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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

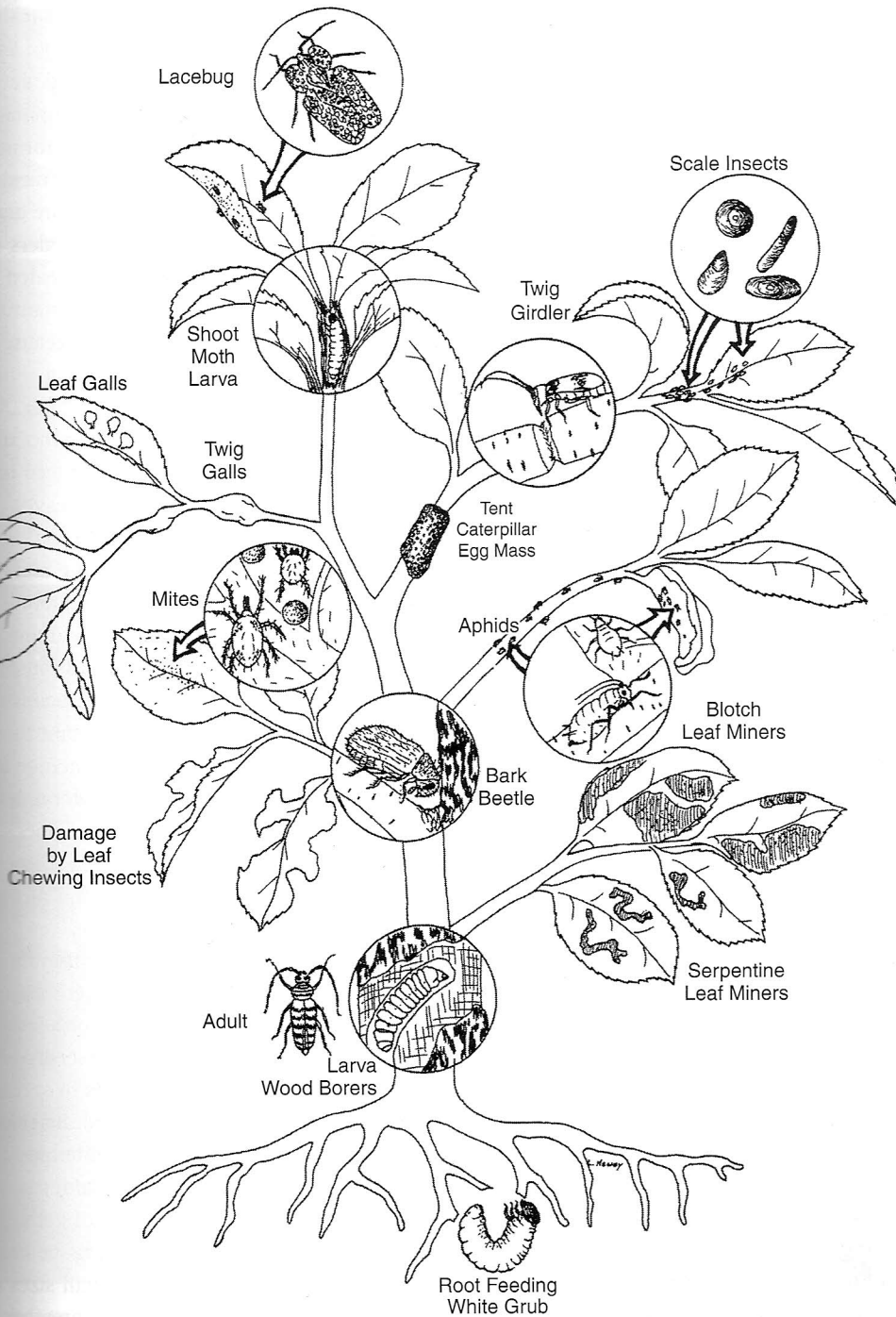


Figure 4.1 Feeding guilds of herbivorous insects and mites that can co-occur on a single host tree including sap-feeders (aphids, scale insects, lacebugs and mites), free-living leaf chewers (tent caterpillars and twig girdlers), leaf miners (blotch and serpentine), borers (shoot moth, bark beetle and 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,

