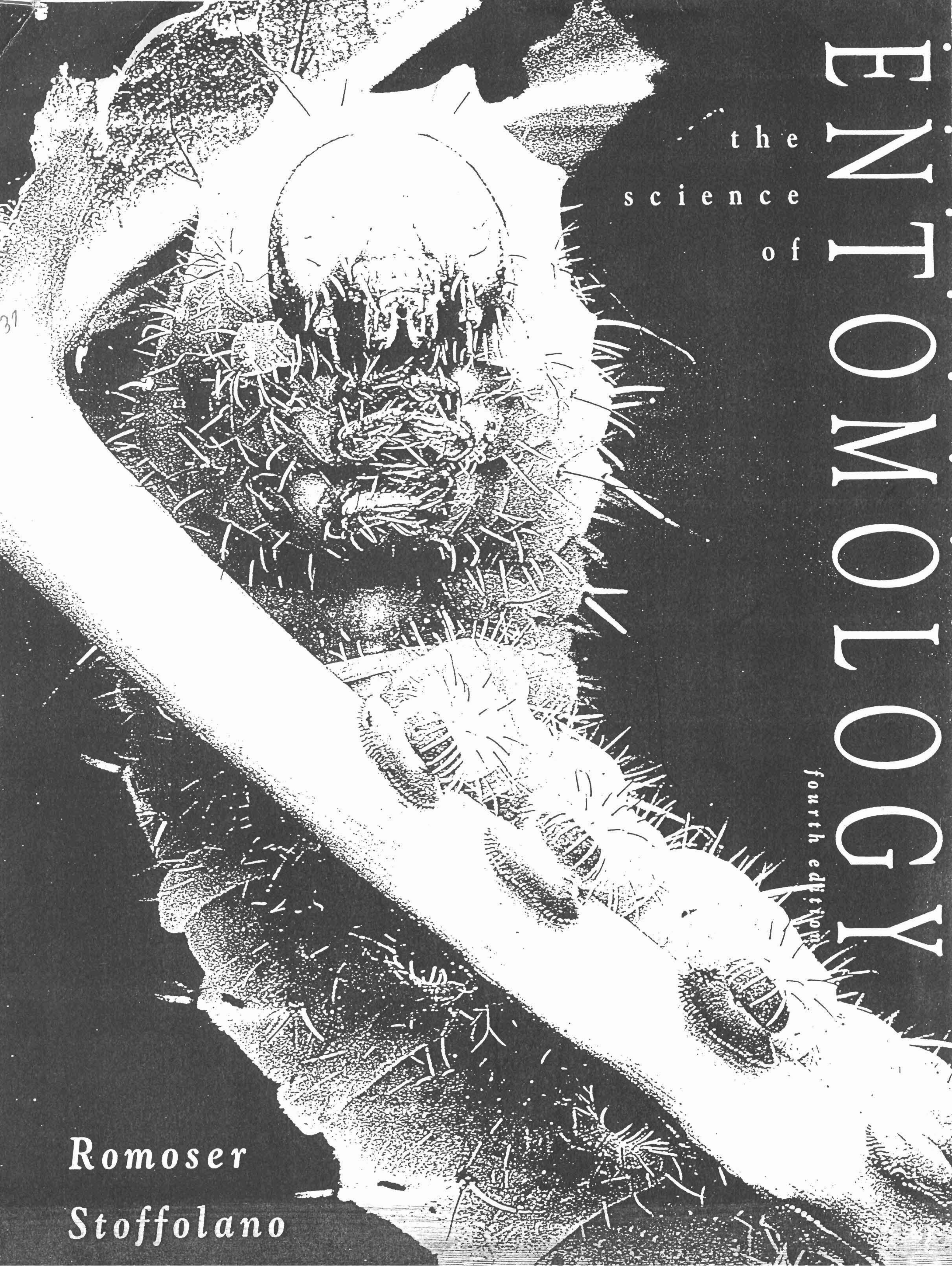

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THE SCIENCE OF ENTOMOLOGY

William S. Romoser
Ohio University

John G. Stoffolano, Jr.
University of Massachusetts

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CHAPTER 10

Insects and Their Environment: Plants

Lowman/Morrow

I've watched you now a full half-hour,
Self-poised upon that yellow flower;
And, little butterfly! indeed
I know not if you sleep or feed.
William Wordsworth, "To a Butterfly"

Humans have always been fascinated by insects, and the majority of their observations occur on the substrate of plants. Plants form the basis of all food chains on earth because they are the only organisms that capture energy from sunlight. In turn, herbivores (of which many are insects) are plant consumers, thereby transferring energy to higher trophic levels (figure 10.1). Insects and plants have evolved together for millions of years, including both antagonistic and mutualistic interactions. Most early observations were simply accounts of plague insects (e.g., the Bible), whereas it is only during the last 75 years that insects on plants have been more carefully studied. Why has the biology of insects on plants received such extensive recent attention? There are a number of reasons for this:

1. Insect population fluctuations have a direct impact on human health and food supplies.
2. Insects are abundant, small and easy to raise, observe, and manipulate in scientific experiments.
3. Unlike many parts of ecosystems, insect-plant relationships have at least one (often two) sessile components, making the study of their relationships very convenient.
4. Insects and plants have evolved in response to each other, and scientists are curious about how these relationships developed.
5. Insects and plants together are perhaps three quarters of the known species on Earth, and the specific insects that feed on plants may represent one quarter of life on Earth (figure 10.2).

During the last 75 years of research on insects and plants, science has advanced enormously. Even as late as 1982 it was hypothesized that nearly 1,000,000 species of insects inhabited the earth (Strong et al. 1984; Richards and Davies 1977). But recent research in tropical rain forest tree canopies has led to a drastic revision of this estimate. Only 10 years later, in 1992, we now think that there may be as many as 30,000,000 insects, a 30-fold increase! (Erwin 1982, Wilson 1988, but see Gaston 1991). Most of that increase appears to be a consequence of insect communities in forests (both in trees and in soils), which may be much more complex and abundant than previously thought.

In this section, we shall look at the ecological relationships of insects and plants, comparing the abundance of insects on structurally simple plants and working up to the more complex distributions of insects in forests. In ecology, scientists often test *hypotheses,* which is an assumption based on careful deduction. Experiments to test an hypothesis comprise observations, experiments in the field or in the lab, and the interpretation of results that leads to either an acceptance or rejection of the original hypothesis. We will look at several examples of experimental ecology in our discussion of plants and insects.

Insects are associated with plants for a number of reasons. The most important relationship involves food supply: many insects on plants are herbivorous or phytophagous (*phyto* = plant, *phagous* = feeding). Others, however, use plants for territory, protection, mating, traveling, communal roosting, and other activities.

The colonization of habitats by arthropods and their active (but sometimes passive) abilities to colonize a site have been the subject of extensive research in the last decade. It is assumed that most arthropods colonize a habitat primarily because conditions are suitable for survival, and that species will co-exist if other populations

Figure 10.1 The energy pyramid of a land-based community. Note that a large proportion of the energy is lost between trophic levels. Trophic levels are pictured and labeled on the left.

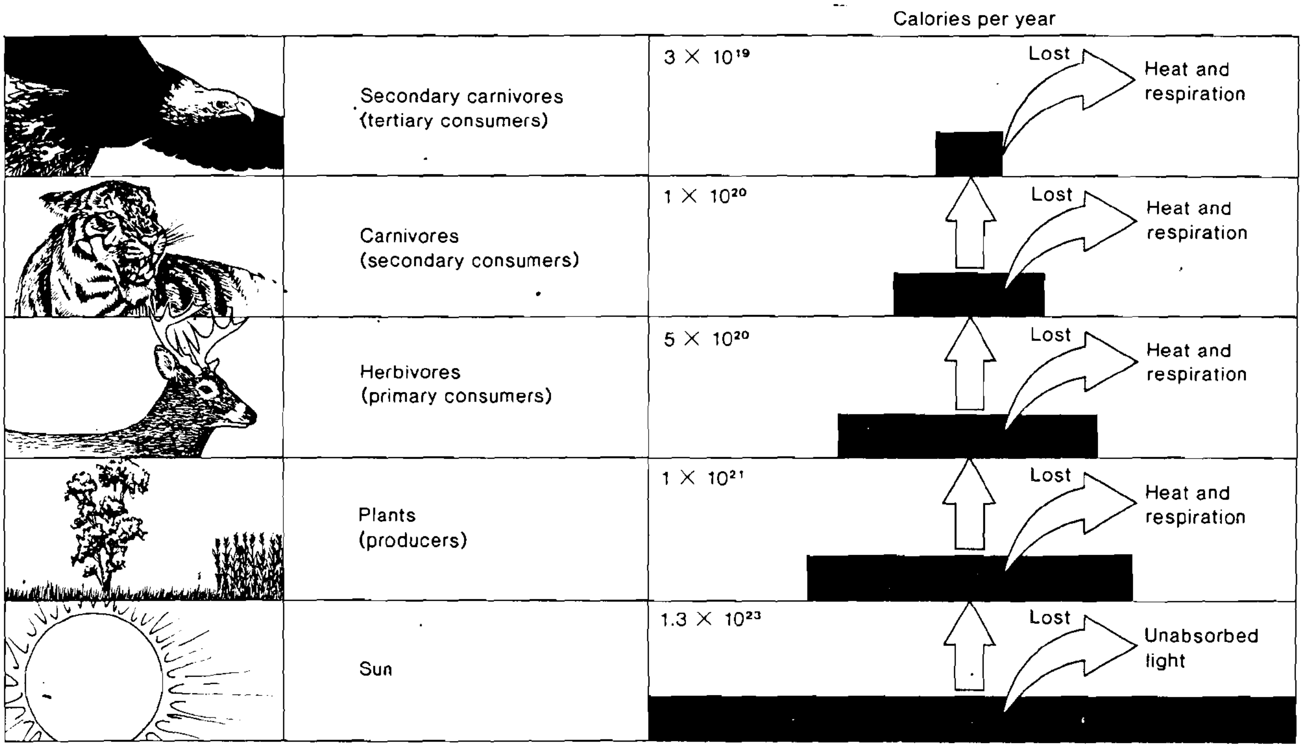
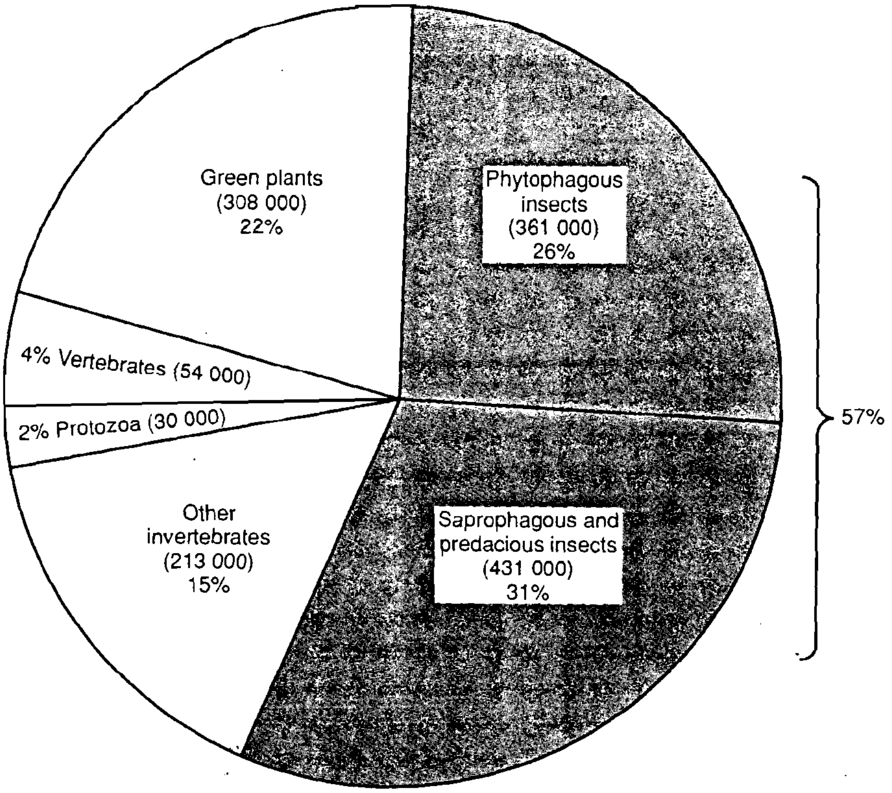


Figure 10.2 The number and proportions of species in major taxa, excluding fungi, algae and microbes. The proportion of phytophages is based on estimates for British insects, assuming that proportions in the world as a whole are broadly similar. *After Strong et al., 1984.*



do not inhibit them or outcompete them. This perhaps originates from the original views by a plant ecologist named Gleason (1926) who advocated that communities are comprised of individual populations, with a continuum of species along an environmental or habitat gradient. Gleason's definition of a community is in contrast to another biologist, Clements (1916), who advocated communities as "organisms" comprised of highly interdependent populations. The individualistic view of Gleason and the organismic view of Clements both have come in and out of fashion over time, but draw attention to the importance of populations and their interactions in any community.

Populations of insects in communities fluctuate more extensively than do populations of longer-lived organisms. These oscillations impart both positive and negative aspects to field studies on insects: insects are easier to study because several generations and population cycles can occur during one season, but population dynamics may be more difficult to interpret because numbers may fluctuate wildly over a relatively short period of time. Functional groups of insects in a community exist at two levels: populations of a species, and guilds of similar, but different species that perform the same role (e.g., sap-sucking insects).

