4 Plant and herbivore interactions

In their classic paper entitled "Butterflies and plants: a study in coevolution," Ehrlich and Raven (1964) envisioned an "arms race" between plants and herbivores, whereby each player exerted reciprocal selective pressure on the other that resulted in evolutionary change. Thus, the arms race between plants and herbivores emphasizes an ongoing reciprocal interplay with plants erecting defenses, herbivores breaking defenses with novel offenses, plants countering with new defenses and so on through evolutionary time (Mitter *et al.* 1991, Herrera and Pellmyr 2002, Thompson 2005). Moreover, "breakthroughs" in plant defense or herbivore offense are thought to create "adaptive zones" that promote speciation, lineage diversification and thus the generation of biodiversity. However, an apparent dilemma arises because plants in general have longer generation times and lower recombination rates than their insect herbivores (and especially plant pathogens), which should hinder their ability to keep pace in the evolutionary arms race (Whitham 1983). Yet, plants have clearly done so.

While the concepts of arms races and coevolution are useful as an overall theme in this chapter, we do not wish to imply that coevolution is a general phenomenon in the interaction between plants and insect herbivores. Strong cases can be developed for coevolution among mutualists (Chapter 6) and parasite–host relationships (Chapter 8), but there is a shortage of sound evidence that insect herbivores have impacted plant traits in a coevolutionary manner (Futuyma and Agrawal 2009).

In this chapter, we will explore the issue of plant–herbivore interactions in much greater depth and attempt to resolve the apparent disadvantage of plants in their arms race with herbivores. Before doing so, however, we need to learn far more about the players themselves, examine the effects of plants on herbivores at the individual and population levels, and discover more about the complex world of plant–insect interactions. Toward this end, we will elaborate on the incredible taxonomic and ecological diversity of insect herbivores and their variable feeding styles, investigate the barriers (e.g., nutrition and allelochemistry) that plants pose to herbivore attack, explore the counter-ploys herbivores have evolved to overcome plant defenses, visit plant defense theory, determine how herbivores and plants affect each other's distribution and abundance, and examine how such information might be exploited to better manage pest herbivores in agricultural and forest systems. The latter is particularly crucial, given that billions of dollars of potential crop yield are lost directly (herbivory) and indirectly (vectors of plant pathogens) to the feeding activities of insect herbivores (Allard *et al.* 2003, Oerke 2006).

4.1 Taxonomic occurrence of phytophagy

At least half of the estimated 2–10 million described species of extant insects are herbivores (phytophages), feeding on living plant material (Southwood 1973, Speight *et al.* 1999, 2008, Gullan and Cranston 2005, Triplehorn and Johnson 2005). Moreover, fossil evidence for the occurrence of phytophagy (e.g., herbivory, leaf mines, galls and the galleries of wood borers) dates far back in geologic time with numerous records in the Triassic (220 MYA) and Carboniferous (330 MYA) Periods, suggesting that this feeding style is indeed an ancient one (Labandeira and Phillips 1996, Labandeira 2002). Despite the richness of phytophagous species, the habit of herbivory occurs predominantly in only nine of the 29 orders of insects: Orthoptera (grasshoppers and relatives), Phasmatodea (stick insects), Thysanoptera (thrips), Hemiptera (e.g. true bugs, leafhoppers, planthoppers, aphids and scale insects), Psocoptera (bark lice), Coleoptera (beetles), Hymenoptera (sawflies), Lepidoptera (butterflies and moths) and Diptera (flies). Notably, most species of Lepidoptera and Phasmatodea (>95%) and the majority of Orthoptera, Thysanoptera and Hemiptera taxa (>80%) are phytophagous, with a lower incidence of herbivory in the Coleoptera (~35%), Diptera (~30%) and Hymenoptera (~15%). If one includes insect species that consume dead or dying plant material (detritivores, decomposers and shredders) in the category of "herbivores," then the prevalence of phytophagy increases substantially, as this feeding habit occurs in the three orders of non-insect Hexapods (Protura, Diplura and Collembola) as well as in 16 orders of insects. Of the terrestrial detritivores, the most noteworthy by far are the wood-feeding Isoptera (termites), whereas in aquatic systems Trichoptera (caddisflies), Plecoptera (stoneflies) and Diptera (flies) often dominate the feeding assemblage.