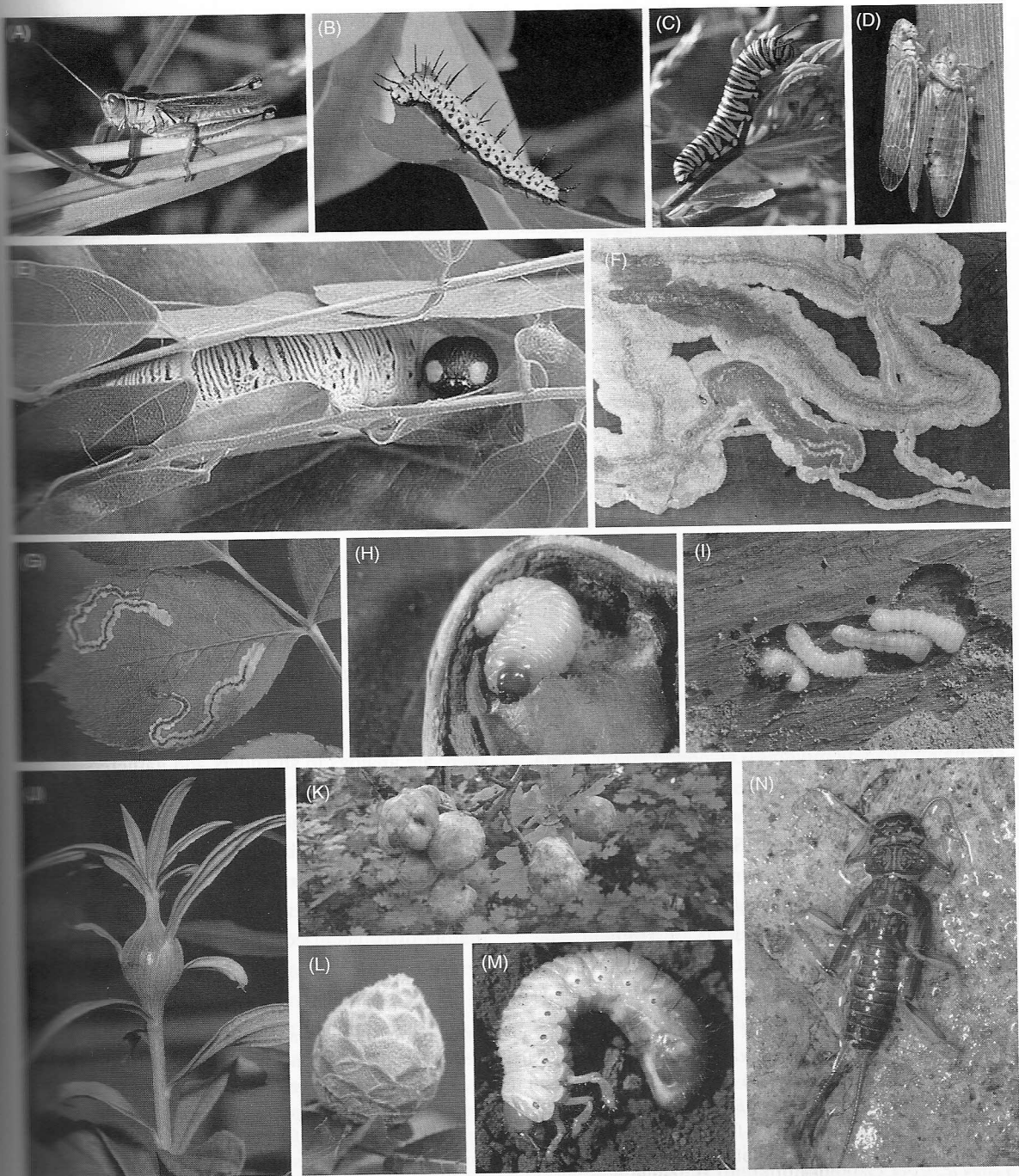


Figure 4.2 Diversity of feeding guilds represented by insect herbivores. Free living mandibulate herbivores include (A) a grasshopper, (B) lepidopteran larva, *Heliconius charitonius*, and (C) caterpillar of the monarch butterfly *Danaus plexippus*. Free-living sap-feeders such as the planthopper *Prokelisia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

discrete feeding guilds. For instance, within taxonomic groups there are species that feed in different niches, such as aphids on leaves, stems, bark and roots (Dixon 1998) and lepidopteran representatives that can be assigned to virtually all mandibulate feeding guilds like free-living folivores, leaf miners and rollers, wood borers, seed feeders, detritivores and even predators (Covell 1984, Powell *et al.* 1998). Moreover, within a single species, there can be changes in feeding guild throughout development such as occur when miners shift to become free-living folivores and when sap-feeders switch from mesophyll to phloem feeding (Powell *et al.* 1998, Lamp *et al.* 2004). Nonetheless, categorizing herbivores into specific feeding guilds lends organization to the diverse array of feeding strategies that exists for insect herbivores. During the course of evolutionary time, phylogenetic analysis reveals changes in the feeding strategy of numerous herbivorous insect groups (e.g., from concealed to external feeding in the Lepidoptera) (Powell *et al.* 1998) and later in this chapter we will explore underlying causes and the opportunities such shifts offer for radiation and diversification.

4.3 Plant barriers to herbivore attack

Even though half of the world fauna of insects is phytophagous, the restricted occurrence of phytophagy as a predominant feeding habit to only 9 (~30%) of the 29 insect orders (Southwood 1973, Ødegaard 2000, Gullan and Cranston 2005) suggests that plants have evolved formidable barriers to insect attack. These barriers include nutritional constraints, mechanical and allelochemical defenses, defensive forces of natural enemies, and features of plant phenology and spatial distribution that render plants inherently difficult to exploit. We will explore each of these obstacles in due course, but suffice it to say for now that once plant barriers are overcome, the evolution of phytophagy vastly accelerates herbivore diversification (Mitter *et al.* 1988, 1991, Winkler and Mitter 2007).

4.3.1 Plant nutrition, ecological stoichiometry and constraints on phytophagous insects

Ecological stoichiometry, the study of the relative balance of key elements in organisms from different trophic levels, provides an integrative approach for analyzing plant–herbivore interactions and specifically the constraints that nutrient-deficient food places on consumers (Elser *et al.* 2000, Fagan *et al.* 2002, Sterner and Elser 2002). All organisms are composed of the same major elements, namely carbon (C), nitrogen (N) and phosphorus (P), but the relative balance of these elements differs dramatically among organisms occupying different trophic levels. Importantly, nutritional imbalances created by organisms feeding at lower trophic levels on nutrient-deficient (N and P) food can severely hamper their ability to meet nutrient demands, grow and reproduce. For example, insect herbivores and detritivores have strikingly higher nitrogen (~10% N) and phosphorus (~0.5% P) contents than their host plants (~2% N, ~0.05% P) or detrital resources (~2% N, ~0.03% P) (Elser *et al.* 2000, Fagan *et al.* 2002, Cross *et al.* 2003, Denno and Fagan 2003). Historically, the stoichiometric mismatch in N content (%) and C:N ratio between plants and insect herbivores has been recognized for decades as imposing fundamental limitations on nitrogen acquisition (McNeill and Southwood 1978, Mattson 1980, White 1993, Awmack and Leather 2002, Matsumura *et al.* 2004, Figure 4.3A–C). Similarly, phosphorous limitation has been shown to have widespread effects in aquatic systems (Sterner and Elser 2002), but only recently has it been shown to adversely affect terrestrial insect herbivores (Schade *et al.* 2003, Perkins *et al.* 2004). In one case where N and P limitations have been compared in the same insect (the planthopper *Prokelisia dolus*), N limitation imposes more severe constraints on growth (Huberty and Denno 2006b), but more studies are needed to confirm any general pattern.