It is interesting to note that one plant can comprise a community with its resident populations of insects, whereas one ecosystem can also comprise a community, with many plants housing many populations of insects. For our purposes, an *insect community* is defined as populations of insects that interact on or in the vicinity of a common host plant.

The reasons for differences in numbers of both populations and guilds of insects on plants are many. We discuss three in this chapter: structural complexity and age of host plant, nutrition and toxicity of plant tissues, and evolution of mutualistic relationships.

Structural Complexity and Age of Host Plants

Insects on Structurally Simple Plants

It is well established that plant-dominated ecosystems have more insects than landscapes that do not. For example, volcanic peaks and alpine aeolian systems (i.e., regions that depend upon wind to import both energy and nutrients), have very sparse arthropod faunas (Edwards 1987), and as areas develop soils and then vegetation (termed *succession,* a classic sequence whereby a region undergoes development of soils and vegetation, often bare soil to field to shrubs to scrub to forest), a larger variety of plants is established, followed by a greater fauna of insects. As succession of the landscape leads to greater complexity, it is hypothesized that increased complexity of plants results in greater insect fauna. The numb insects increase as plant size increases: monocots to we to perennial herbs to shrubs to trees (Lawton 1983).

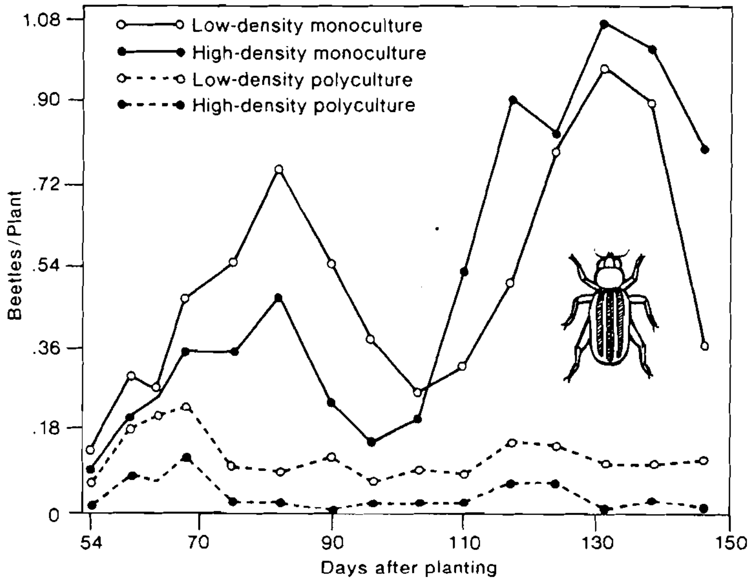
Monocultures (single-dominant groups of a species versus polyculture) of cereal grains or other crop plants are both structurally and taxonomically simple, but their resident populations of insects have extremely complex behaviors (reviewed in Liss et al. 1986). On the one hand, populations of insects in monocultures tend to be taxonomically less diverse than insect communities in more diverse habitats; but on the other hand, their populations may fluctuate enormously with subtle changes in the quality and availability of food. Price (1976) examined seasonal changes in arthropods on soybean plants, with predictable increases in numbers as the season progressed, followed by decreases in numbers as the plants underwent senescence. The number of species fluctuated from 0 to 30 during a three-month period. Bach (1980) examined the population dynamics of insects on cucumbers in monocultures and in polycultures. She found that the populations of striped cucumber beetles (*Acalymma vittatum*) were higher in monocultures than in polycultures (figure 10.3). This is an example which supports the *resource concentration hypothesis* (Root 1973), which predicts that insect herbivores will reach larger per plant populations in areas with high densities of host plants than in regions where host plants are patchy or rare. The *enemies hypothesis* is an alternative idea that predators and parasitoids should control numbers of insects more effectively in mixed stands than in pure stands.

Both of these hypotheses are pertinent in recent experimental ecology. The relationships between insects and crop plants are studied extensively in a discipline called integrated pest management (IPM; see chapter 16). This topic is of obvious importance to the survival of human beings because we depend upon crop plants for our nutrition and try to minimize the losses of cereal crops to insect epidemics. Because crop plants are usually herbaceous and grown in monocultures, their structural simplicity poses a challenge to agriculturalists to protect the crops from excessive build-up of insect populations.

Insects on Structurally-Complex Plants

Lawton (1983) further hypothesized that plants offering a greater variety of resources (e.g., more leaves or branches) will support more individuals and more species of insects. Very little experimental evidence exists to support this hypothesis, however, because it is difficult to test. In one experiment, Bach (1981) found higher numbers of specialist chrysomelid beetles on vertically-grown (versus horizontal) cucumbers. This suggests that insects prefer the structurally vertical plant with its more complex arrangement of stems. With larger populations, species are more likely to persist on a plant despite predation,

Figure 10.3 Mean number of striped cucumber beetles (*Acalymma vittata*) on cucumber plants (*Cucumis sativus*) in garden plots in monocultures, or in polycultures planted with corn (*Zea mays*) and broccoli (*Brassica oleracea*). Density of cucumber plants (289 or 144/100 m^2), by itself, has little influence on beetle density.
After Bach (1980).



inclement weather, and so forth. Following Lawton's (1983) original progression, shrubs, saplings and ground vegetation are slightly more structurally complex than low-growing herbaceous monocultures.

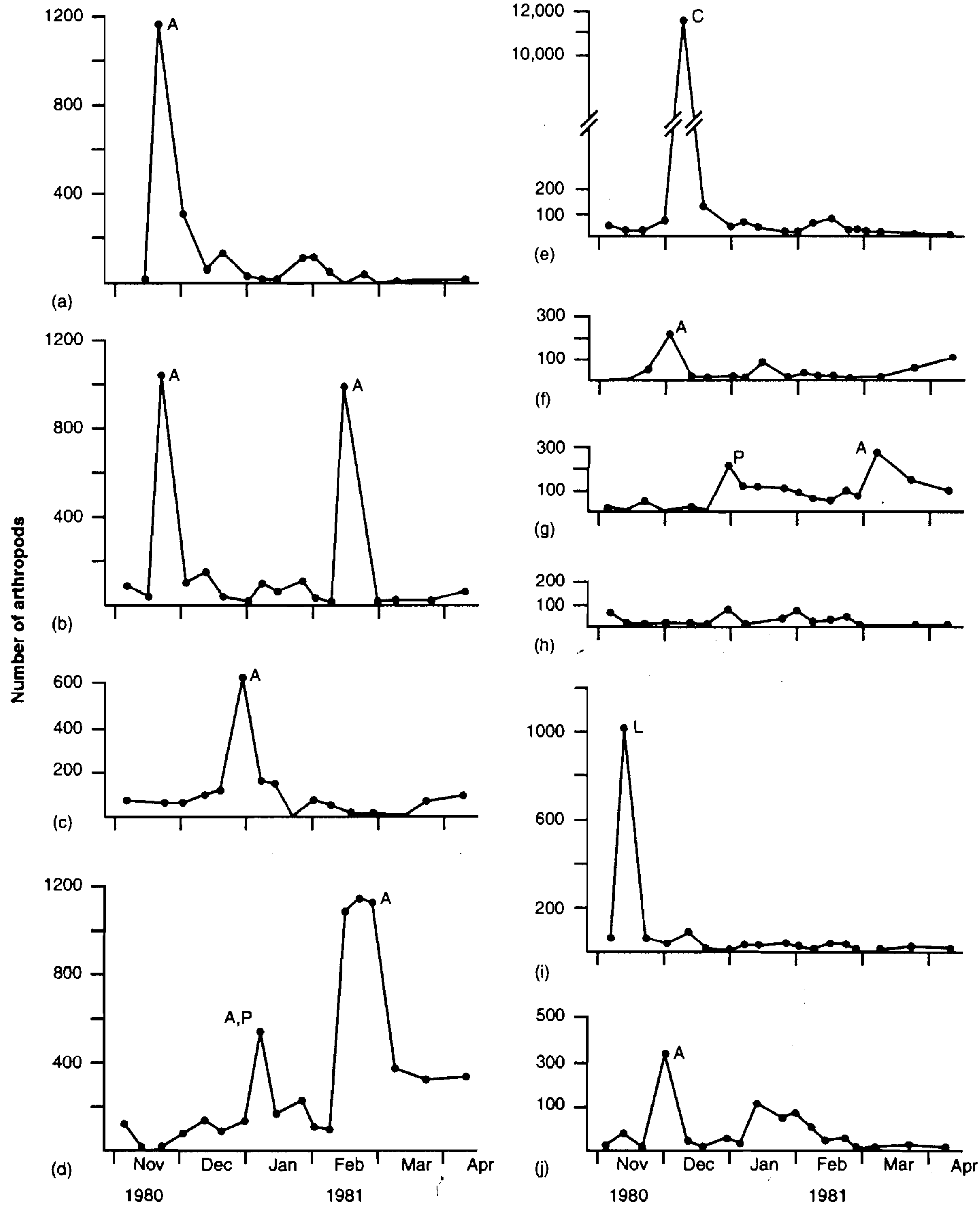
Some studies indicate that numbers of individuals (not just species) also vary with increasing structural complexity of the host plant. Saplings of eucalypts and closely related angophoras in Australia were examined for abundance of arthropods over time, with the result that numbers fluctuated seasonally from 0 to 20,000 (figure 10.4). Some of these insects (e.g., Diptera and other flying insects) appeared to be situated on a plant as a result of chance, and were travelers; others such as the ants and aphids were residents and also very prolific. This combination of transient and permanent residents on a plant accounted for the high variability in numbers of insects on the eucalypt saplings. Other factors such as foliage quality and *phenology* (seasonal patterns of growth-related activities) of the leaves affected the numbers on a seasonal basis. These numbers appear to be extremely high, but eucalypts seem adapted to relatively large insect populations as compared to their northern temperate forest counterparts (see section on forests). Mature eucalypts have been observed to have many tens of thousands of Christmas beetles (*Anoplognathes* sp. Scarabaeidae) feeding in their canopies (Heatwole and Lowman 1986).

Studies comparing the abundance of insects on seedlings, saplings, and adult trees are rare because of the obvious time and energy required. It is possible to infer relationships of insect abundance from studies on herbivory, however, which is an indirect measure of the numbers of insects on plants. Coley (1983) examined the herbivory of rain forest saplings in Panama. Persistent, late successional species had greater defenses of leaf material and subsequently lower numbers of herbivores per tree than pioneer or early successional species of saplings. Similar results were obtained for herbivory of mature rain forest canopy trees in Australia, whereby the gap-colonizing giant stinging tree (*Dendrocnide excelsa*) had higher herbivory than the late successional red cedar (*Toona australis*) and sassafras (*Doryphora sassafras*) (42%, 5%, and 13% annual leaf area losses, respectively) (Lowman 1985).

According to the structural complexity hypothesis, trees and forest communities house the most abundant and diverse insect populations. In his classic work, Southwood (1961) (see also Southwood et al. 1982a, b) made extensive measurements of the arthropod fauna of various deciduous trees. He used an insecticide spray which harvested all insects within the canopy and essentially provided a "snapshot" of each tree at one point in time. This technique, called *fogging*, is useful for obtaining a comprehensive count of all insects within a complex structure such as a tree canopy. Comparisons among trees and continents showed a fairly consistent proportion of different trophic levels of insects: one-quarter phytophagous by species but over one-half by weight, one-quarter parasitoids by species but less than one-sixteenth by weight, one-quarter predators by species and the same proportion by weight, one-sixth scavengers by species and

Figure 10.4 Seasonal changes in numbers of insects on 10 individual eucalypti saplings growing in close proximity in an old field near Armidale, NSW, Australia. Arthropods responsible for peaks include ants (A); psyllids (P); Christmas beetles (C); leafhoppers (L). Sapling species are *Angophora floribuda (a, b)*; *Eucalyptus caliginosa (c, d)*; *E. blakelyi (e, f)*; *E. melliodora (g, h)*; and *E. viminalis (i, j)*.

Data from Heatwole, Lowman, Donovan, and McCoy.



Species

Individuals

Biomass

Figure 10.5 Composition of the arthropod fauna of trees in terms of major guilds, expressed as mean number of species, number of individuals, and biomass, based on comparable samples from six species of tree in Britain and six in South Africa. C = chewers, S = sap-suckers, E = epiphyte fauna, Sc = scavenging (dead wood, and so on) fauna, PR = predators, P = parasitoids, A = ants, T = tourists.

by weight, and the remainder split amongst tourists (visitors to the tree), epiphyte fauna, and ants (figure 10.5). In total, they found between 180 and 425 species of insects for *Salix alba* and *Quercus* canopies, respectively, using a composite of both fogging and observation methods.

Insects on Plants of Different Ages

It is assumed that insects have coevolved with plants for a long time, so the older, more complex and more highly-evolved ecosystems may have richer insect faunas and more complex relationships between plants and insects. Once again, these hypotheses are difficult to test because they involve evolutionary time and cannot be manipulated experimentally. Biologists can look at different members of one group, however, and compare the differences of the plant-insect relationships they observe.

One well-studied group of plants are the thistles. Europe, especially the Mediterranean region, has a large and ancient thistle flora used by more than 50 genera of insects. Most of these species are *host-specific* (feed just on thistles) and an especially large guild feeds inside the flower heads. One tribe of thistles migrated to North

America and speciated extensively. But the diversity of insects on these thistles is low, apparently because few thistle-feeding taxa accompanied their ancestors as they migrated from Europe over the Bering Strait land connection in the late Miocene (Zwolfer 1988).