4.2 Diet breadth, feeding strategies and herbivore guilds

Most plant species support complex assemblages of herbivores that collectively exploit almost every plant part (Figure 4.1). Synthesizing the incredible diversity of feeding styles and foraging strategies of insect herbivores is a daunting task, but can be simplified by categorizing herbivores according to their **diet breadth** (host-plant range) and **feeding guild** (a group of species exploiting the same resource in a similar manner; *sensu* Root 1973, 2001). Regarding host range, insect herbivores can be **monophagous** (specialists that feed on a single plant

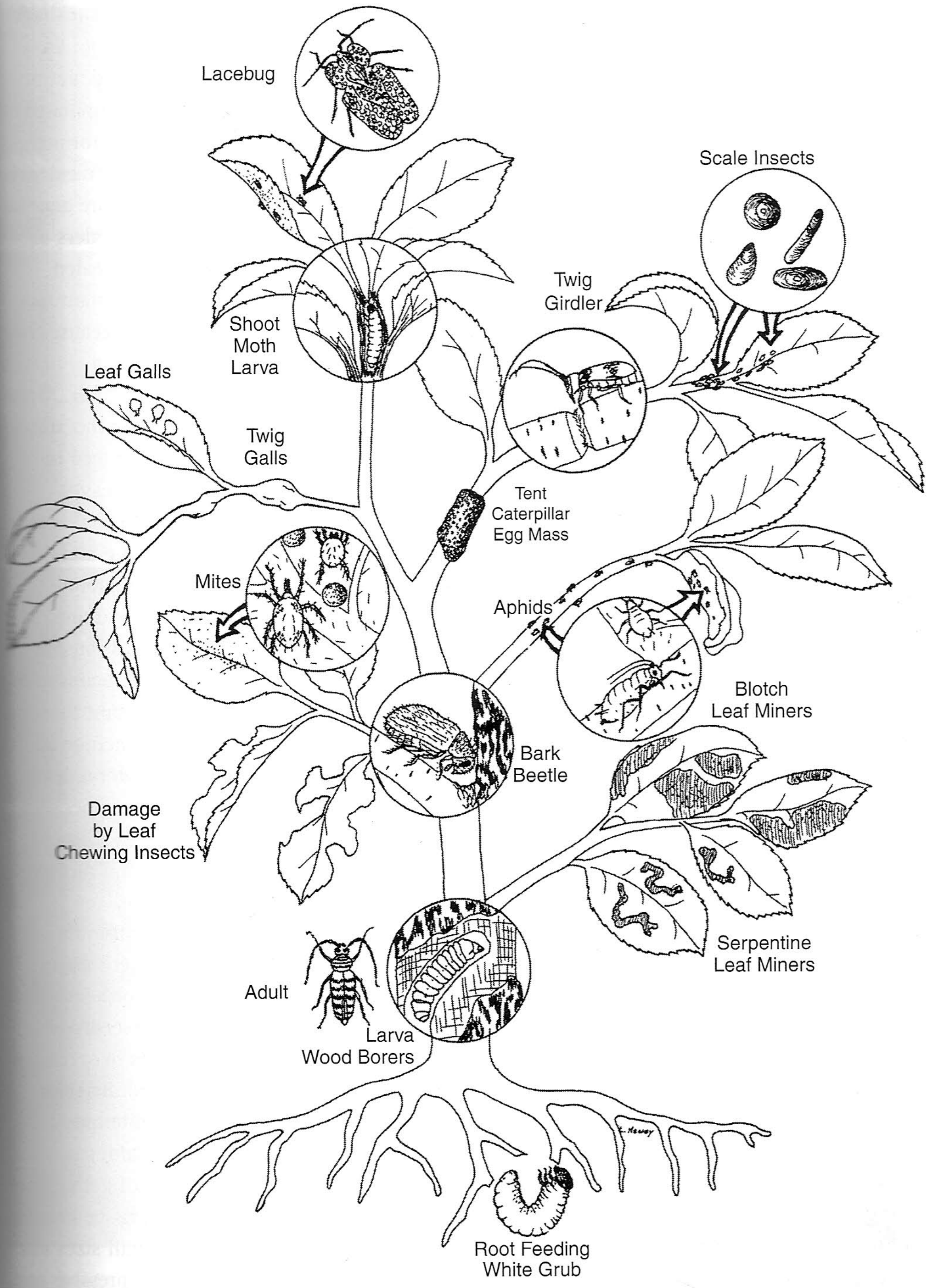

Figure 4.1 Feeding guilds of herbivorous insects and mites that can co-occur on a single host tree including sap-feeders (aphids, scale insects, lacebugs and mites), free-living leaf chewers (tent caterpillars and twig girdlers), leaf miners (blotch and serpentine), borers (shoot moth, bark beetle and wood borer), gall inducers (leaf and twig galls) and root feeders (white grubs). From Johnson and Lyon (1991).