(A)

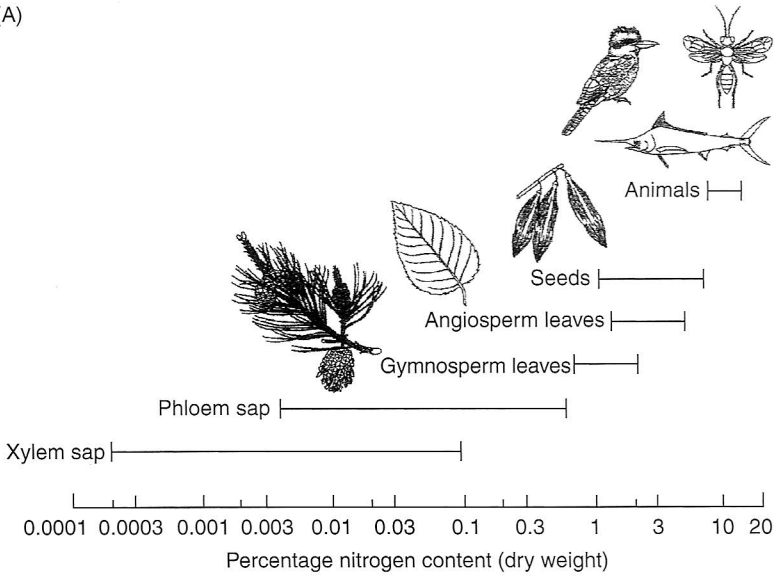
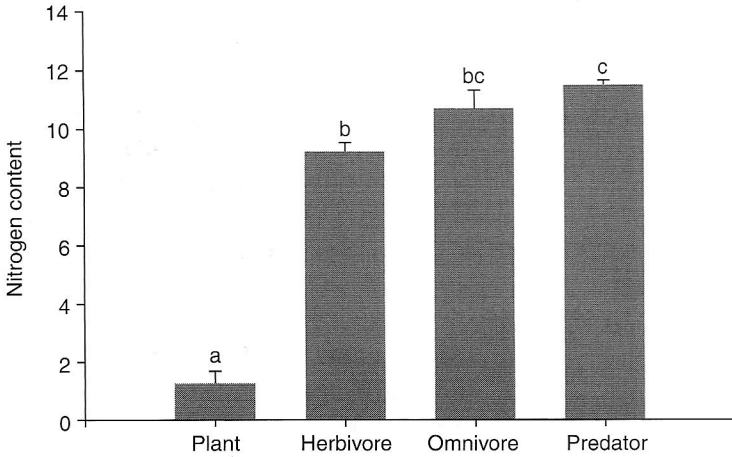
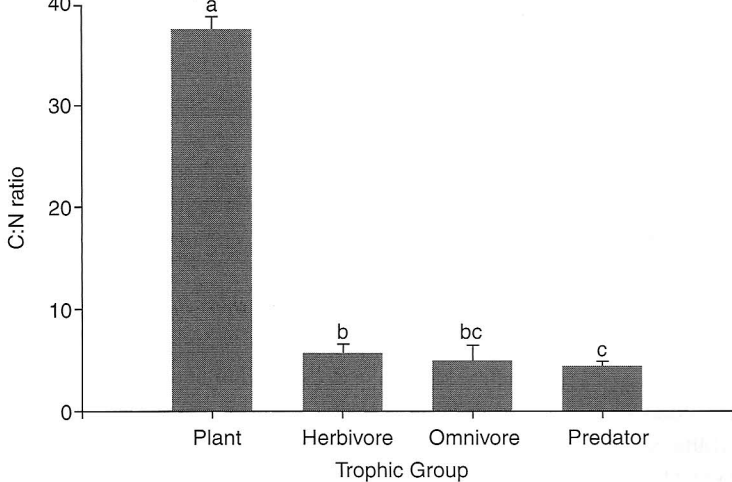


Figure 4.3 (A) Nitrogen content of plant tissues and animals. Original from Mattson (1980); adopted from Speight *et al.* (1999). Nitrogen content (B) and C:N ratio (C) of plants, herbivores, omnivores and predators. Notice the increase in N content and decrease in C:N ratio moving up the food chain from lower to higher trophic levels. From Matsumura *et al.* (2004).

(B)



(C)



The nutritional mismatch between plants and herbivorous insects persists even though there is considerable variation in the nitrogen content of the different plant groups and plant tissues they exploit (Mattson 1980, Slansky and Scriber 1985, Fagan *et al.* 2002, Figure 4.3A). Of all plant tissues, dead wood and the sap of vascular tissues (xylem and phloem) have the lowest concentrations of nitrogen, whereas reproductive structures, especially seeds, have the highest reported concentrations. The nitrogen content of detritus is also exceptionally low, but can be enhanced when it is enriched with fungi and bacteria (Slansky and Scriber 1985, Cross *et al.* 2003). Overall, phytophagous insects face two obvious problems; not only must they obtain critical nutrients (N and P) from nutrient-poor food, but they must also process and eliminate excess amounts of carbon in doing so (Raven 1983, White 1993, Elser *et al.* 2000). For active consumers that use carbon-based energy for foraging or dispersal, the need to eliminate carbon to achieve elemental balance may be less (Stern and Elser 2002, Denno and Fagan 2003).