A perhaps older and more complex web of relationships exists between *Heliconius* butterflies and plants in neotropical rain forests. These butterflies have a variety of interactions with their sessile hosts; adults are brightly colored, a warning to would-be predators that they retain the toxins their larvae obtained from their passion vine hosts. Warning is enhanced by gregarious feeding of larvae, communal roosting of adults and participation of adults in mimetic complexes with other distasteful butterfly species (there are two kinds of mimics: Batesian mimics are palatable species that look like distasteful, or dangerous, model species; Müllerian mimics are distasteful and look like other distasteful species; see chapter 9). Butterflies eat pollen of widely scattered *Anguria* vines; young butterflies learn *trap lines* (regular routes traveled by pollinators to visit the same plants repeatedly) by following older adults when they leave the roost. Some passion vines make fake insect eggs and attract ants to escape larval attack (Turner 1981). Figure 10.6 illustrates the complex interactions and the range of relationships that have evolved between *Heliconius* and their hosts.

Other studies have shown that older trees have more phytophagous insects than younger ones (Banerjee 1981 on tea trees) and that older forests have a richer fauna than younger ones (Southwood et al. 1982a, b). Southwood (1961) compared the numbers of insects between dominant native trees and introduced trees in Britain, Sweden, Russia and Cyprus. They found that the older tree community averaged higher numbers of resident insects, as compared to introduced, less well-established tree species (presumably where the trees and insects have had less time to reach an equilibrium).

Plant Nutrition and Herbivory

Plants are the largest and most readily available source of food in terrestrial communities. Phytophagous insects have the capacity under ideal conditions to increase by a geometric progression (exponentially). But this capacity is rarely realized in nature. In an influential paper, Hairston et al. (1960) observed that plants seem to be damaged extensively only when natural enemies (parasitoids and predators) of herbivores are absent, due, for instance, to the greater sensitivity of enemies to pesticides or introductions of herbivores without their enemies. From this they deduced that herbivore populations are controlled by their natural enemies rather than by availability of food, in contrast to plants and carnivores, which they argued are controlled by competition for resources.

In some cases predation, parasitism, and disease control the abundance of herbivores, but experiments to test these regulatory effects are difficult to conduct (Price 1987, Price et al. 1990). Why then is the world green? Hairston et al. (1960) assumed that anything green is food for herbivores just as different antelope species are equally good for large predators. As we shall see, this assumption has proved false.

Herbivorous insect species are very abundant, comprising perhaps half of all individuals found in nature. However, out of 32 orders of insects, only 9 feed on living plants (figure 10.7). This suggests that plants are a formidable evolutionary barrier that most groups have not been able to overcome. But the high diversity of insect species within these orders suggests that, once these barriers are surmounted, insect groups radiate extensively (Mitter et al. 1988).

Ways of Eating Plants

Plants are complex and variable structures. The nutritious parts of plants, cytoplasm and fluids, are surrounded by wooden walls that insects cannot directly digest (see chapter 4), so they must mechanically disrupt or otherwise circumvent them. Insects have evolved specific morphological, physiological, behavioral and other adaptations to cope with and use plants. The large size of plants in comparison to insect herbivores has been associated with the evolution of insect specialists that feed on a particular plant part. Insects can be classified into several feeding *guilds*, or groups, that have similar styles of exploiting plants for food.

Chewers

Chewing is the most common way in which insects process plant material, including leaves, stems, flowers, pollen, seeds, and roots. In the orders Orthoptera, Coleoptera, Hymenoptera and Phasmida both juvenile and adult stages have chewing mouthparts. In the Diptera and most Lepidoptera, only the larvae chew their food. Because most of the material eaten by chewing insects includes tough cell walls, the mandibular surfaces are exposed to considerable wear and are replaced at each molt.

Miners and Borers

Larvae of many insects and some adult beetles feed within plant tissues. Leaf miners are chewing insects that eat one or more of the tissue layers between the intact upper and lower epidermis of leaves. As the insect tunnels its way through a leaf, it leaves a mine whose pattern is often characteristic for the species. Except in the Diptera, miners tend to be flattened to accommodate the dimensions of the leaf. Like other insects that feed inside growing tissues, miners often feed on one or a small

Figure 10.6 Interlocking of the adaptations of *Heliconius* and their associated plants in the tropical American rain forests. Arrows indicate causal relations, in most cases via natural selection.

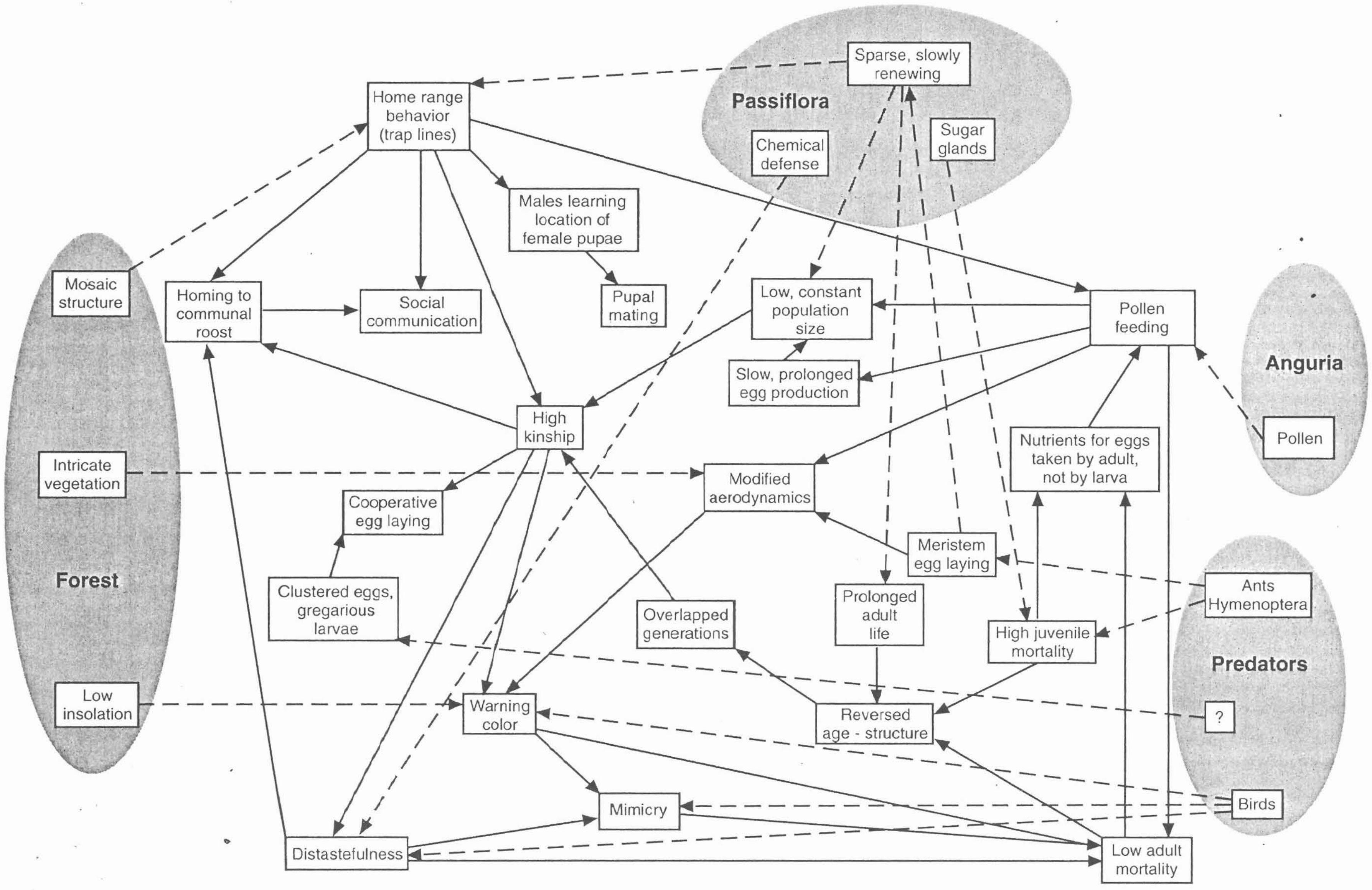
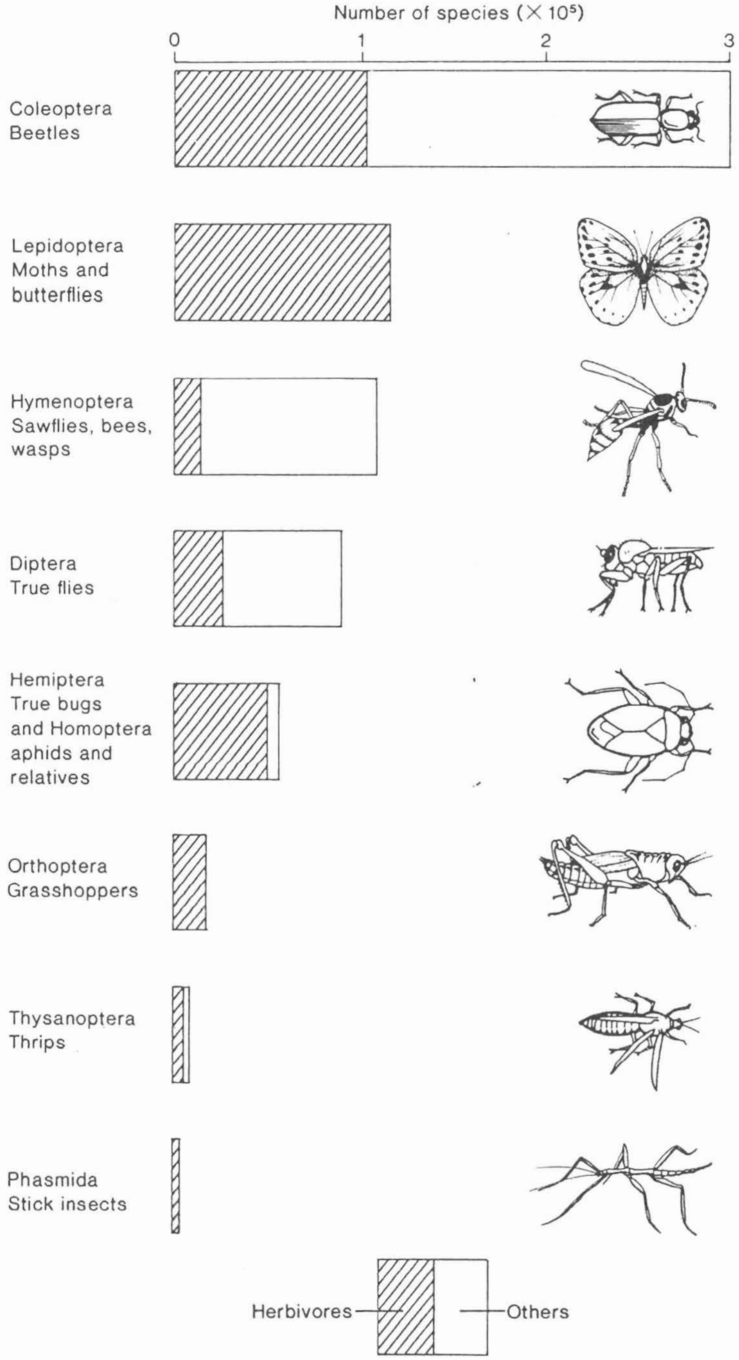


Figure 10.7 The size of the insect orders containing significant numbers of herbivores.

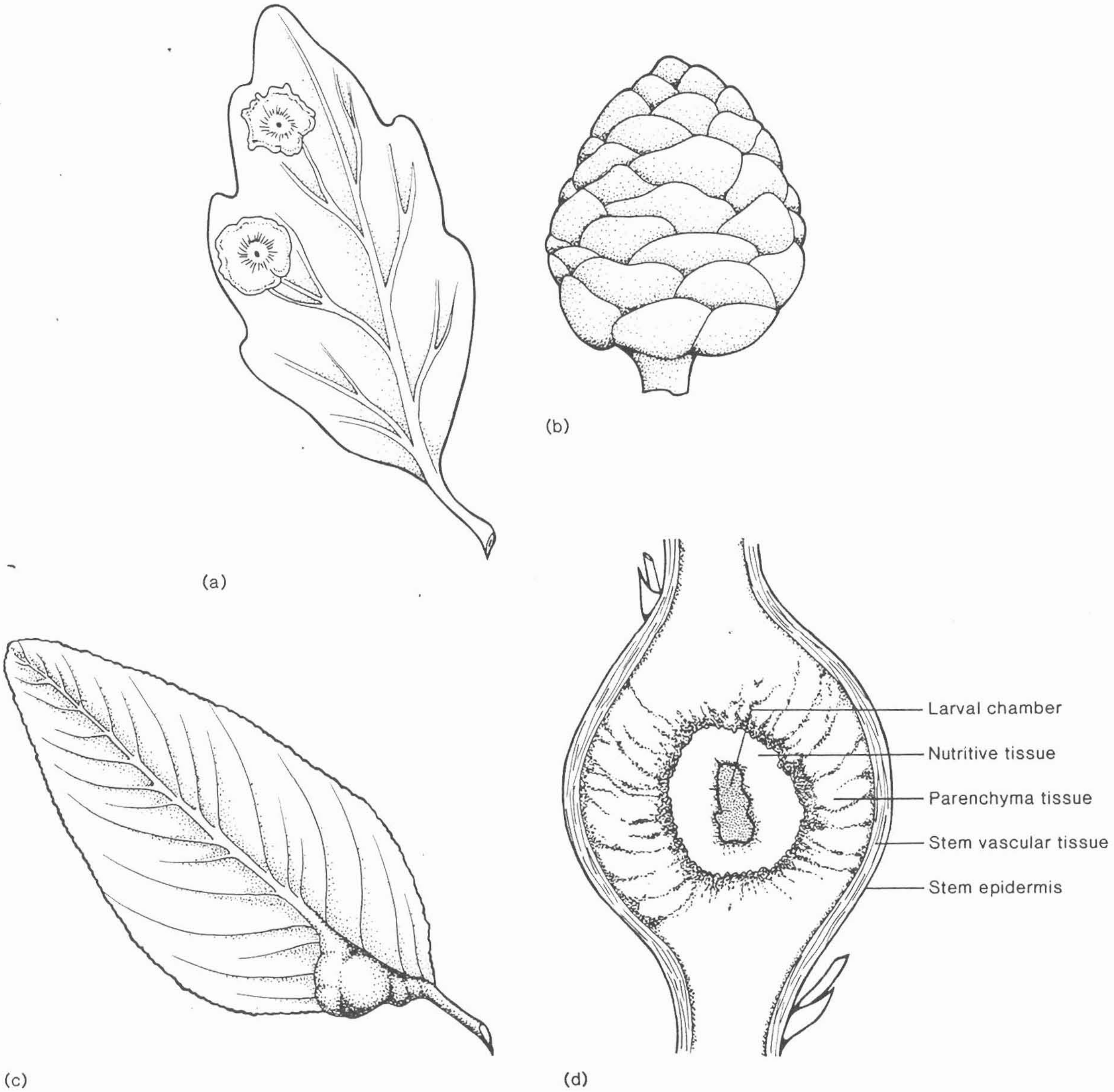
The size of the order taken from Borror et al., 1976 and Richards and Davies, 1977. Proportion of herbivores in each order taken from Price, 1977, except for Thysanoptera, which was estimated from Lewis, 1973; as appeared in Weis and Berenbaum, Plant-Animal Interactions, *1989.*