species or plants in the same genus), **oligophagous** (species that feed on plants in several genera, but within the same family) or **polyphagous** (generalists that exploit plants in more than one family) (Strong *et al.* 1984a, Bernays and Chapman 1994). Using swallowtail butterflies as an example, the Oregon swallowtail (*Papilio oregonius*) is monophagous, feeding exclusively on the composite *Artemisia dracunculoides* throughout its range, the short-tailed swallowtail (*Papilio brevicauda*) is oligophagous feeding on several genera of plants in the Apiaceae and the anise swallowtail (*Papilio zelicaon*) is polyphagous exploiting 69 plants in 32 genera in two plant families (Thompson 1998). The fall webworm (*Hyphantria cunea*) and gypsy moth (*Lymantria dispar*) are extremely polyphagous, feeding on over 600 plant species representing dozens of plant families (Miller and Hanson 1989). Complicating matters of diet breadth determination is the fact that herbivores can be locally monophagous, but geographically polyphagous, whereby they specialize on different host-plant taxa elsewhere in their geographic range (Singer and Wee 2005).

Historically, the perception has been that most insect herbivores are monophagous (>70% of species), but this view is based largely on regional assessments of specific taxa such as aphids, planthoppers, butterflies and agromyzid flies, mostly from temperate latitudes (Wilson *et al.* 1994, Dixon 1998, Janz *et al.* 2001). Recent evidence for assemblages of tropical insect herbivores suggests that levels of monophagy may be lower than temperate estimates, at least for some taxa (Basset *et al.* 1996, Mawdsley and Stork 1997, Ødegaard *et al.* 2000). Later in this chapter, factors that enhance or constrain diet breadth, influence host shifts and promote speciation and diversification will be considered.

Insect herbivores can be characterized by their feeding strategy or **guild**, and indeed they exhibit an incredible array of feeding styles on living, dying and dead plant resources (Kirby 1992, Gullan and Cranston 2005, Figure 4.2). Feeding guild is ultimately affected by a variety of factors, including mouthpart type (chewing versus piercing-sucking), the microhabitat where herbivores feed (e.g., leaves, stems, bark, roots, fruits, seeds, dead wood, detritus and fungi), and how plant material is manipulated or processed (e.g., leaf tiers, leaf rollers, gall formers, shredders, collectors and scrapers). For convenience, feeding strategies can be grouped into more general categories such as **chewers** versus **sap-feeders** or **free-living feeders (exophages)** and **concealed feeders (endophages)**. Notably, it is important to distinguish particular herbivore guilds, because they often respond differently to plant nutrition, allelochemistry and natural-enemy attack (e.g., Gross 1991, Inbar *et al.* 1999a, Huberty and Denno 2004).

Of the **free-living chewers**, those that feed in exposed locations on the plant (e.g., on leaves, flowers, pollen, seed heads and fallen seeds), Lepidoptera and Coleoptera are by far the most diverse and abundant followed by Orthoptera (grasshoppers), Hymenoptera (sawflies and ants) and Phasmatodea (stick insects) (Gullan and Cranston 2005). Many chewing insects also feed in concealed locations within living, dying or dead plant tissues. Important guilds of **concealed feeders** include **leaf tiers** (Lepidoptera), **leaf rollers** (Lepidoptera), **leaf miners** that feed internally between the upper and lower epidermis (Lepidoptera, Coleoptera, Diptera, Hymenoptera), **stem borers** (Lepidoptera, Coleoptera, Hymenoptera), **wood borers** (Coleoptera, Lepidoptera, Hymenoptera) that feed within the branches or trunks of woody plants where they consume the bark, cambium, sapwood or heartwood, **fruit borers** (Diptera, Lepidoptera) and **seed/pod borers** that feed internally within seeds or seed pods (Coleoptera, Lepidoptera, Hymenoptera). By their feeding and oviposition activity, mandibulate herbivores (Hymenoptera, Diptera, Lepidoptera and Coleoptera) also induce the formation of galls (structures arising from aberrant plant tissue growth) in which they reside. The diversity of gall sizes and shapes produced by **gall-inducers** is impressive and galls can be induced on most plant tissues. Mandibulate **root feeders** (Lepidoptera, Coleoptera,