Nitrogen and phosphorus limitation have been featured in studies of phytophagous insect nutrition due to their fundamental roles in protein and RNA synthesis, and maintaining elemental balance (C:N:P) in an organism is essential for metabolism and cell function (Stern and Elser 2002). Despite elemental mismatches between herbivorous insects and their host plants, herbivores are able to maintain their elemental body composition, at least to some degree, via homeostatic mechanisms. Homeostatic regulation in phytophagous insects occurs by the selective uptake, assimilation, storage and excretion of nutrients (Darchambeau *et al.* 2003, Trier and Mattson 2003). A noteworthy case involves sap-feeders (hemipterans such as aphids, leafhoppers and scale insects) that feed in phloem or xylem tissues where they encounter very low concentrations of nitrogen and much higher levels of sugars in the cell sap (Dixon 1998). Homeostasis is achieved by the selective retention of amino nitrogen and elimination of

excess sugars as honeydew, a process that is achieved by a unique midgut arrangement known as a filter chamber whereby most sugar-rich liquid bypasses the absorptive midgut and is excreted. However, homeostasis does not occur without cost, which explains why there are such severe growth penalties when herbivores develop on nutrient-poor foods (Stern and Elser 2002, Raubenheimer and Simpson 2004).

Given that herbivorous insects are fundamentally nitrogen limited, it is not surprising that elevated host plant quality (%N), either that which occurs naturally or via nitrogen fertilization, can promote increased growth, reproduction and remarkable population outbreaks (McNeill and Southwood 1978, Mattson 1980, Cook and Denno 1994, Herms 2002). However, not all feeding guilds respond similarly to elevated plant nutrition nor do species within the same guild (Scriber 1984, Kytö *et al.* 1996, Awmack and Leather 2002). In general, sap-feeders (e.g., aphids, planthoppers, leafhoppers, scale insects and mirid plant bugs) show consistent population increases on N-enriched host plants, whereas chewing herbivores (e.g., beetles, caterpillars and sawflies) range the gamut of responses including increases, decreases and no change (McNeill and Southwood 1978, Mattson 1980, Strauss 1987, Kytö *et al.* 1996, Awmack and Leather 2002, Denno *et al.* 2003). Unlike mandibulate herbivores, sap-feeders may be more responsive to enhanced plant nitrogen because they feed in vascular tissues, where they benefit from increased soluble nitrogen and yet avoid elevated levels of N-based allelochemicals (e.g. HCN) that are compartmentalized in other leaf tissues (Raven 1983, Huberty and Denno 2004). Likewise, the high reproductive potential characteristic of many sap-feeders may promote their escape from natural enemies on N-enriched host plants, a factor that can compromise potential population increases of slower-growing herbivores. Within the same feeding guild (e.g., leafhoppers and delphacid planthoppers), variable population responses of herbivores to N-enriched host plants have been attributed to

species-specific differences in colonization ability, feeding compensation and the level of plant nitrogen at which maximum nitrogen utilization efficiency is achieved (Prestidge 1982, Prestidge and McNeill 1982, Denno *et al.* 2002, Huberty and Denno 2006a).

Although responses of insect herbivores to plant nitrogen can be compromised at the population level by other factors, there is widespread support for the adverse effects of nitrogen limitation on performance at the individual level (Strong *et al.* 1984a, White 1993, Awmack and Leather 2002). There are many examples showing that phytophagous insects in general survive better, grow faster, molt into larger adults and are more fecund if they develop on nitrogen-rich host plants. Their increased performance on N-rich plants is often attributed to increased feeding rates and enhanced nitrogen assimilation and growth efficiencies (Mattson 1980, Slansky and Scriber 1985, Awmack and Leather 2002). Moreover, the extremely slow growth rates (years) of dead-wood borers (cerambycid and buprestid beetles, moths and wood wasps), several aquatic detritivores (stoneflies) and some xylem feeders (17 and 13 year cicadas), all groups that feed on extremely nitrogen-poor food resources, provide further testament to nitrogen limitation (Iverson 1974, Pritchard and Berté 1987, Motomori *et al.* 2001).

Although ecological stoichiometry provides a broad context for highlighting the general nutritional constraints that consumers face, it does not emphasize important details such as the appropriate form of the macronutrient ingested (e.g., nitrogen-containing toxins), amino acid balance in the diet or the need for non-synthesizable nutrients (e.g., sterols required for molting hormone) and limiting trace elements and water-soluble vitamins (e.g., thiamine, riboflavin and ascorbic acid), all of which are necessary for metabolism and development (Prestidge and McNeill 1982, Bernays and Simpson 1990, Singer *et al.* 2002, Singer and Bernays 2003). Moreover, the water content of plants affects cell turgor pressure and the ability of sap-feeders to

access plant nitrogen (Huberty and Denno 2004). Similarly, the nitrogen utilization efficiency of chewing herbivores is often diminished under conditions of lowered foliar water content (Slansky and Scriber 1985). Thus, plant condition such as water content and other dietary factors can hinder herbivore performance beyond the general constraints imposed by contrasts in macronutrient stoichiometry with their host plant (Scriber and Slansky 1981).

4.3.2 Coping with nutrient-deficient host plants

Because insect herbivores are inherently nutrient limited, they have evolved a variety of adaptations or feeding strategies that maximize encounters with nutrient-rich resources or buffer them against nutrient deficiencies in their diet (McNeill and Southwood 1978, Cook and Denno 1994, Karban and Agrawal 2002). These adaptations can be organized into six general categories:

- (1) Feeding compensation
- (2) Selection of nitrogen-rich feeding sites and/or diet mixing
- (3) Life-cycle synchronization with nutrient-rich resources
- (4) Manipulation of plant physiology by forming nutrient sinks
- (5) Obtaining nitrogen from non-plant sources
- (6) An evolutionary shift in body nutrient composition.