number of related plant species. Leaf-mining insects are found in the Lepidoptera, Diptera, Hymenoptera, and Coleoptera. The greatest diversity of forms and number of leaf-mining species are in the Lepidoptera, followed by the fly family Argromyzidae (Hespenheide 1991).

Boring insects live in the woody tissues of plants. The abundance and long-term availability of food provided by tree trunks permits growth to a large size. The larvae of *Syleutes boisduvale* (Cossidae), for instance, attain a length of 18 cm (Waterhouse 1970). In addition, the low nutritive value of wood tends to result in long life cycles. As an aid in using wood for food, some borers inoculate the wood with fungi that attack the plant and upon which the larvae feed. Dutch elm disease is caused by a xylem-blocking fungus introduced by the elm bark beetle, *Scolytus scolytus*. Other borers attack the living cambium

Figure 10.8 Insects galls. (*a*) *Andricus pattersonae* (Hymenoptera; Cynipidae) on leaf of blue oak. (*b*) Pine-cone willow gall caused by *Rhabdophaga strobiloides* (Diptera; Cecidomyiidae). (*c*) *Pemphigus betae* (Homoptera; Aphididae) on *Populus angustifolia*. (*d*) Longitudinal section through the goldenrod ball gall caused by *Eurosta solidaginins* (Diptera; Tephritidae).
(a) After Essig; (b) Redrawn from Boreal Labs key card; (c) from Whitham 1978; (d) from Abrahamson, 1989.



and vascular tissues, which can devastate the host. Bark beetles in the family Scolytidae are examples (Mitton and Sturgeon 1982).

Gall-Forming Insects

Many phytophagous insects induce the production of abnormal growth reactions, *galls,* in the tissues of their host plants, inside which they live and feed. Galls are found in buds, leaves, stems, flowers, or roots and their shape and location are often characteristic of the plant and insect species concerned (figure 10.8 *a–d*). In galls initiated by species with chewing larvae the insect resides in an inner chamber lined by nutritive tissue upon which the insect feeds. The gall is entirely a product of the plant, developing in response to a chemical stimulus from the secretions of the insect. The diversity of gall types and the biology of host and gall can be explored in books by Meyer (1987) and Ananthkrishnan (1984).

Gallmakers (also called gallers) reach their peak of diversity on dicots, the broad-leaved flowering plants. In North America and Europe, 85% of gall-forming species are found on the oak (especially *Quercus*), rose, and sunflower families. In South America, galls are especially common on legumes, and in Australia half of all known gallmakers are found on plants in the Myrtaceae, especially on *Eucalyptus* trees (Meyer 1987). Gallers are found primarily in the Diptera (Cecidomyiidae) and Hymenoptera (Cynipidae), but there are some representatives in the Hymenoptera (Chalcidoidea, Agaonidae), Coleoptera, Thysanoptera and Lepidoptera and in the fluid-feeding Homoptera (Aphididae, Apiomorphinae) (Waterhouse 1970).

Sucking Insects

Some insects avoid the need to fragment plant tissues by using highly modified mouthparts (see chapter 2) to pierce the plant epidermis and suck plant fluids. In this way, true bugs (Hemiptera), aphids and their relatives (Homoptera), and Thysanoptera avoid consuming indigestible structural components of the plant as well as toxic materials produced by the plant.

Sucking insects survive on several types of plant fluids. Thrips pierce and macerate the contents of individual cells with their stylets and then suck the liquified material through their proboscis. Other species (e.g., the meadow spittlebug, 13- and 17-year periodical cicadas) tap xylem vessels, from which they get a very dilute nutrient solution. But most hemipteran species insert their beaks directly into phloem cells to tap the more nutritious fluid there. Phloem fluid is a sugar solution with low concentrations of necessary nutrients. The specialized filter chamber digestive system that allows phloem feeders to make use of this fluid is described in chapter 4.

The feeding of Hemiptera and Homoptera involves negligible mechanical injury to plant tissues. However, saliva injected by some species may be toxic and sucking mouthparts are often involved in the transmission of viral diseases. So some insects are of more importance as plant-disease vectors than for the direct damage they inflict by feeding.

Seed-Eaters

Seed-eaters (and seedling-eaters) are the only true plant predators among insects because they kill plants by consuming them. Herbivores that consume stems, leaves, buds, or fluids are likened to parasites because the host is not killed (Price 1980); rather a growth module of the plant (either branch or leaf) may be removed, and the plant can grow a replacement part. Seeds are a rich source of protein and are used by both sucking and chewing insects. Seed beetles (Bruchidae) are one of the largest groups infesting seeds. Janzen's (1971a) studies of this group in the neotropics led to the development of some important ideas in ecology (e.g., predator satiation, seed shadows).

Plants As Food

Plants, permanently rooted to a spot, cannot flee from their consumer. Therefore, it is easy to assume that plants are an available and abundant food. But their immobility is the only "advantageous" aspect of herbivory! The structural parts of plants vary extensively and require different ways of feeding. Plants are only marginally nutritious, and most plants have a variety of both toxic and physical defenses against consumers. Further, the effects of air pollution on plant quality may exert indirect effects on phytophagous insects (boxed reading 10.1). The wide variety of characteristics plants use to defend against herbivory have been the subject of extensive and exciting research over the past decade, both in natural ecosystems and in crop plants. Some of these characteristics, including structural materials, nitrogen, water, chemical and physical defenses, are described below.

Structural Materials

The rigidity of plants is imparted by the structural carbohydrates cellulose and hemicellulose. As plant tissue ages, these carbohydrates accumulate and tissues become tougher and more difficult for insects to chew or pierce. In studies of Australian rain forest leaves, herbivory of young leaves was 15–40 times greater than of old leaves, and leaf toughness increased similarly (Loman and Fox 1983). There is a large amount of energy bound up in cellulose and hemicellulose, but insects cannot digest them since they do not produce cellulase, which is necessary to break down cellulose. The bulk of what almost all chewing insects eat is consequently indigestible. Important exceptions to this are insects such as termites, leaf cutting ants, and bark beetles, which have internal or external mutualistic associations with microbes or fungi that can produce cellulase (see chapter 4). Plants also produce waxes, cuticle, and other indigestible structural materials and concentrations of these, in addition to cellulose and lignin, increase as tissues age. They are especially high in tissues of plants growing in high light, dry or nutrient poor habitats where the vegetation is referred to as sclerophyllous (hard leaf) (Morrow 1983).

Nitrogen

Insects are more than 50% protein and 7% to 14% nitrogen by dry mass because they use protein as a major component of their structural compounds (e.g., arthropodin, sclerotin; see chapter 2). In contrast, plants have nitrogen levels that are much lower, from 0.5% to 8% nitrogen (figure 10.9), so insects must concentrate large amounts of protein from a very dilute source. As the nitrogen content of their food increases, insects become more efficient at extracting it (figure 10.10*a*). Many studies demonstrate increased growth (figure 10.10*b*),

Figure 10.9 Variation in nitrogen content of animals, fungi, and different plant tissues. Bars span the range of typical values. *Data from Strong et al., 1984.*

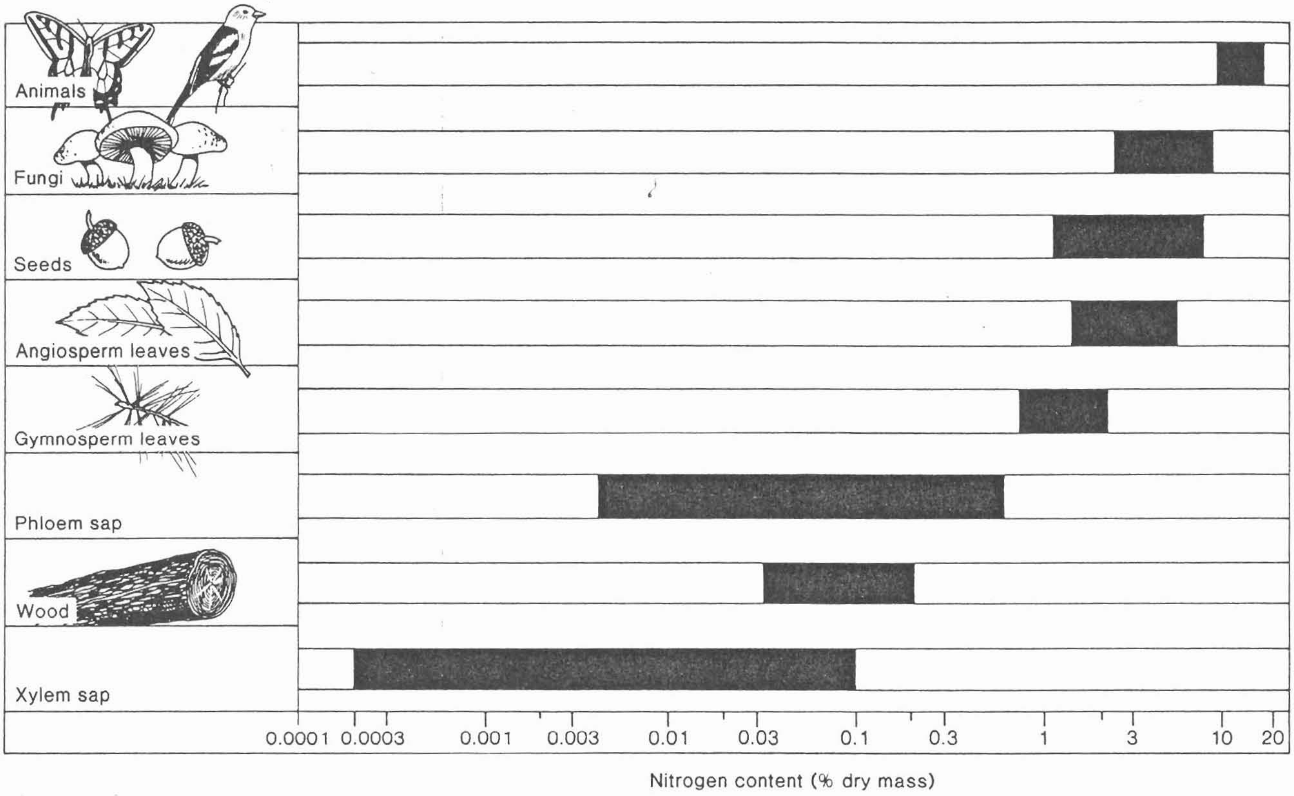
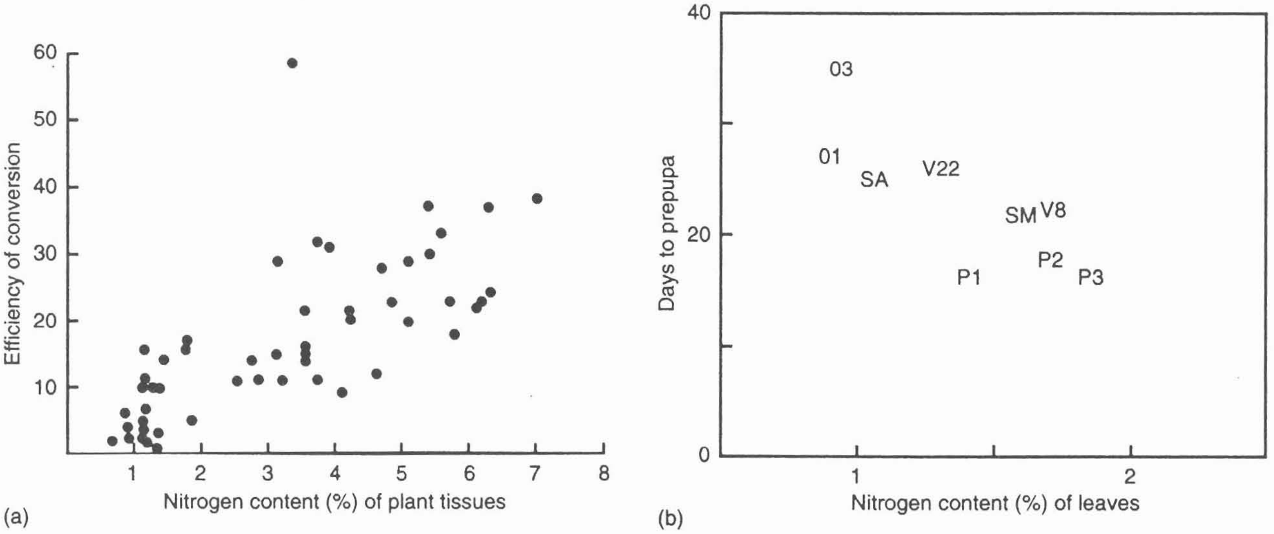


Figure 10.10 (*a*) Efficiency of conversion (biomass gained/biomass consumed) for various invertebrate phytophages as a function of the nitrogen content of their food (Mattson 1980). Low-nitrogen diets are used inefficiently because the rate of feeding and of throughput in the gut are increased to compensate for low food quality; therefore, digestion is less efficient. (*b*) Effect of leaf nitrogen content on development rate of *Paropsis atomaria* larvae (Coleoptera; Chrysomelidae). The number of days from hatching until most larvae in a cohort become prepupae decreases as nitrogen content increases (Morrow and Fox 1980). Percentage nitrogen × 6.25 gives an estimate of protein content (Waldbauer 1968).



