctonus rufipennis*, infestations are commonly initiated in wind-thrown trees but then spread to and kill dominant and co-dominant standing green Engelmann spruce, *Picea engelmannii* (Schmid & Freye 1976). The result is a significant change in species composition to subalpine fir, *Abies lesiocarpa*, when this species is present as a component, or a change in age composition of Engelmann spruce itself by release of suppressed trees of this species in the understory. Outbreaks of this beetle have occurred only at intervals of ca 50 yr, and it appears to be important in maintenance of Engelmann spruce stands (Miller 1970).

The role of the mountain pine beetle, *Dendroctonus ponderosae*, on any particular lodgepole pine site depends on whether lodgepole is seral or the persistent, climax type. In seral stands the continued role of this beetle depends upon fire, as lodgepole pine is perpetuated by periodic fires on these sites (Amman 1977); here the beetle has a beneficial economic as well as ecological role, killing the trees at an age whereby maximum timber productivity is maintained (Amman 1977, Safranyik et al. 1974).

In the mixed conifer forests of California's westside Sierra Nevada, both the mountain pine beetle and the western pine beetle, *D. brevicornis*, kill weakened ponderosa pines. In some situations trees are weakened by a root disease caused by *Verticicladiella wagneri*, which seems to occur in pockets. Beetle activity is common in these centers (Goheen & Cobb 1980). Susceptibility to beetle attack has also been associated with photochemical

oxidant injury (Cobb et al. 1968). Other factors (e.g., *Ips*) may become involved. *Dendroctonus*, again in combination with root disease, seem to be important in succession to a mixed forest of very large trees. The key host, ponderosa pine, is shade intolerant and the pioneer species, whereas white fir, Douglas-fir, sugar pine, incense cedar, and black oak (also present) are all variously shade tolerant. Ponderosa invades open sites after fire or logging or both. The pine stands are nearly pure for several years until a canopy is formed and gradually the shade-tolerant species become established in the understory. As the crowded pines become older, they are thinned by root disease and *D. brevicornis* and the shade-tolerant species are "released." After a number of years, with the further influence of ground fires, an open, mixed stand of very large trees results.

What we have given here is only suggestive of the varied roles insects play in temperate forest succession, composition, and maintenance. (Cf. overviews by Mattson 1977, Rafes 1966.) From an understanding of these relationships one might have been able to predict some of the many adverse consequences that have ensued from ignoring these relationships and growing forest monocultures (cf. Knight & Heikkinen 1980, McFadden et al. 1981).

22.4 INFLUENCES OF INSECTS ON PLANT POPULATIONS AND COMMUNITIES IN TROPICAL FORESTS

Leaving aside the pollinators (Chapter 20), the herbivore load of a tropical plant population poses two major classes of influence on the members of the plant population. First, and mostly unappreciated, the long-standing existence of this herbivore load has selected for the plant to expend a substantial part of its resources on defensive traits such as resins, latex, polyphenols, toxic proteins, alkaloids, uncommon amino acids, cardiac glucosides, cyanogenic glucosides, indigestible storage polysaccharides, cyanolipids, phytoalexins, lignins, essential oils, urticating hairs, hard seed coats, heartwood, thick bark, and so on (e.g., Levin 1976, Rosenthal & Janzen 1979); that is to say that despite Hairston et al.'s (1960) opinion, the world is not always so green. Conceivably, cellulose may have been evolutionarily chosen over other structural polysaccharides because of its indigestibility to most herbivores. In any event, the plant pays a high price for its cellulose resistance in that it, likewise, cannot digest cellulose and thereby is deprived of recovering an energy-rich resource when an organ is discarded. This greatly restricts the plant's options for tissue repair and replacement. These observations should cause rejection of estimates of insect impact based only on amount of leaf surface eaten, estimates that usually range from 1 to 10% if averaged over many species in a habitat (e.g., Leigh 1975).

Secondly, herbivores cause two kinds of more direct damage to plants, and tropical insects are no exception: (1) There is the direct *parasitism*

through sucking sap, eating leaves, and boring in stems, storage organs, and cambium. This damage lowers the fitness of the plant through reduction of progeny. This occurs because the damaged plant has directly lost resources and also loses competitive status, which in turn leads to lowered resource availability. (2) There is direct *predation* on seeds (and less commonly, seedlings) from the flower to already dispersed seeds (e.g., Janzen 1980). Just as we cannot know (anticipate) if introduction of yet another species of herbivore will result in a change in density or distribution of the host (prey) plant population, we cannot know the effect that a given species component of the herbivore load is having on a plant population unless we remove the species and see what happens, taking into account compensatory actions by other fractions of the herbivore load. We should add that herbivore loads illustrate very well the generality that herbivores compete *indirectly* through the medium of the resource and defense "budget" of the plant, as well as directly. Two herbivores may be in intense competition but never encounter each other or each other's direct damage (Janzen 1973). In short, a shoot tip eater affects the root feeder; the beetle that induces protease inhibitor formation in leaves by feeding on them may make the leaf inedible for a caterpillar.

Can we say anything unique about the impact of tropical phytophagous insects, parasites, and predators on their hosts and prey? First, there is much observational and circumstantial evidence and a bit of experimentation suggesting that, in tropical forests rich in tree species, insects are generally more effective at eliminating or severely reducing seed crops than in other forests. When the members of a population of large trees lose 50–70% of their seed crops to a single bruchid (e.g., *Pithecellobium saman* or *Merobruchus columbinus*—Janzen 1977), they have also had their tries at recruitment reduced by that much. Recruitment is a highly stochastic event. In the tropics every square meter has a finite but very small probability of bearing a member of a tree's descendants in future years and the number of tries is very important in determining equilibrium density of adult trees present in the habitat (Janzen 1970). Why might insects be more destructive as seed predators in many tropical forests than in temperate forests? This may be because the climate is less effective at depressing their densities between major pulses of their food (seed crops), because their prey populations (the seeds) are not so thoroughly missing in between peaks of seed production in the tropics and because relatively fewer tree species are involved in supraannual synchronized seeding cycles than is so in extratropical regions (e.g., Janzen 1971, 1976, cf. Section 22.2.2.1).