Feeding compensation: By increasing their feeding rate on nitrogen-deficient plant resources, insect herbivores can partially offset the problem of satisfying their nutrient demands, a phenomenon which occurs in a wide diversity of sap-feeders (Hemiptera: aphids, planthoppers and leafhoppers), chewing herbivores (Orthoptera, Coleoptera, Lepidoptera and Hymenoptera) and detritivores (Plecoptera and Trichoptera) (Iverson 1974, McNeill and Southwood 1978, Bernays and Simpson 1990,

Simpson and Simpson 1990, Slansky 1993, Yang and Joern 1994, Kause *et al.* 1999, Swan and Palmer 2006). Feeding compensation, however, is not a completely effective solution to problems of nutrient acquisition because of physiological constraints such as gut capacity and throughput time that limit the degree to which eating more can compensate for eating nutrient-poor food (Simpson and Simpson 1990). For instance, correlated with increased feeding rate on nutrient-deficient food are a shorter gut-retention time and often decreased digestion and nitrogen assimilation. Moreover, increasing consumption rate to compensate for a deficiency in one nutrient may lead to an excess of other carbon-rich compounds or dietary toxins that can negatively affect growth and survival (Slansky and Wheeler 1992, Awmack and Leather 2002). Also, if feeding compensation results in delayed development, then herbivores may also experience higher exposure to natural enemies, the so-called slow-growth-high-mortality hypothesis (Price *et al.* 1980, Benrey and Denno 1997, Kaplan *et al.* 2007).

Selection of nitrogen-rich feeding sites and diet mixing: Specialized sap-feeders that are generally less affected by compartmentalized allelochemicals show very strong preferences for nitrogen-rich feeding sites (Mattson 1980, Cook and Denno 1994, Awmack and Leather 2002). Feeding sites where high concentrations of nitrogen occur include actively growing meristems, young leaves, inflorescences, pods, seeds and senescing leaves, and sap-feeders such as aphids often aggregate at these sites, where their performance is dramatically enhanced. Many sap-feeders also shift their feeding position from low- to high-nitrogen sites with the seasonal decline in leaf nitrogen that occurs in many plant species (McNeill and Southwood 1978, Scriber and Slansky 1981). A frequent spatial shift is from leaves to more nitrogen-rich inflorescences or seed heads with the onset of flowering. Chewing folivores (Lepidoptera, Coleoptera, Hymenoptera) show more variable responses than sap-feeders with regard to selecting the most nitrogen-rich feeding sites on a plant,

namely young compared to mature leaves (Raupp and Denno 1983). In general, specialist defoliators, which are better adapted than generalists to deal with allelochemicals concentrated in young leaves, show stronger feeding preferences for nitrogen-rich young leaves, but there are exceptions (Raupp and Denno 1983, Awmack and Leather 2002). Although performance is often potentially greater on nitrogen-rich plant tissues, specialized herbivores do not always select such sites for oviposition or feeding because performance is compromised by high concentrations of performance-reducing allelochemicals, increased risk of enemy attack or because herbivores forage selectively elsewhere on the plant for toxins that they sequester for defense (Damman 1987, Awmack and Leather 2002).

Among polyphagous herbivores, such as many grasshoppers and lepidopterans, there is certainly evidence that high-nitrogen diets are selected to meet nutrient demands (Bernays and Simpson 1990, Joern 2000, Awmack and Leather 2002). Similarly, many detritivores like the leaf-shredding caddisfly *Hydatophylax* selectively colonize high-nitrogen litter over less nutritious choices (Cummins and Klug 1979, Motomori *et al.* 2001). However, diet mixing (feeding on more than one plant species or food resource) is a common feeding strategy in many herbivorous insects (e.g., numerous grasshoppers and caterpillars) and detritivores as well (e.g., stoneflies and caddisflies) (Joern 2000, Behmer *et al.* 2001, Singer and Bernays 2003, Swan and Palmer 2006). Some herbivores (e.g., many grasshoppers) and detritivores (e.g., stoneflies), and predators for that matter, in fact grow faster and exhibit higher fitness on mixed compared to single-resource diets (MacFarlane and Thorsteinson 1980, Mayntz *et al.* 2005, Swan and Palmer 2006), whereas others do not (several heteropterans and lepidopterans) (Bernays and Minkenberg 1997). Diet-mixing theory, in partial contrast to ecological stoichiometry, emphasizes achieving dietary balance by foraging selectively on limiting macro-nutrients such as protein and carbohydrate (Behmer *et al.* 2001, Raubenheimer and

Simpson 2004, Raubenheimer and Jones 2006). Grasshopper species, for instance, grow best on diets composed of a specific proportion of protein and carbohydrate, their so-called nutritional "intake target." When fed diets deviating in protein-carbohydrate composition from their intake target, performance is reduced. So, it is not surprising that grasshoppers forage selectively on a dietary smorgasbord of protein and carbohydrate choices to achieve their intake target, although targets do differ among species.

Diet mixing theory extends from **optimal-diet theory**, which itself stems from **optimal-foraging theory** (Sih and Christensen 2001). The essential predictions of optimal-diet theory are that foragers should conform as follows:

- (1) They should prefer food items that yield more energy per unit handling time.
- (2) Individuals should drop low-value items from their diet as higher-value options become available.
- (3) They should obey a quantitative threshold rule as to when specific food types should be included or excluded from the diet (Charnov 1976, Sih and Christensen 2001).

The observation that diet mixing can be more beneficial to consumers than simply feeding on the most nitrogen-rich resource challenges the more singular focus of ecological stoichiometry and has led to a multitude of multifaceted hypotheses to explain diet choice and mixing by polyphagous herbivores and omnivores (Bernays and Bright 1993, Joern and Behmer 1997, Joern 2000, Behmer *et al.* 2002, Singer and Bernays 2003, Raubenheimer and Simpson 2004, Raubenheimer and Jones 2006). Besides achieving nutrient balance, alternative hypotheses for diet mixing include feeding on nutrient-deficient resources when superior alternatives are rare, diluting toxins that are ingested from nutritious food resources, diet sampling to assess optimal resources and minimizing exposure to natural enemies. Future development of

food-selection theory should seek to combine the constructs of stoichiometry with the complementary views of diet-mixing theory (see Raubenheimer and Simpson 2004). Overall, however, there is overwhelming evidence that nitrogen and phosphorus limitation are pivotal factors directing the feeding strategies of insect herbivores.