BOXED READING 10.1

Pollution Induced Changes in Plant Quality

There is growing evidence that air pollution changes insect performance and levels of attack on plants (Riemer and Whittaker 1989). At the broadest level we might suspect that the nitrogen compounds in air pollution and increased CO_2 would affect levels of structural carbohydrates and concentration and composition of leaf proteins. Air pollution has resulted in dramatic inputs of nitrogen to the environment over the last 30 years. Emissions of NO^3 come largely from fossil fuel combustion and NH^4 from fertilizer applications (which have quadrupled since 1945) and intensive livestock operations (Wedin and Tilman 1992). Insect responses to fertilized and to pollution stressed plants are variable and we are not now able to predict how these factors alone, much less together, will influence insect populations.

The consequences of increasing atmospheric CO_2 levels on interactions between plants and their herbivores have been examined in a small number of studies. Some plants grown at high CO_2 levels had lower nitrogen levels, presumably because of dilution by cellulose and other carbon-based compounds, and insects increased their consumption of high CO_2 plants by 20% to 80%. Despite this, they grew more slowly than larvae on plants grown at ambient CO_2 levels (Bazzaz 1990). In contrast, sagebrush grown at high CO_2 was more readily digested by grasshoppers (Johnson and Lincoln 1991). Clearly, the direct and indirect effects of air pollution are not going to be easy to predict.

survival, fecundity, and longevity with increases in nitrogen. It would appear to be advantageous for insects to maximize their consumption of this limiting resource.

One way for insects to increase nitrogen intake is to eat more, but there is a limit to how much they can compensate for low quality food in this manner. *Eucalyptus* leaves must have at least 1% nitrogen in order for larvae of the chrysomelid beetle *Paropsis atomaria* to gain more nitrogen than they excrete in their frass (Fox and Macauley 1977). For grasshoppers and larvae of *Prodentia eridania*, the break-even level of plant nitrogen is 3% (Mattson 1980). But nitrogen content is more complex than nitrogen concentration alone implies. For example, when nitrogen levels are elevated by fertilization, insects do not benefit as predicted from studies of plants that have naturally high nitrogen levels or levels elevated as a result of stress (Morrow 1983).

The relative proportions of amino acids that make up plant and insect proteins are different. In artificial diets, Karowe and Martin (1989) found that the respiration rate of *Spodoptera eridania* larvae depended upon the amino acid composition, but not upon the quantity of protein. Southwood (1973) concluded that predatory insects convert animal proteins to biomass more efficiently than herbivores convert plant protein. One major difference is in the ratio of phenylalanine to other amino acids. Plants produce relatively small amounts, whereas insects require large amounts to make chitin. Grasshoppers, for example, have significantly increased growth rates when phenylalanine is added to their diet (Bernays 1982).

The nitrogen content of plants varies considerably between plant species, tissues (figure 10.9), and with season. Actively growing tissues require high levels of nitrogen to support protein synthesis, but once the tissue is fully expanded, synthesis shifts to structural carbohydrates and nitrogen levels become diluted. The deciduous oak, *Quercus robur*, has leaf nitrogen levels of about 5% at bud burst in late April, 2.5% nitrogen when fully expanded and 1.5% just before leaves are shed in October (Scriber and Slansky 1981). The equivalent values for *Eucalyptus pauciflora*, an evergreen tree in nutrient poor, high altitude sites are 2%, 1.5%, and 1.2% nitrogen (Morrow 1983).

Nitrogen levels in phloem fluids also are variable. When the plant is actively growing and later when nitrogen is being retrieved from leaves before they are dropped, the concentration of nitrogen transported in the phloem may reach 0.6%. In between these periods, levels may drop to .03%, and the proportions of amino acids change (Mattson 1980). Phloem-tapping insects such as the green spruce aphid, *Elatobium abietinum*, respond to this nitrogen change by producing winged alates that disperse from the plant in late spring to find alternative hosts (McNeill and Southwood 1978).

Water

The water content of foliage varies from 45% to 95% of fresh weight. All else being equal, leaves with high water content (e.g., expanding leaves or leaves of annual plants) are digested most efficiently and support the highest rates of growth (Scriber and Slansky 1981). Leaf water content is correlated with nitrogen content, and both decrease with increasing levels of structural materials.

Adaptations have evolved in higher plants that enable these plants to deal with the harsh realities of extracting water and nutrients from dry land. The specialized ways of plant feeding that have evolved in phytophagous insects provide evidence that plants have passed difficult nutritional problems for insects to overcome.

Insects that have evolved the ability to use particular host plants exert selection pressures that favor the evolution of defenses in those hosts. We will consider these "co-evolutionary" interactions later. Here we simply outline the main characteristics of plant defenses.

Plant Defenses

Plant defenses against phytophagous organisms of all sorts fall into two basic categories: physical defenses and chemical defenses that are toxic or deterrent, or actively interfere with digestion.

Physical Defenses

Plants commonly have tough surfaces that make them hard to pierce, bite, and chew. Toughness is endowed by thick cell walls with high levels of lignin and by deposits of surface waxes. Silica crystals are common in epidermal cells of grasses and horsetails, *Equisetum,* and abrade the mandibles of herbivores.

Many plants are covered by small hairs called *trichomes,* or *pubescence.* These hairs come in many different forms: long, short, thin, sharp, flattened, slippery, and with or without glands (Levin 1973). Leaves and stems of *Passiflora adenopoda* are covered with small hooked hairs that protect it from larvae of *Heliconius* which are specialized feeders on passion vines. Where hooked hairs pierce the larva's skin, hemolymph drains out and the larvae dries up and dies (figure 10.11*a,b*). Trichomes are an important defense in some crop plants. For example, soybeans without trichomes supported an average of 30 leafhoppers per plant, and those with trichomes had just 2.7 (Singh et al. 1971).

In contrast, the leaves of the giant stinging tree (Urticaceae, *Dendrochide excelsa*) in tropical Australian rain forests are densely covered with stinging hairs, as the name implies. Observations by Lowman (1985) have shown that a host-specific beetle, *Hoplostinis viridipenis,* is undeterred by these defenses. The leaves lost an average of 32% leaf surface area during a lifetime. Stinging hairs may have evolved as a defense against mammalian herbivores in Asia, but are less effective against insects (figure 10.11*c*). While defenses can be ineffective against some herbivores, they may deter other potential herbivores, and so the plant has won at least those battles.

Chemical Defenses

Plants are the original pharmacies. Among the compounds they produce are vanilla, salicylic acid (aspirin), caffeine, nicotine, morphine, pyrethrum and tannins. Frankel (1959) argued convincingly that the diverse array of compounds produced by plants are defenses against herbivores. An enormous literature now exists on relationships between plant toxins and herbivores that support his view. This literature can be tapped through review volumes such as Rosenthal and Janzen (1979), Rosenthal and Berenbaum (1992), and Harborne (1988) and journals such as *Chemical Ecology.*

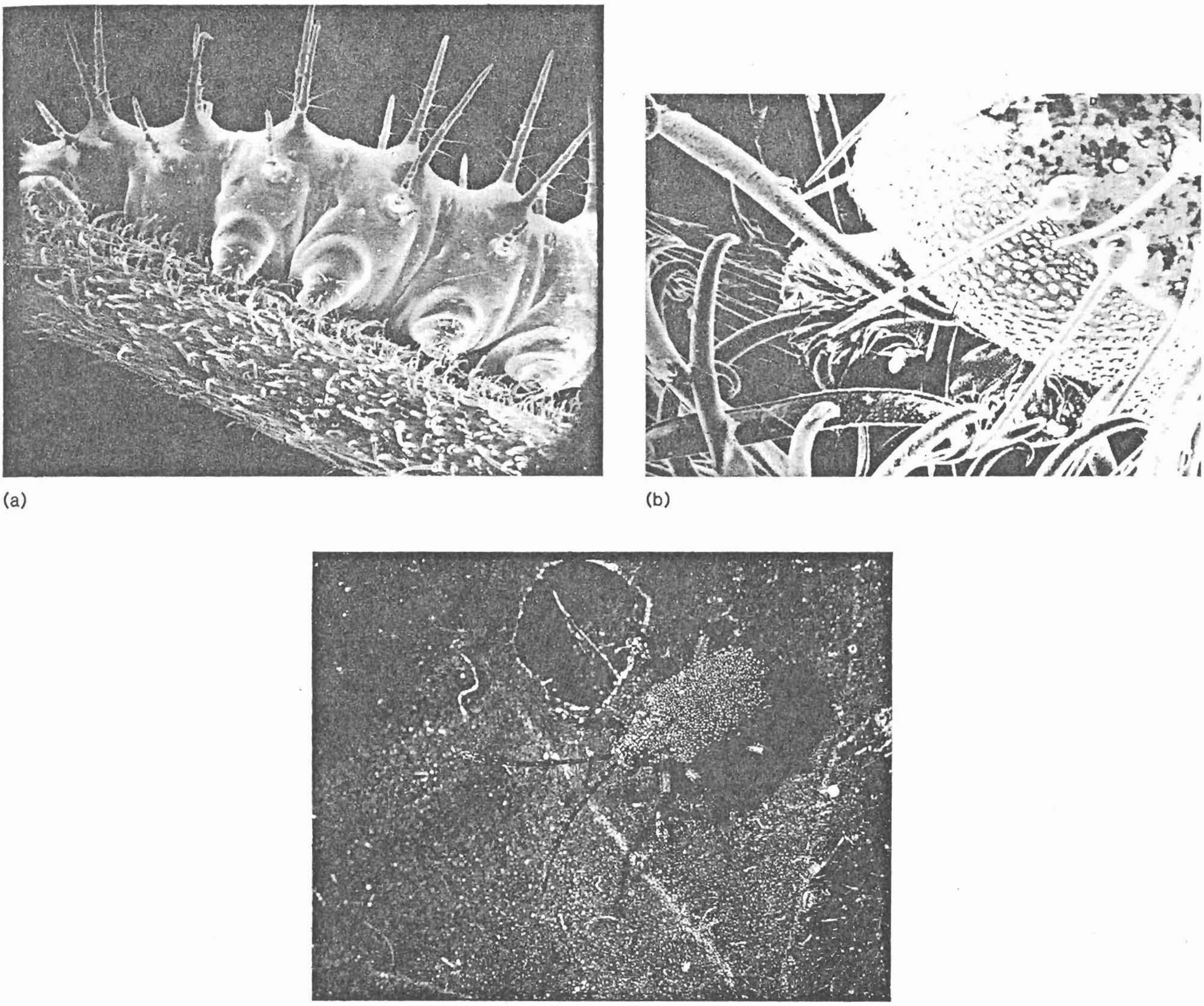
Defensive chemicals, also called *allelochemics,* or *secondary compounds,* are produced from biosynthetic pathways related to the primary metabolic pathways (figure 10.12) common to all or large numbers of organisms. Plants produce an incredibly diverse array of these compounds and all of them can be traced back to a very limited number of precursors, acetyl coenzyme A, mevalonic acid, and shikimic acid (Waterman and Mole 1989). Allelochemics can poison the physiological systems of herbivores, many of which are the same as those of plants. Plants avoid poisoning by isolating allelochemicals from physiologically active sites, for instance in glands, resin ducts, or vacuoles. Or they may be stored as inactive precursors that become damaging only when metabolized by the herbivore or when the plant is damaged. For instance, free hydrogen cyanide, which poisons mitochondrial respiration, is released from damaged clover leaves when cells are ruptured and cyanogenic glycosides and glycosidases come together (Jones 1973). Free cyanide can deter insects and is even more toxic to mammalian herbivores (Bernays 1982).