Secondly, Janzen (pers. comm.) has considered that foliage removal for specific species of plants by tropical leaf eaters in *deciduous* tropical forests is as severe or more severe than that in extratropical deciduous forests. That it is severe in any sense may seem surprising. In any year there is substantial defoliation of certain species by their strongly to highly oligophagous herbivores, and the next year a different set of plant species have

their turn being severely defoliated. The *forest* never appears to be heavily defoliated since there are likely to be 50–200 species of large woody plants within view at one time, but in species-rich tropical deciduous forests there is often a heavy shower of herbivore frass and 30–100% defoliation of some 5–30 species during the first 2 months of a rainy season (Janzen 1981). Gray (1972) has also viewed insect impacts in tropical forests to be much greater than commonly viewed by entomologists.

Thirdly, it is our impression that a given amount of defoliation of a tropical deciduous tree leads to larger losses in status, wood increment, future seed yields, height increment, and so on, than is the case with an average extratropical deciduous tree. We suspect this may be because extratropical trees are more accustomed to dealing with a variety of damages and physiological challenges (and therefore carry the reserves and have the physiological machinery for using them) than are their tropical counterparts. We suspect, too, that extratropical trees customarily have larger reserves because they are storing for mast crops at long intervals and because they are storing for heavy flushes at spring growth. Tropical plants, perhaps, may operate on a smaller margin of error than their extratropical counterparts.

Since the tropics are so rich in phytophagous insect species, it is tempting to assume that a tropical plant will be attacked by a larger array of insect species than a comparable extratropical plant of the same size and age. This does not appear to be so. Some studies in a Costa Rican deciduous forest with a flora of about 600 species of broad-leaved plants suggest that, if anything, an average tree there may have fewer species of insects to deal with than its extratropical counterpart.

If one thinks in units of years, everything happens faster in the tropics. Losses in status due to herbivore damage appear to be resolved more rapidly in tropical than in extratropical vegetation. Thus, if a noctuid larva eats off several terminal apices of a 2-m tall tree sapling in a tropical forest, the resultant loss in height may easily be adequate to result in that sapling losing out in competition with other saplings and being dead and gone in less than a year. The intense shading and continuously salubrious climate may cause a telescoping of the competitive process. However, we badly need more experiments in both temperate and tropical forests to substantiate such impressions as these from field observations.

Phytosociologists in northern latitudes have long gotten away with looking at only edaphic and climatic correlates with micro- and macro-habitat plant distributions. They rather ignored the insects and stressed the physical factors in defining the habitats in which plant recruitment can occur. However, in tropical habitats, and as we have seen, in temperate ones, it is certainly not safe to assume that the reason a tree species lives only in riparian bottomland vegetation, for example, is because that is a moist site during the dry season. We desperately need experiments on this subject in both tropical and extratropical forests.

The tropics are often thought of as extremely species-rich in trees ("di-

verse" in a sloppier terminology), but there are enormous areas of tropical vegetation where only one or a few species of trees (or other life forms) constitute the bulk of the plant matter. Even in some very species-rich forests there occasionally are single species that constitute up to 30% of the stand (e.g., Hartshorn 1975). Mangrove swamp forests are the best known examples; here virtually all of the self-supporting vegetation may be made up of 1–20 species of trees of tall to moderate height. This vegetation—leaves, bark, wood, seeds—is extremely rich in tannin, a powerful digestion inhibitor. There are herbivorous insects in mangrove forests, but it is clear that the bulk of the plant parts are simply inedible. Likewise, these plants grow very slowly compared to growth rates of trees on normal terrestrial sites. In short, they have traded their competitive ability for protection from herbivores and can get away with it because they live in a special edaphic habitat in which allospecific competitors have little chance of surviving. Another tropical habitat poor in tree species is a forest above about 2000–5000 m in elevation. These forests are continually cool and are commonly dominated by Fagaceae, Lauraceae, and Gymnosperms.

Perhaps the most interesting low-diversity tropical forests lie on white sand soils in Malasia. These "dipterocarp forests" have an upper canopy made up largely (50–90%) of 1–15 species of Dipterocarpaceae and an understory of many (up to some 400) species of smaller trees (e.g., Janzen 1974). Looking only at these dipterocarps, it is striking that they have foliar and reproductive biologies extremely similar to that of a hypothetical tree such as an oak in a mixed conifer–oak–ash stand in temperate United States; yet, these are evergreen rainforest trees by anybody's definition. They produce seeds in supraannual pulses that are highly synchronous at both the population and community levels. These seeds are heavily preyed upon by vertebrates and insects (several being weevils with roles like acorn curculios), but these animals are sufficiently satiated that dense lawns of dipterocarp seedlings appear after a seeding year, just as occurs in temperate climate oaks and pines after a seed year. The seeds are dispersed only a short distance from the parent. The adult trees appear to be site specialists and are rich in resins and tannins, and they appear to have similar relationships with forest insects as do evergreen oak and conifer trees in temperate climates. In short, in these habitats trees of this family have largely beaten the competitor and herbivore challenges and by and large come to dominate the system (Janzen 1974, 1978).

22.5 CONCLUSION

It would be sufficient if the scope and detail of concepts and roles of insects in the dynamics and regulation of other organisms as discussed in this chapter were to stimulate a deeper probing of the role of insects in the whole economy of nature.

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