Life-cycle synchronization with nutrient-rich resources in time (diapause) and space (dispersal). There is tremendous spatial and phenological variation in plant quality (nutrition and allelochemistry) that occurs within and among plant species (McNeill and Southwood 1978, Hunter *et al.* 1997, Dixon 1998, Awmack and Leather 2002). In general, the nitrogen content of plants such as grasses, forbs and trees follows a distinct seasonal pattern. Leaf nitrogen is highest in spring following bud break, declines rapidly thereafter to a summer low and then rises again during autumn when nutrients from senescing foliage are being translocated to roots. However, among individuals of the same plant species, there is remarkable temporal and spatial variation in the onset of this progression and in the maximum nutrient content that ultimately occurs. Also, within the same habitat, various plant species peak in nitrogen content at different times. Failure to synchronize reproduction and development with "windows of high-nitrogen opportunity" can have drastic consequences for herbivore performance and survival (McNeill and Southwood 1978, Cook and Denno 1994, Hunter *et al.* 1997, Dixon 1998). Two life-history traits, namely **diapause** and **dispersal**, allow herbivores to synchronize reproduction and development with optimal plant nutrition in time and space respectively (Denno 1994a).

Several of the best examples of "nitrogen tracking" occur in the sap-feeding guild (McNeill and Southwood 1978, Dixon 1998). For instance, population size of the Green Spruce aphid (*Elatobium abietinum*) mirrors changes in the amino nitrogen content of its host with peak reproduction occurring in spring when trees are most nutritious (Figure 4.4).

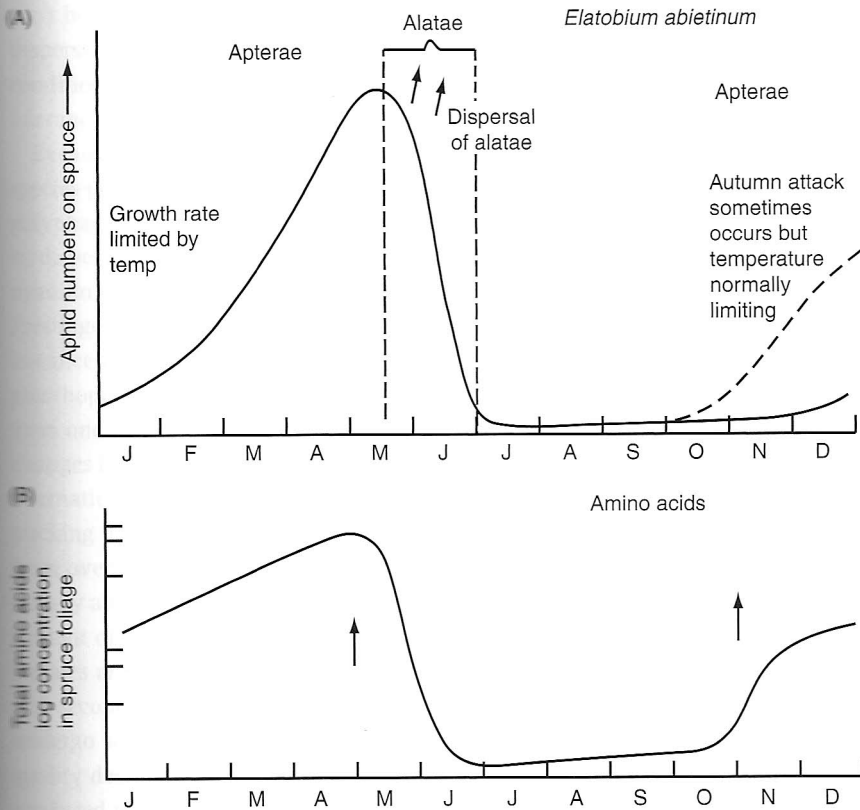


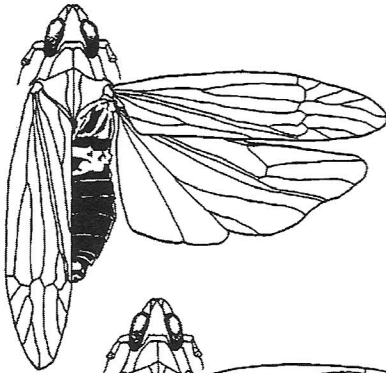
Figure 4.4 (A) Fluctuations in the abundance of the Green Spruce aphid *Elatobium abietinum* in relation to (B) seasonal changes in the amino nitrogen content of its host tree. Fluctuations in aphid population size mirror changes in the amino nitrogen content of spruce with peak reproduction occurring in spring when trees are most nutritious and dispersal (production of winged alatae) is coincident with a precipitous drop in tree amino nitrogen in early summer, when wingless parthenogenetic females (apterae) are present. From McNeill and Southwood (1978).

A second population rise often occurs during autumn and is associated with the mobilization of amino nitrogen and its back translocation to roots. Notably, the production of winged adults (alatae) that can disperse to more nutritious trees elsewhere occurs in summer when there is a precipitous drop in the amino nitrogen content of the resident tree.