We can roughly categorize allelochemicals into two groups, those that exacerbate the already low nutritional value of plants and those that are toxic to basic metabolic processes. The first group are variously referred to as *digestive reducers, quantitative, immobile,* or *carbon-based defenses.* Passively or actively, they make food less nutritious (table 10.1). Eating becomes a more time consuming process and increases the length of time an insect is exposed to predators, parasites and environmental hazards. These chemicals generally are present in high concentrations (e.g., up to 23% of the dry mass of Sitka spruce bark is lignin and 21% of eucalyptus leaves may be essential oil) and their effectiveness is dose dependent (Wainhouse et al. 1990). Quantitative compounds accumulate as tissues age and the plant does not scavenge their largely carbon components before shedding the structure (hence, *immobile* compounds). Compared to the next group of allelochemics, digestion reducers are not very diverse.

The second group of allelochemics are referred to as *toxic, qualitative,* or *mobile compounds.* Qualitative compounds are present and effective in small concentrations (generally less than 5% leaf dry weight) and target essential functions of the herbivorous animals such as respiration, DNA repair, transmission of nerve impulses, and hormone production (table 10.1). Often they are synthesized and degraded over fairly short periods, hours to weeks, and their component parts end up in other compounds. In the plant they may have nondefensive as well as defensive functions. For instance, nicotine, a potent insecticide, also is used by tobacco plants to transport nitrogen to the shoot from uptake sites in the roots, a

Figure 10.11 Larvae of *Heliconius melpomene* eat many species of *Passiflora* but not *P. adenopoda* for the reason illustrated in these scanning electron micrographs. (*a*) Third instar larva caught on leaf petiole (85×). Proleg marked x is enlarged in (*b*). (*b*) Proleg has hooked trichomes embedded at a, b, and c causing the larval skin to split and hemolymph to drain from the wound (85×). (*c*) Host-specific chrysomelid (*Hoplostinis viridipenis*) feeds on the giant stinging tree in Australian rain forests, obviously undeterred by the hairs. Hairs have a sharp point that on contact detach, injecting poisons whose effects may be felt by humans for up to a month.

(a) and (b): Gilbert, L. F., and SCIENCE: *172, 585–6 (1971),* © *AAAS. (c):* © *M. Lowman.*



(a)

(b)

(c)

Figure 10.12 The ent-kaurene to gibberellin (a hormone) primary pathway probably present in all higher plants. Diterpenoids indicated to the right of the dotted line are secondary metabolites characteristic of goldenrods, *Solidago*, which inhibit feeding by many herbivores.

Modified from Graebe, 1987.

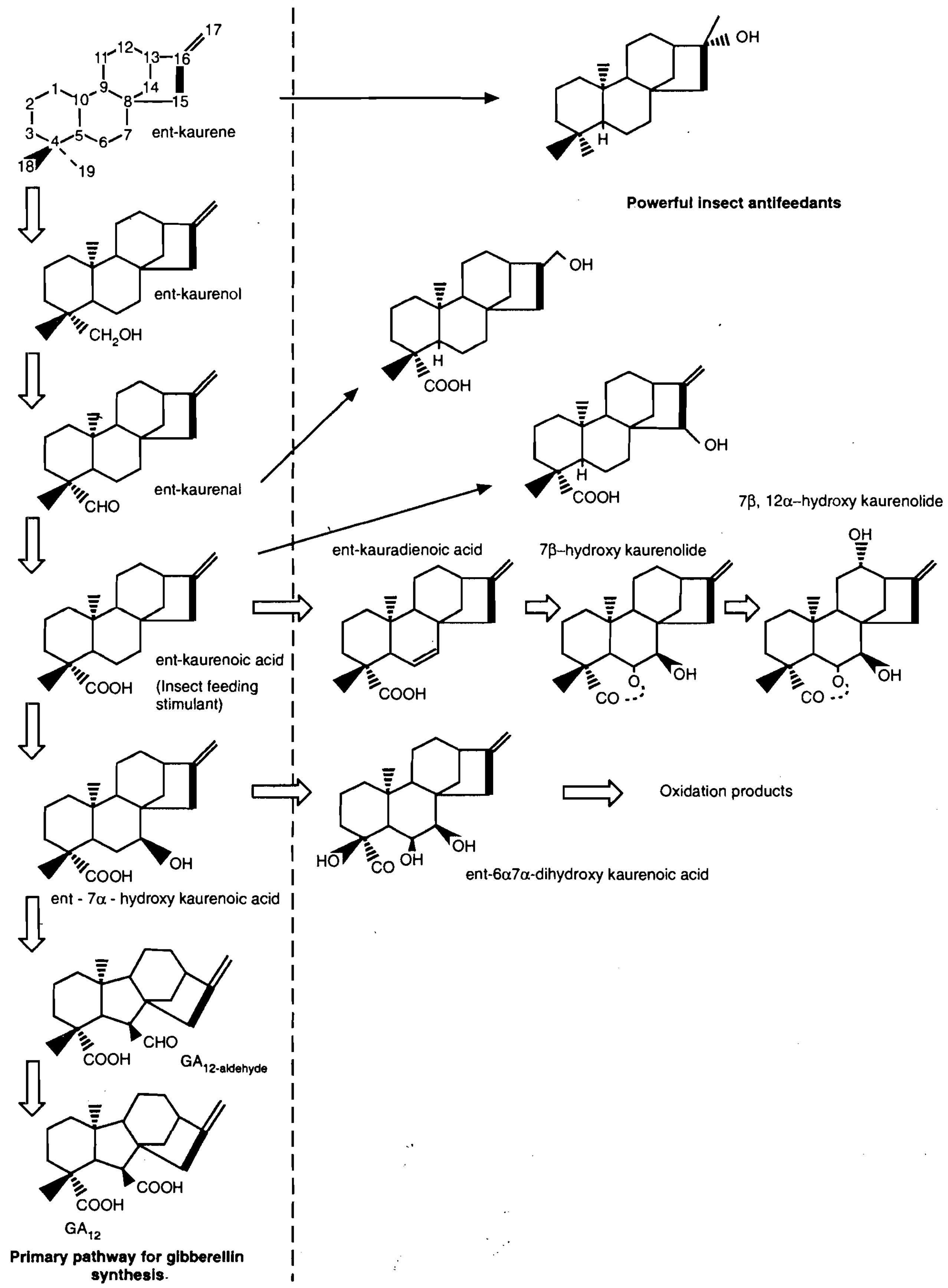


Table 10.1 Selected Plant Products that Reduce Herbivory[a,b]

Chemical group (number identified)	Description	Defensive role
	Quantitative Digestibility Reducers	
Cellulose (1 basic type)	Sugar polymer	Requires gut flora for digestion
Hemicellulose (1 basic type)	Sugar polymer	Requires gut flora for digestion
Lignins (indefinite)	Phenolic polymers	Bind with proteins and carbohydrates
Tannins (indefinite)	Phenolic polymers	Bind with proteins
Silica (1 basic type)	Inorganic crystals	Indigestible
	Qualitative Toxins	
Alkaloids (20,000)	Heterocyclic N-containing	Many; some stop DNA and RNA production
Toxic amino acids (260)	Analogues to protein amino acids	Compete with protein amino acids
Cyanogens (23+)	Glycosides that release HCN	Stops mitochondrial respiration
Glucosinolates (80)	N-containing K salts	Many; endocrine disorders
Proteinase inhibitors (indefinite)	Proteins or polypeptides in subunits	Bind with active site of enzymes
Terpenoids (100,000+)	Polymers of C_5 units	Many; some stop respiration

[a] See Rosenthal and Janzen (1979) for a discussion of other secondary compounds.

[b] C, carbon; H, hydrogen; K, potassium; N, nitrogen; HCN, cyanide.

Some compounds have characteristics of both groups. Silica, for instance, can be viewed as both a physical and a quantitative defense and the defensive properties of cellulose may be coincidental to its primary support function (Howe and Westley 1988).

From *Ecological Relationships of Plants and Animals* by Henry F. Howe and Lynn C. Westley. Copyright © 1988 by Oxford University Press, Inc. Reprinted by permission.

function performed in most plants by other nitrogen-rich but nontoxic compounds such as glutamine and asparagine and amino acids closely related to them (Pate 1973).

Plant defenses may be present in a plant all of the time or they may be produced in response to tissue damage. *Constitutive defenses* are a plant's permanent protection. They include most of the physical defenses like silica crystals and trichomes as well as many digestion reducing and toxic compounds (table 10.1). They help plants survive first encounters with herbivores. *Inducible defenses* are produced after the plant begins to experience damage (Tallamy and Raupp 1991; Haukioja 1991; Weins et al. 1991). The best documented inducible allelochemicals are proteinase inhibitors. These polypeptides and proteins block the catalytic activity of digestive enzymes in the gut by binding to the active site of the enzyme molecule (Ryan 1979, 1983). Proteinase inhibitors are extremely common in the plant kingdom, including the legume family. They are denatured by heat, one of the reasons we cook beans and some other vegetables. See chapter 4 for a brief discussion of how genetic engineers have used the proteinase inhibitor genes to develop plants that are resistant to certain pest insects.

Catching Food: Temporal and Spatial Availability

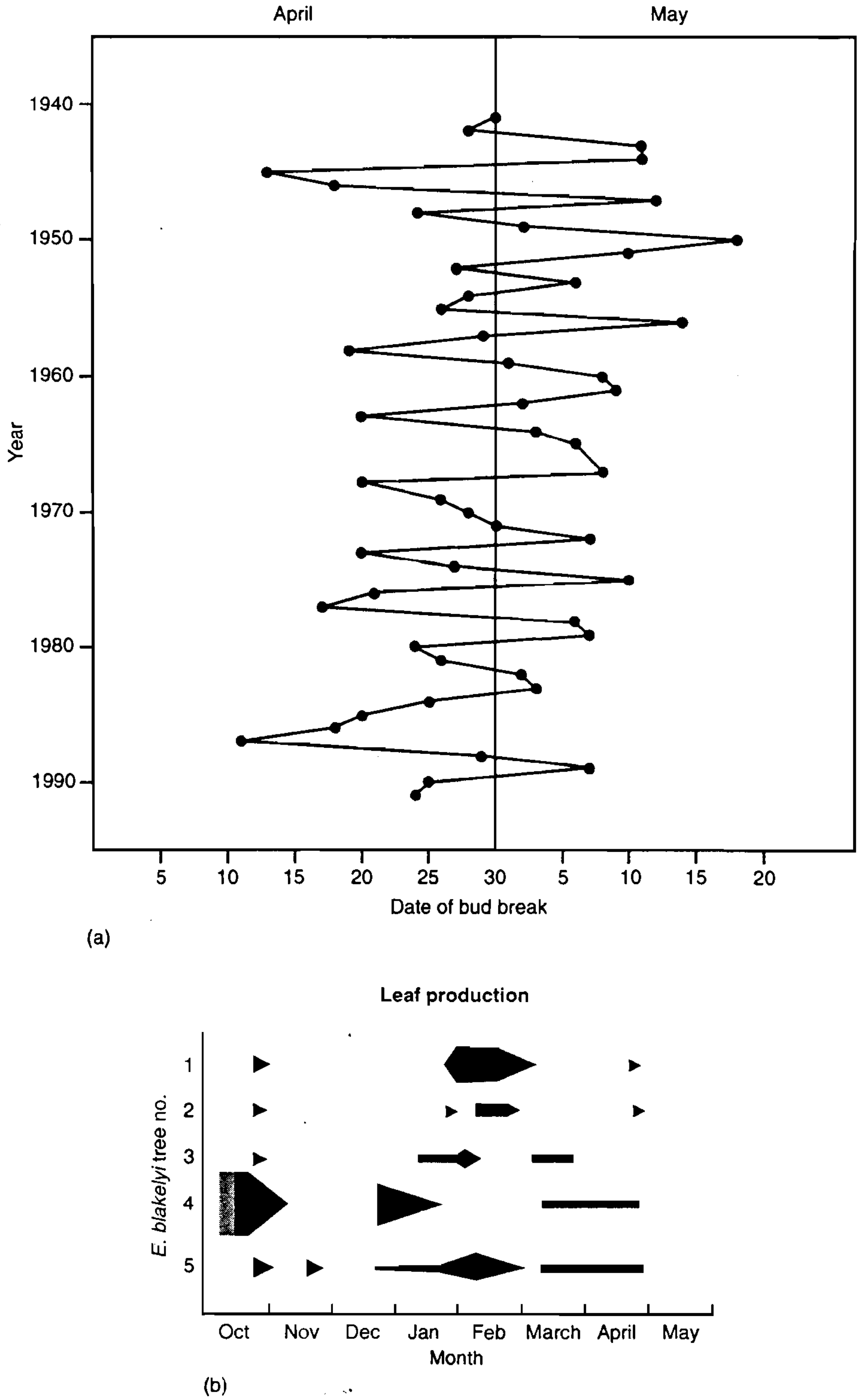
Plants are dynamic. All of the properties so far discussed change with time and in response to biotic and abiotic environmental challenges. The parts of a single plant can vary enormously in their potential to support the growth and reproduction of an insect. These differences have causes ranging from the divergent physical properties of various structures such as leaves and stems, the unequal production, transport and storage of nutrients, and fluctuations in the concentration of toxins and other compounds that interfere with feeding. Plant variation imposes severe constraints on many insects (Whitham 1983; Schultz 1983).