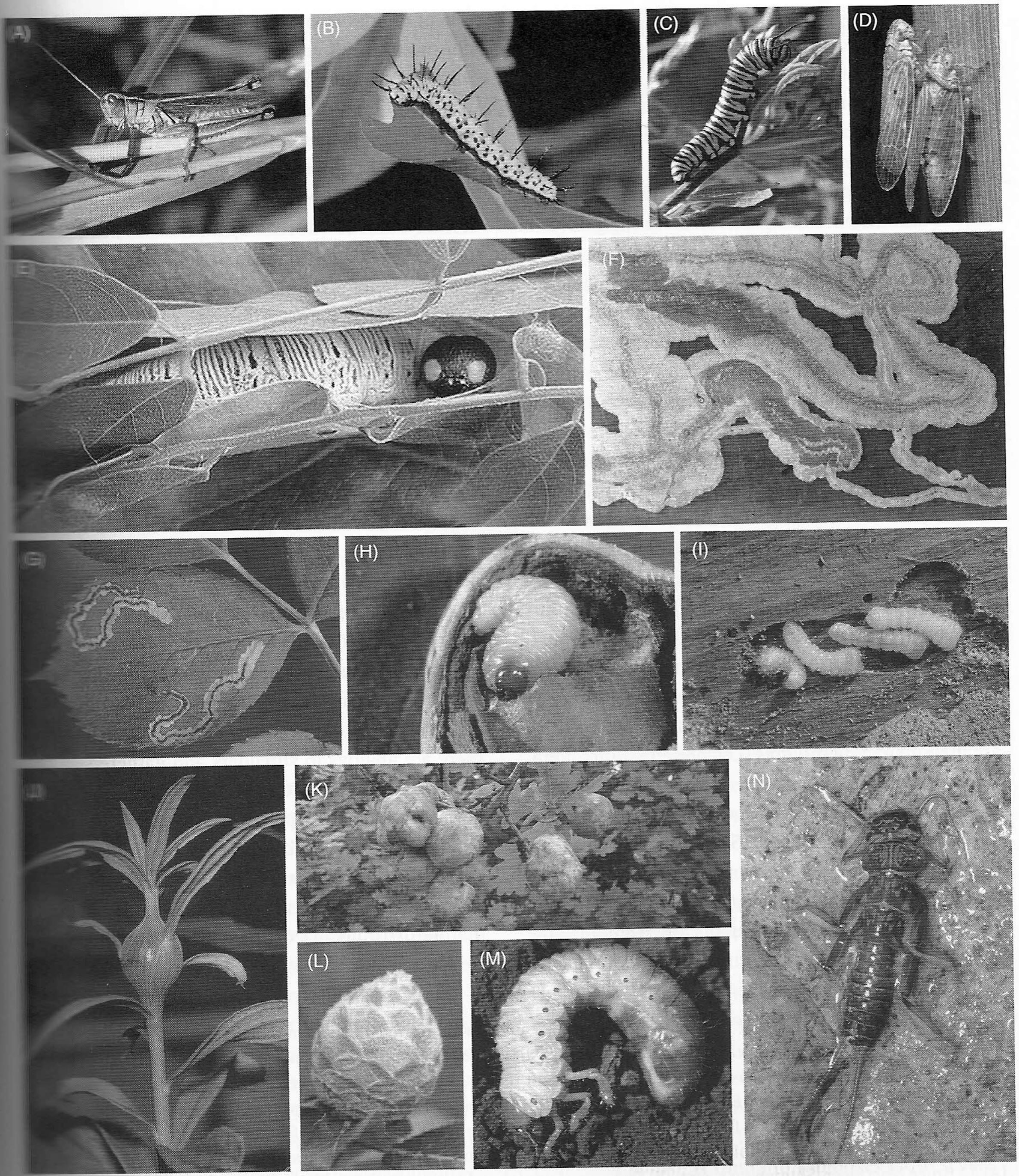

Figure 4.2 Diversity of feeding guilds represented by insect herbivores. Free living mandibulate herbivores include (A) a grasshopper, (B) lepidopteran larva, *Heliconius charitonius*, and (C) caterpillar of the monarch butterfly *Danaus plexippus*. (D) Free-living sap-feeders such as the planthopper *Prokelisia marginata* also feed in exposed positions. Concealed feeders,

Diptera) can be considered concealed feeders simply because they reside in the soil. However, some species feed internally within roots as borers (some Lepidoptera), whereas others feed externally (Coleoptera such as scarab beetles and weevils).