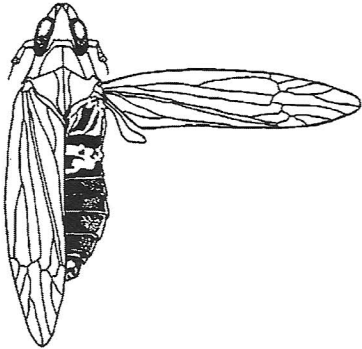
Other monophagous herbivores also synchronize their life histories with high plant nitrogen by dispersing to more nutritious plants. For example, the salt marsh planthopper *Prokelisia marginata* meets its high-nitrogen demands by dispersal, which allows for the escape of deteriorating plant patches and the

colonization of nutrient-rich plants in other habitats where offspring performance is enhanced (Cook and Denno 1994, Denno and Peterson 2000). By contrast, its sympatric congener *P. dolus* is relatively immobile and copes with declining plant nitrogen by compensatory feeding (Huberty and Denno 2006a). A morphological trade-off in investment between flight muscles (*P. marginata*) and the muscles governing ingestion capacity (*P. dolus*) imposes constraints on how these sap-feeders cope with declining plant nitrogen (Figure 4.5). Thus, dispersal and feeding compensation may be two competing mechanisms for satisfying nitrogen demands that

(A)

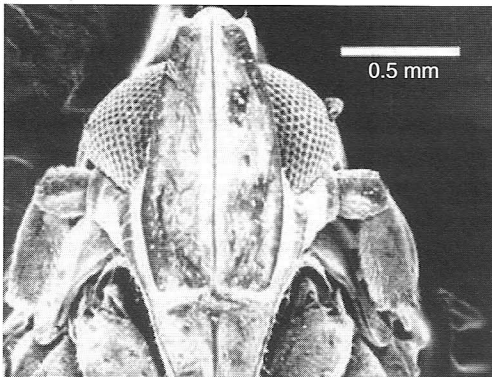


Flight-capable adult of
Prokelisia marginata
with fully developed wings

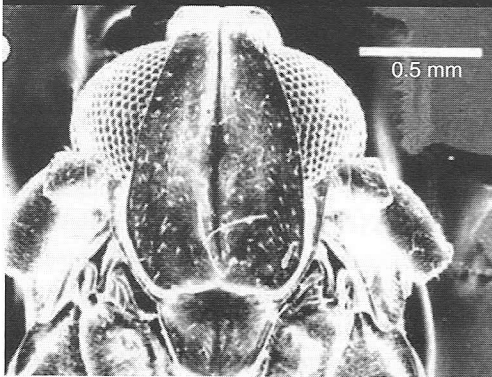


Flightless adult of
Prokelisia dolus
with reduced wings

(B)



Flight-capable adult of
Prokelisia marginata
with narrow face and
reduced subcibarial musculature



Flightless adult of
Prokelisia dolus
with wide face and
enlarged subcibarial musculature

Figure 4.5 (A) Planthoppers are wing-dimorphic as adults with both flight-capable and flightless forms occurring in the same population. Most adults of the planthopper *Prokelisia marginata* are flight capable and meet their nutritional demands

can't both be maximized in the same species. Dispersal allows for avoidance of low-nitrogen conditions, whereas feeding compensation permits tolerance until plant nutrition improves.

Because the nitrogen content of different plant species peaks at different times of the year, polyphagous herbivores can meet nitrogen demands by dispersing to more nutritious plant species as local conditions deteriorate (McNeill and Southwood 1978, Prestidge 1982, Awmack and Leather 2002). For instance the grass bug *Leptopterna dolabrata* and the planthopper *Javesella pellucida* switch host grasses from one generation to the next as they track spatial changes in high-nitrogen availability. Moreover, host alternation in aphids has been linked to nitrogen tracking (Dixon 1998). Host-alternating aphids hatch from overwintering eggs on their primary host, usually a woody tree or shrub. As the amino-nitrogen content of their primary host declines, migratory females are produced that disperse to more nutrient-rich secondary hosts (herbaceous plants) where they undergo several asexual generations until plant quality declines. Subsequently, migratory forms are produced that return to the primary host, where they reproduce and give rise to the egg-laying sexuals. The decrease in quality of the secondary host coincides with the autumn increase in leaf nitrogen content of the primary host.

Other aphid species such as the sycamore aphid *Drepanosiphum platanoides* show similar patterns of precise nitrogen tracking, but do so by entering a reproductive diapause in summer and thus avoiding periods of low nitrogen availability (Dixon 1998).

Some herbivorous insects that overwinter as diapausing eggs on their host trees (e.g., treehoppers) detect plant cues in spring and synchronize egg hatch with the onset of sap flow, thereby ensuring development on nitrogen-rich leaves (Wood *et al.* 1990). Other herbivores such as foliar-feeding caterpillars are less able to predict bud break and thus peak leaf nitrogen (Hunter *et al.* 1997). If larvae hatch just following bud break they experience high performance on nitrogen-rich leaves. However, if they hatch too early bud scales preclude access to developing leaves, and if they hatch too late they incur the adverse effects of declining leaf nitrogen and increasing defensive chemicals, both of which result in lower survival.

Manipulation of plant physiology by forming nutrient sinks: Several species of free-living aphids, gall-inducing insects and lepidopterans modify plant nutritional physiology to their own advantage by creating "nutrient sinks" (Way and Cammell 1970, Larson and Whitham 1991, Inbar *et al.* 1995, Raman *et al.* 2006). When phloem-tapping herbivores feed, they alter the source-sink dynamics of phloem transport by diverting assimilates from neighboring leaves and drawing them toward feeding sites where their performance is dramatically enhanced. Moreover, by feeding in aggregations, some aphids (*Brevicoryne brassicae*) further facilitate the local accumulation of nutrients and increase the strength of the nutrient sink. Similarly, the developing gall of the lepidopteran *Epiblema strenuana* intercepts the normal flow of nutrients and acts as a nutrient sink.

Caption for Figure 4.5 (cont.)

by dispersing to nutrient-rich patches of their host plant where performance is increased. Most adults of *P. dolus* are flightless and do not have this option. From Denno *et al.* (1985). (B) *P. dolus* meets its nitrogen demands by increasing its ingestion rate when plant quality declines. Feeding compensation in *P. dolus* is made possible by a greater investment in thoracic musculature (as evidenced by its wide face where these muscles attach) compared to its congener *P. marginata*, which has reduced compensatory ability. Thus, these planthoppers meet their nutritional demands in different ways and a morphological trade-off in investment between flight muscles (*P. marginata*) and the muscles influencing ingestion capacity (*P. dolus*) imposes constraints on how these sap-feeders cope with declining plant nitrogen. Adapted from Denno *et al.* (1987) and Huberty and Denno (2006a).