The boundaries of those constraints have been studied for the aphid, *Pemphigus betae,* by Whitham and his colleagues. In the spring, females emerge from eggs that overwintered in bark fissures of their cottonwood host tree, *Populus angustifolia* (figure 10.8*c*). Galls started within three days of bud break have the greatest chance of being successful. By day seven, leaves are fully expanded and lignified and cannot be galled. Bud break is nearly simultaneous throughout a tree so there is little room for error in female emergence time. This is not an easy problem to deal with because date of bud break varies between trees within a population (3–7 days) (Whitham 1978) and for individuals from year to year (e.g., figure 10.13*a*).

The gall aphid's temporal problem is exacerbated by spatial problems. On leaves less than 5 cm^2 in area, most galls fail. Above this size, the number of offspring that emerge from the gall increases with leaf size, which is related to the amount of nitrogen the tree sends to a leaf; larger leaves get more than smaller ones. Most leaves are too small and the large leaves are scattered throughout the crown. Females crawl from branch to branch searching for unoccupied large leaves. The females actually fight one another for possession of the best leaves (Whitham 1978). Not unexpectedly, the number of galls on a tree varies enormously from year to year (Moran and Whitham 1988).

Figure 10.13 (*a*) Twenty-six year record of the date of bud burst for tagged branch of an aspen (*Populus*) tree. (*b*) Relative abundance and duration of leaf production on five saplings of *Eucalyptus blakelyi* at a single location in one year. The asynchrony in leaf initiation, which increases as the (southern hemisphere) growing season progresses, is caused by individual responses of trees to different levels and timing of insect defoliation.

(a) Data from Hodson, 1991. (b) Data of L. R. Fox.



Trees in the large genus *Eucalyptus* have a very different leafing phenology. They initiate new leaves whenever it is sufficiently warm and wet and they are especially prone to do this in response to damage, for example, fire or insect attack. This behavior can result in continuous growth or in bursts of growth (figure 10.13*b*). Unlike the narrow window of time available for *P. betae* to exploit cottonwood, eucalypt insects can have multiple large windows. This is probably one of the factors responsible for the high levels of damage eucalypts sustain most years (Fox and Morrow 1983, 1986; Morrow and Fox 1989). Furthermore, insect attack opens these windows wider because trees respond to attack by producing new flushes of growth, which the insects then eat. This is a major contributing factor in the widespread eucalypt dieback in rural regions of Australia (Heatwole and Lowman 1986), widespread tree decline that has ranked amongst the most severe in the world. Outbreaks of psyllids, beetles, and other insects repeatedly defoliate the canopies of eucalypts until mortality occurs. Defoliation can reach 275% per year, because the insects defoliate the canopy each time it refoliates. The stress of repeated defoliation is all the more significant because the eucalypts already face other stresses, for example, widespread clearing of adjacent forest, soil compaction from livestock, recurrent droughts, and depletion of many insectivorous bird populations.

Recently, Whitham (1989) has shown that hybrid cottonwood trees support several orders of magnitude more gall aphids than the parent species. A contributing factor may be the increased time over which bud burst occurs in the hybrid zone, 21 days versus 3–7 days in the parent zone (T. G. Whitham, unpublished data).

Mutualism and Coevolution

Every organism must obtain enough food to maintain itself long enough to reproduce if it is to pass its genes to the next generation. As an organism proceeds from conception to reproductive maturity, it must constantly obtain food and at the same time avoid becoming food for some other organism. Organisms that are unable to do this successfully, for whatever reason, are maladapted and leave few descendants. Although a number of environmental factors are undoubtedly involved in the selection process, examination of specific adaptations often leads to the identification of specific selecting agents. Such is the case when we examine adaptation associated with many interspecific interactions. Organisms that are closely associated ecologically often act as agents of selection reciprocally; that is, they act as selecting agents on one another. There is good evidence that many organisms have done so for long periods of geologic time. These organisms are said to have coevolved.

Examination of several examples of coevolution reveals two types of interactions. Two different species or guilds of species that have coevolved to the extent that they benefit one another are termed *mutualistic*. In this case, the presence of both enhances the reproductive success of both. Alternatively, two species may engage in a kind of genetic warfare whereby one adapts a mechanism of offense providing increased access to the other as food, only to have the other "respond," in the evolutionary sense, with a defense. Examples include predators and prey, parasites and hosts, and herbivores and plants. For a comprehensive introduction to coevolution, see Thompson (1982, 1989).

Figure 10.14 Bull's horn acacia branches (*Acacia cornigera*) are occupied by an aggressive stinging ant (*Pseudomyrmex ferruginea*). Ants live in the thorns and feed on starchy Beltian bodies and sugar-rich secretions from extrafloral nectaries. The ants clear vegetation around host trees and attack insect and mammalian herbivores that might eat the foliage.

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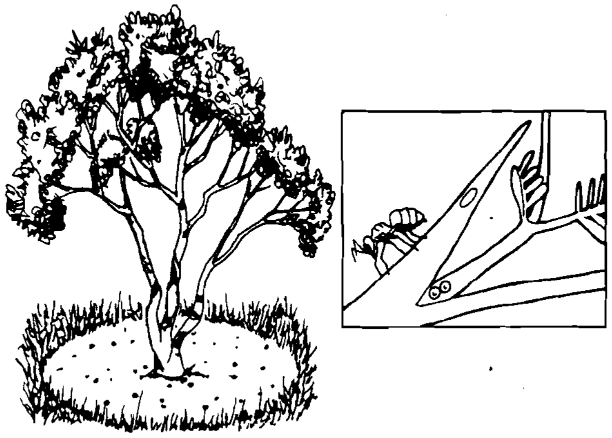


We give two examples of mutualisms here: ants and plants and plants and their pollinators.

Ants and Plants

Some species of ants in the neotropics live in acacia trees. An aggressive stinging ant (*Pseudomyrmex ferruginea*) nests in the hollow thorns of the bull's-horn acacia (*Acacia cornigera*) and feeds on nutrient-rich Beltian bodies and sugar secretions from extrafloral nectaries present on all the leaves. In return the ants attack herbivores and clear vegetation surrounding their acacia tree (figure 10.14). Acacias without ants have lower growth rates and are often killed by herbivores, fire, or crowding from other plants (Janzen 1966). In this case, the mutualism is *obligate*, neither the ant nor the acacia survives without the other.

More common than obligate mutualism is *facultative mutualism* (i.e., the interaction occurs under some conditions but not others). One of the most common kind of facultative mutualism is between the many species of plants with extrafloral nectaries and the many ant species that seek nectar. While searching for nectaries, ants may prey upon herbivores they encounter. Both mutualists benefit from the interaction but neither is dependent upon it. Tilman's (1978) study of ants, cherries, and tent caterpillars is an excellent example of facultative mutualism.

Plants have a mutualistic relationship with many ants for the purposes of seed dispersal. Ants benefit by gaining a food source, and plants benefit by having their distributions extended (because ants invariably drop some seeds on their way back to the colony). There are two major variations in this phenomenon: some ants feed upon the seeds (and so plant dispersal depends upon the frequency of seeds dropped); and some ants feed upon an *elaiosome* (fat body) that is attached to a seed, thereby ignoring the seed which is left to germinate (Handel and Beattie 1990). This latter relationship, termed *myrmecochory* (from the Greek for "ant," *myrmex,* and for "dispersal," *kore*) insures complete dispersal of all the seeds of a plant that are harvested by ants. The ants benefit from consumption of the elaiosome, and the plants benefit from effective seed dispersal. Elaiosomes have been found in taxonomically diverse plants, including northern temperate wild flowers (e.g., *Trillium* and *Viola*), tropical epiphytes and vines, and Australian arid shrubs (e.g., *Acacia*). The morphologically and taxonomically diverse origins of elaiosomes indicates convergent evolution: originally they protected seeds from predation but gradually changed into food lures for ants. Even the biochemical attractants contained within the elaiosomes have been identified, with some proving to be the same from plants found on different continents!

Other ants have special relationships with plants whereby they cultivate fungal gardens (providing nutrients for the ants) in exchange for shelter and a supply of plant material that the ants harvest from outside the nest. Huxley (1978) studied ant-plants in New Guinea that have evolved bulbous chambers to house their ant partners and Thompson (1981) explores how these associations may have arisen. Huxley and Cutler (1991) provide a review of anti-plant interactivities.

Plants and Pollinators

Flowers and their pollinators have developed specialized relationships over evolutionary time. The first winged insects were present 300 million years ago in the Carboniferous, long before the development of flowers (Smart and Hughes 1972). The first flowers appeared in the fossil record approximately 225 million years ago and were small (those of the gymnosperm order Bennettitales), so presumably they had insect pollinators. They are termed *entomophilous* (pollinated by insects that feed on pollen, nectar, or on the flower itself). At about the same time the first holometabolous insects appeared. The adults of these insects were adapted to feed on different foods from the larvae. This alteration of food supply between different life stages greatly enhanced the opportunities of insects to specialize upon leaves as larvae and upon pollen as adults. The radiation of Lepidoptera, an insect order whose coevolution in pollination ecology is well studied, began during the early Cenozoic, and today we appreciate a wide variety of specific relationships between pollinators and plants.

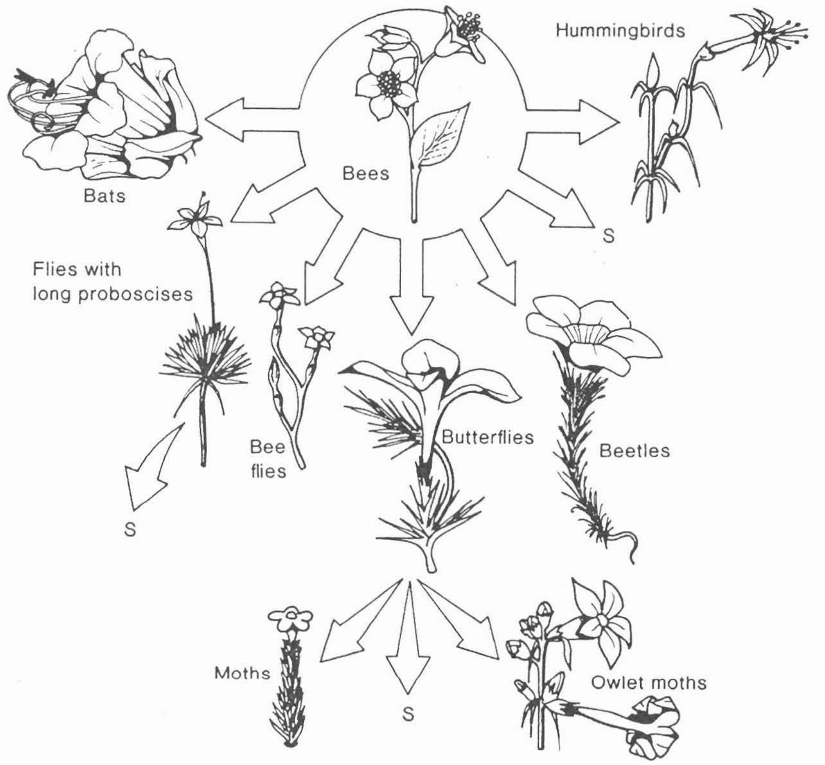
Sexual reproduction in flowering plants is accomplished by the transfer of pollen from the anther of a male flower to the stigma of a female flower. When a pollen grain contacts a stigma, the male germ cell in the pollen grain eventually unites with the female germ cell or egg, and a fertile seed develops. When the seed is exposed to the proper conditions in or on an appropriate substrate, it will give rise to a new plant. The transfer of pollen from a male to a female flower is accomplished primarily by the wind or by the activities of insects that associate with plants. Examples of wind-pollinated plants include cereal plants such as wheat and corn, ragweed (of hay fever fame), and many species of trees. The flowers of these plants, which are generally small with weakly developed petals, do not produce nectar, and produce dry pollen grains that are easily picked up by the wind.

The evolution of pollination involved the processes of *divergence* (whereby organisms become different) and *convergence* (whereby organisms become more similar over time). Fossil evidence indicates that animal mutualists changed more significantly over evolutionary time as compared to flowering plants, which have remained remarkably stable over the last few million years. However, some plant families exhibit classic specialization of reproductive parts that attract specific pollinators. A good example is the phlox family, which evolved from one bee-pollinated flower to a variety of flower heads that have different types of pollinators (figure 10.15).

Many factors affect the complex relationships between flowers and their insect pollinators. These include the nutritional rewards of pollen and nectar, as well as the physical features such as shape, color, and scent of flowers; the phenology (i.e., seasonal availability) of flowers in relation to population dynamics of insects; the growth structure of flowers (clusters versus solitary); the plant community surrounding a flower (i.e., competition from other plants present); and, of course, competition from other pollinators. With all these factors to account for, it is obvious how complex plant-pollinator relationships are for biologists to unravel!

In pollination, both partners enjoy a mutual benefit from the relationship. The plant is propagated, and the pollinator enjoys a calorific reward. An interesting aspect of the energetics of the plant-pollinator mutualism was investigated by Baker and Baker (1973). It has long been known that nectar contains various sugars and is used as an energy source for pollinators, but insects also require

Figure 10.15 The phlox family (*Polemoniaceae*) illustrates divergence of flower form due to selection from different pollinators. Self-pollination (S) evolved independently in several of these adaptive branches.
From Barth, 1985; after Grant and Grant, 1965.



the molecules with which to synthesize proteins (amino acids) which presumably had to be found elsewhere (e.g., in Lepidoptera, from larvae feeding upon leaves). The Bakers surveyed 266 species of flowering plants in California and found that nectar contained amino acids in many species, with relative amounts of amino acids highest in specialized lepidopteran-pollinated flowers.