Free-living **sap-feeders** (Hemiptera, Thysanoptera) feed by inserting their stylets into various plant tissues and they are categorized accordingly as **phloem feeders** (e.g., aphids, planthoppers, treehoppers, leafhoppers, scale insects), **xylem feeders** (cicadas, spittlebugs) and **epidermis/mesophyll/parenchyma feeders** (heteropterans and thrips) that insert their mouthparts into non-vascular tissues (Gullan and Cranston 2005). Numerous sap-feeders are also notorious **gall-inducers** (Hemiptera and Thysanoptera), and like their mandibulate counterparts, they (aphids, psyllids and thrips) induce an incredible variety of gall architectures. Several groups of sap-feeders (aphids, mealybugs and scale insects) also feed externally on roots beneath the soil surface.

In aquatic systems, feeding guilds of herbivorous/detritivorous insects are pigeonholed more into functional groups (Merritt and Cummins 1996, Barbour *et al.* 1999, Gullan and Cranston 2005). There are mandibulate herbivores (Lepidoptera, Coleoptera, Diptera) and a few sap-feeders (Hemiptera such as water boatman) that feed externally or internally on living macrophytes or algae. **Shredders** (some Plecoptera, Trichoptera, Coleoptera and Diptera) feed on living or decomposing plant tissues. **Collectors** feed on plant fragments and decomposing bits of organic matter smaller than those usually consumed by shredders. Collectors are often divided into **filter feeders** that strain minute particles from the water column (e.g., blackfly larvae and net-building Trichoptera) and **gatherers** that feed on organic matter on the streambed (several Ephemeroptera, Coleoptera, Trichoptera, Diptera). Notably, shredders break up detritus into smaller fragments, making it available for collectors. **Scrapers** (Ephemeroptera, Coleoptera, Trichoptera, Lepidoptera and Diptera) graze on surface vegetation or on algae that is attached to submerged substrates. Many of the feeding guilds of aquatic insects are omnivorous and consume a variety of microorganisms along with the plant material they ingest.

Terrestrial detritivores, decomposers and dead-wood feeders (e.g., Collembola, Isoptera, Blattodea, Coleoptera) are not often subdivided into feeding guilds, even though they occupy a huge diversity of microhabitats above and below the soil surface (Kirby 1992). Perhaps part of the difficulty in sorting soil and wood-dwelling groups into feeding guilds is that, like their aquatic counterparts, many groups are omnivorous, consuming various combinations of detritus, fungi and dead arthropods. Nonetheless, there are analogs to shredders and gatherers in that larger species (e.g., Isoptera, Coleoptera) process detritus into smaller pieces and fecal material that can then be handled by smaller consumers (e.g., Collembola) (Gullan and Cranston 2005).

From this discourse, it would be wrong to conclude that herbivorous insects are easily pigeonholed into

Caption for Figure 4.2 (*cont.*)
such as (E) the leaf-tying larva of the silver-spotted skipper *Epargyreus clarus*, (F) a leaf-mining larva feeding inside a mangrove leaf, (G) a serpentine leaf miner, (H) the seed-feeding weevil *Curculio nucum* in a hazel nut and (I) wood-boring cerambycid beetle larvae, all feed internally in various plant tissues. Gall inducers, such as (J) the tephritid fly *Eurosta solidaginis*, (K) the cynipid wasp *Biorhiza pallida* and (L) the cecidomyiid fly *Rhabdophaga strobiloides* are also concealed feeders. A great diversity of root-feeders such as (M) the white grub *Melolontha vulgaris* feed beneath the soil surface. Shredders, such as (N) a nymph of a stonefly, feed on living or decomposing plant tissues in aquatic habitats. Photo credits: (A) © Bruce MacQueen/Shutterstock.com, (B) Steve Kaufman/photolibrary, (C) © Ron Rowan Photography/ Shutterstock.com, (D) © Dwight Kuhn, (E) Dale Clark, Dallas County Lepidopterists' Society, (F) Kevin Schafer/photolibrary, (G) Geoff Kidd/photolibrary, (H) Bartomeu Borrell/photolibrary, (I) Keith Douglas/photolibrary, (J) Warren Abrahamson, (K) Brian Hainault, (L) Daniel Mosquin, (M) ©iStockphoto.com/fotosav, (N) Martin Siepmann/photolibrary. See color plate section.