Plants and pollinators not only have complex relationships in terms of energy exchange, but their structures ensure long-term consequences such as regulation of the pollination process. The promotion of *outcrossing* (whereby a plant gets pollen from another individual, not from itself) was studied by Heinrich (1979), who found several interesting patterns: flowers may evolve to restrict visits to pollinators, excluding "robbers" that take the rewards without transferring pollen; plants evolve different levels of nutritional reward and stand densities to regulate the number of flowers that insects are encouraged to visit; plants can control the amount of the calorific reward in relation to the size and behavior of the pollinator (e.g., bumble bees require more energy than a small fly).

Distinct correlations can be made between the anatomical and physiological characteristics of the flowers of a given species and the anatomy, physiology, and behavior of their insect pollinators. Among the characteristics of flowers attractive to insects are:

1. The production of particular scents.
2. Color, size and shape of petals.
3. Patterns of stripes or spots on petals.
4. Separation or nonseparation of petals.
5. Shape of flower.

Scent production is often important in attracting a pollinator and in determining behavior. Flowers pollinated by flies, which breed in dung and carrion, may actually mimic the odor of dung or rotten meat, so "fly flowers" commonly have a disagreeable odor to humans. Conversely, "butterfly and moth flowers" usually have a sweet smell. Honeybees are attracted to blue, purple, and yellow flowers, but cannot "see" red flowers. Many insects are attracted to patterns of ultraviolet light. The shape of nectaries are often suited to restrict undesirable species and to encourage the pollinator species.

Over the course of evolution, many pollinators have adapted to using particular flowers. A good example of this is the orchid family, the majority of whose members have specific pollinators and structurally complex flowers to pollinate. Some orchids produce scents that mimic the effects of sex pheromones, stimulating the insects both visually and tactilely. Another interesting family is the figs with 600 species, each of which has a specialized wasp pollinator. Pollinators that visit only one taxon of plant are termed *monolectic* (versus *polylectic* pollinators that visit many different taxon). What is the evolutionary advantage of visiting only one taxon? In the case of fig wasps, they not only pollinate the fig flowers but also lay eggs in the floral receptacle called a *synconium.* This structure provides a safe home for the wasp larva, which consumes the ovule in which it was placed. Upon emergence, it can easily find a mate and fly to another ripe fruit, thereby completing its life cycle within one tree canopy. In this sense, monolectic behavior offers a secure existence to the host-specific fig wasp.

Even the foraging dynamics of pollinators can be a complex coevolved process. For example, euglossine bees forage for food throughout kilometers of tropical forest and frequently return to the same plants (Janzen 1971b). This trap-lining behavior is advantageous because outcrossing occurs despite the very low plant densities characteristic of many tropical tree species. Only one of several flowers must produce nectar each day, and floral morphology can become specialized for pollinators that can learn their way around a forest and that are usually also efficient (and do not waste pollen). Because smaller amounts of energy are required to ensure pollination, tropical trees can reproduce much earlier in their life span and also save energy for other more competitive aspects of survival (e.g., getting light and nutrients). Floral visibility is also less important and can be effective even under the shaded, complex tropical canopy.

The most common insect pollinators are members of the orders Coleoptera, Lepidoptera, Diptera, and Hymenoptera. Their most common adaptations include elongated mouthparts that allow them to get nectar from flowers with deep nectaries, plumose (featherlike) hairs on the body to which pollen clings, and various specialized pollen-collecting and/or transporting structures such as the corbiculae (pollen baskets; see figure 2.37*a*) on the hind tibiae of honeybees. The relationships of plants and insect pollinators are an exciting aspect of ecological research, because coevolution is a dynamic process and there are so many groups of insects and plants yet to study. The topic of insect-plant interactions is covered by Prince et al. (1991) and Abrahamson (1989).

Insects in Forests as an Example of Community Aspects of Insects and Plants

Insects form a community within a plant, and similarly insects and plants together form part of a larger community or ecosystem. Although insect epidemics can occur anywhere (even in deserts), forests generally contain the most diverse and abundant fauna of invertebrates. This is because forests contain a wide diversity of plants (trees, shrubs, herbs, mosses, lichens, ferns, and algae, each with its own insect fauna); are slow-growing and older than many surrounding early successional ecosystems; and offer a large selection of food sources of different ages, palatabilities, and nutritive qualities. The relatively long time scale involved in forest succession allows for colonization and more complex levels of interactions of organisms to become established.

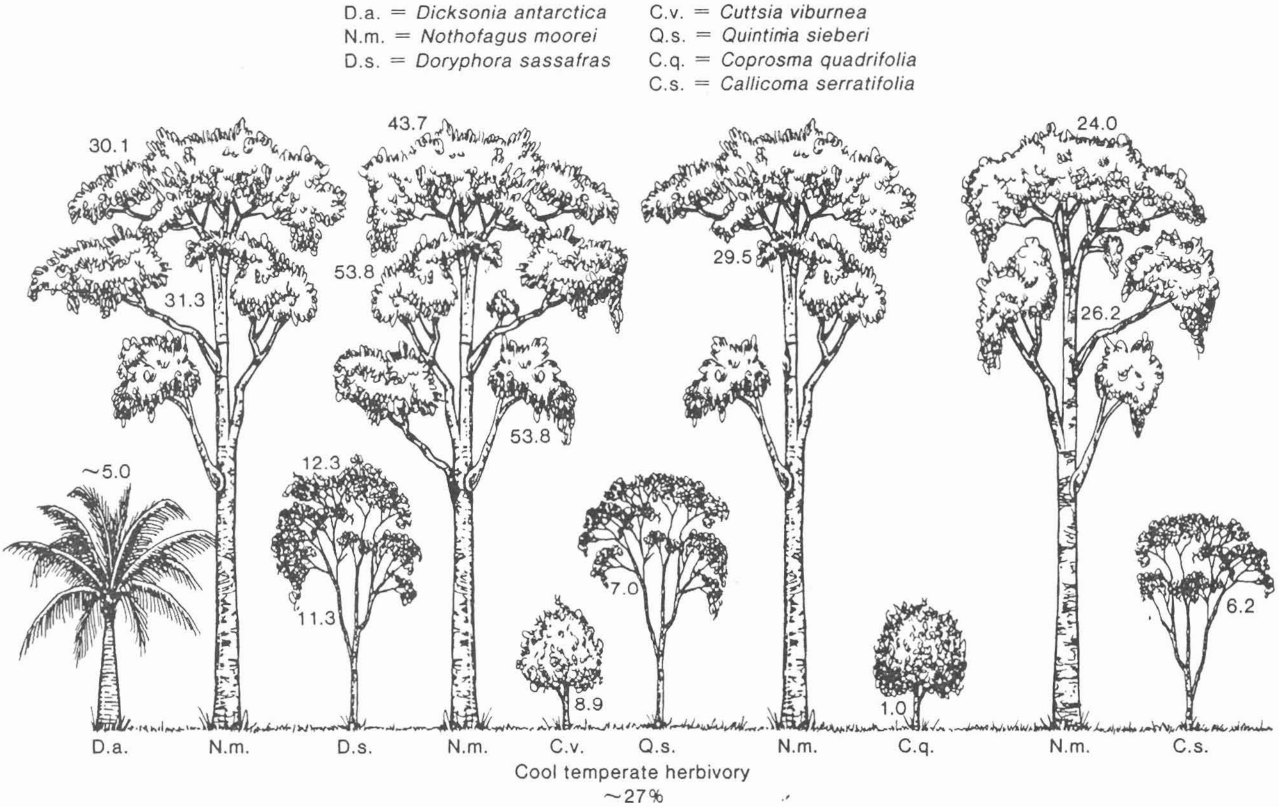
Insects in forests are difficult to study, but represent a great challenge due to the anticipated diversity that will be found there. Whereas biologists can count and measure the number of mollusks on the intertidal rock platform (a relatively two-dimensional habitat), it is nearly impossible to view the invertebrates of a forest due to its structural density, complexity, and height. These logistic problems have led many scientists to study insects in other habitats; hence, a paucity of literature exists on forest insects, except in outbreaks in which numbers are easier to obtain.

In recent years, biologists have become particularly interested in insects of rain forests for two reasons. These habitats are endangered by human activity, and the need to study them before they are reduced to fragments or to clearings is paramount. Second, rain forests contain the greatest wealth of insect species anywhere in the world (Wilson 1988). Despite the fact that they occupy less than 7% of terrestrial habitats, they have a variety of plants and a relatively homogeneous wet climate that has enabled the evolution of a wealth of species. Wilson (1987) found 43 species of ants in one leguminous tree in the tropical rain forests of Peru, equivalent to the ant fauna of the entire British Isles! And Erwin (1982) found 1,080 species of Coleoptera by fogging four rain tree forest canopies in Brazil. What was more astounding than the diversity, however, was the fact that 83% were endemic to only one site. Only 3.2% of the species were shared among all four sites, indicating that almost every tree canopy in the tropics may have a specialized insect fauna!

In subtropical understory vegetation in Australia, Lowman (1982) sampled insect densities that ranged from 65 to 650 per 100 m^3 throughout different months of the year. So, even in the relatively benign climates of the tropics and subtropics, insect seasonality is very pronounced. This suggests that biologists studying tropical insects need to consider many factors in their sampling design and replication: numbers and diversity of tree species, age of forest, season of year, day versus night, phenology of foliage, and weather, to name a few.

Herbivory levels are often more commonly measured in vegetation than are the insects that cause the damage. This is partly because herbivores are often hard to see, feeding only intermittently or at night. Herbivory serves as an important indicator of insect abundance, particularly in such ecosystems such as rain forests where the herbivores are especially difficult to observe and count.

Figure 10.16 Herbivory in canopies of cool temperate rain forest, dominated by Antarctic beech (*Nothofagus moorei*). Each number represents mean amount of leaf surface area removed annually by insects (%).
Data from M. Lowman.



For example, high levels of herbivory in the cool temperate rain forests of Australia led Lowman to look for the insect(s) responsible for this high defoliation. Like many aspects of field biology, searching for an insect in a complex mosaic of green foliage is equivalent to finding a needle in a haystack. Fortuitous observations led to the discovery of a new genus of chrysomelid beetle whose larvae are prolific but only during a 10-day period in spring (October) every year. This herbivore, *Novocastria nothofagi,* eats only the Antarctic beech trees that dominate the cool temperate rain forests in New South Wales. The beetle larvae emerge synchronously with the leaf emergence and defoliate over one half of the new leaves, contributing significantly to the overall 30.5% annual leaf surface removal for beech canopies (figure 10.16).

This new beetle is just one of a vast fauna of yet-to-be-discovered insects in this rain forest type alone! No one can predict the actual numbers of insects and plants becoming extinct as rain forests are continually cleared, but the urgency to document, study, and preserve the ecology and biodiversity of what remains has become an important issue of international priority today.

How many insects are found in a tree? This question appears simple and straightforward, but is actually very complicated and not well-defined. There are many logistic aspects (previously mentioned) challenging biologists who aspire to find all the insects in a tree. In addition, factors that lead to variability in the numbers of insects inhabiting a tree, as previously mentioned, the methods of counting insects in trees are not well established, and ecologists face challenges to merely locate all insects in a tree, much less count them! Some insect orders characteristically feed on leaf surfaces (Coleoptera, Hemiptera, Phasmida, and Lepidoptera larvae) and are best sampled with sweep nets or with beating trays. Other orders are often involved with temporary feeding on trees (e.g., pollinators) and occupy the air spaces between trees (Diptera, Lepidoptera, some Hymenoptera). Some insects are nocturnal and may be collected with light traps. Insects associated with the soils and roots of trees are difficult to quantify. Pitfall traps offer opportunities to collect ground insects, but once again they are not comprehensive in their ability to quantify the abundance of organisms. Insects in the wood and root systems of trees usually go uncounted. There are no comprehensive methods to measure insect abundance, although the use of sweep nets is perhaps the most widely-used technique. It is obvious that numbers of insects in trees are vastly underestimated.

Fogging is perhaps the most comprehensive method of documenting the numbers of insects on trees. It involves the dispersal of an insecticide throughout the upper tree canopy, usually with a spraying device. The insects are collected on sheets at ground level after the insecticide has been effective. The sampling technique requires windless conditions with careful attention paid to season, time of day, and forest structure and composition for replication. This method fails to collect insects in the bark and roots, and may underestimate numbers of large insects that may be more resistant to insecticide.

The paradox of insect outbreaks and forest trees is a vast and complex topic, summarized in an entire volume (Barbosa and Schultz 1987). Trees are sessile, long-lived, and extremely reliable food sources for insects, particularly in forests where the amount of foliage ranges from 1–9 t ha^{-1} yr^{-1} (Van Cleve et al. 1983). More than 120 lepidopteran species feed upon *Quercus robur,* yet very few reach outbreak levels (Feeny 1970). Insects are very fecund and are renowned for their ability to adapt to large persistent food supplies (agricultural fields, trees), so it is surprising that outbreaks are not more commonplace. Of the vast numbers of herbivores on western American trees, only 31 species are considered pests (Furniss and Carolin 1977). Only 16 of these are defoliators (with 15 as feeders in bark or wood), and three of the 16 are introduced (e.g., gypsy moth). The number of native pests on this apparently abundant food supply is extremely low!

Whether or not insects are considered pests is an *anthropocentric* (human-centered) view, and oftentimes the fluctuations in insect numbers are a consequence of human activities. The eucalypt dieback in Australia and the gypsy moth outbreaks in the eastern United States are good examples. As long as insects continue to fluctuate in numbers over time and space and as long as they continue to compete with humans as herbivores, we will continue to study the complex interactions of insects on plants.