Seed-feeding insects can also manipulate seed development to their own advantage (von Aderkas *et al.* 2005). For example, the seed chalcid *Megastigmus spermatrophus* (Hymenoptera: Torymidae) deposits eggs in the ovules of Douglas fir (*Pseudotsuga menziesii*) cones. Oviposition prevents the expected degeneration of unfertilized ovules and at the same time induces the accumulation of energy reserves, which larvae require for development.

Nutrients from non-plant sources: There are two primary ways that insect herbivores obtain supplemental nutrients from sources other than their host plant, namely by feeding at higher trophic levels and/or from symbionts, microorganisms living in intimate association with their insect host. An extensive literature documents cases of "herbivorous insects" occasionally or frequently feeding at higher trophic levels, where nitrogen is more concentrated in the diet (McNeill and Southwood 1978, Polis 1981, Whitman *et al.* 1994, Douglas 1998, Agrawal *et al.* 1999a, Coll and Guershon 2002, Denno and Fagan 2003, Figure 4.3). These instances include cannibalism, intraguild predation, scavenging on carcasses and feeding on other nitrogen-rich food sources such as dung. A vast array of herbivores exhibit these behaviors, including Orthoptera, Hemiptera, Thysanoptera, Lepidoptera, Coleoptera, Diptera and Hymenoptera. Detritivores such as Trichoptera engage in cannibalism and predation as well (Wissinger *et al.* 1996). By supplementing their diets with nitrogen from other sources, both herbivores and detritivores can increase their growth and fecundity remarkably (Anderson and McFadyen 1976, McNeill and Southwood 1978, Coll and Guershon 2002). Upon hatching, many first-instar caterpillars (e.g., *Ascia monuste*) seek nitrogen-rich meals by regularly consuming their own egg chorion or the eggs of nearby conspecifics (Barros-Bellanda and Zucoloto 2001), whereas other taxa (cockroaches and lepidopterans) often consume their exuviae and partially recover lost nitrogen (Mira 2000). Factors that further motivate herbivores to seek nutrients

from other sources include food depletion, reductions in plant quality, high population density and physiological state, such as when females are in the process of maturing eggs (Simpson *et al.* 2006). If plant quality is poor and nitrogen is not available from other sources, females may resorb eggs or embryos, thereby enhancing their own survival (Ohgushi 1996, Awmack and Leather 2002).

Numerous orders of insects have member species that harbor a variety of symbiotic microorganisms such as bacteria, fungi and protozoans (Bourtzis and Miller 2006). Symbiotic mutualists are completely dependent on their hosts, but in turn provide them with nutrients (e.g., amino acids, sterols and vitamins), chemicals that are either rare, absent altogether, or tied up in non-digestible forms in plant diets (Liadouze *et al.* 1995, Baumann *et al.* 1997, Douglas 1998, Bourtzis and Miller 2006). Symbionts are over-represented in groups of insects that feed on nutritionally-poor food or imbalanced diets suggesting that housing symbionts is an adaptation to meet nutrient demands. For example, symbionts occur in phloem and xylem feeders (Hemiptera: aphids, psyllids, whiteflies, scale insects, planthoppers, leafhoppers and cicadas), some folivores (Hymenoptera: leafcutter ants), wood feeders in the Coleoptera (bark, ambrosia beetles and some scarabs and weevils) and Isoptera (termites) and a few omnivores (Blattodea: wood roaches) (Baumann *et al.* 1997, Gullan and Cranston 2005, Bourtzis and Miller 2006). Notably, symbionts are known to occur in predatory insects that feed on more nitrogen-rich food. Microbial symbionts can occur external to the insect's body (ecto-symbiotic fungus grown by leafcutter ants) or within the host (endo-symbiotic gut protozoans in termites), and can be either extracellular (bacteria and protozoans in the guts of termites and cockroaches) or intracellular (bacteria in the specialized mycetome cells of aphids (see Chapter 6 on Mutualism).

The role of symbionts in host nutrition has been examined by ridding hosts of symbionts with

antibiotics, heat-shock treatments or otherwise sterilizing them and then comparing the performance of so-called aposymbiotic hosts with symbiotic control groups (Chen *et al.* 1981, Campbell 1989, Douglas 1996, 1998). When symbionts are deactivated, hosts grow slower, molt to smaller adults or exhibit reduced fecundity, a result that has been shown for aphids, planthoppers, bark beetles and termites (Chen *et al.* 1981, Fox *et al.* 1992, Yoshimura *et al.* 1993, Liadouze *et al.* 1995). Moreover, some herbivores such as leafcutter ants (e.g. *Atta*) culture fungal symbionts in their subterranean nests and bark beetles (e.g. *Ips*, *Dendroctonus*) and ambrosia beetles (e.g. *Platypus*) vector them among host trees during colonization (Beaver 1989, Cherrett *et al.* 1989, Fox *et al.* 1992). Depending on the species, these herbivores feed on the ecto-symbiotic fungus either exclusively (*Atta*) or in part (*Ips*), thereby providing essential nutrients for growth and population increase that are available in very limited amounts in leaf tissue or wood. Termites as a group have evolved a variety of mutualisms with different microorganisms that aid in wood digestion, nitrogen acquisition and ultimately balancing their own C:N content when feeding on very carbon-rich food (Breznak 1982, Higashi *et al.* 1992). For the most part, gut microorganisms such as protozoans, bacteria and fungi are required for cellulose digestion (Breznak 1982; Martin 1991). Moreover, several lineages of termites enhance nitrogen intake by harboring bacterial gut symbionts that either fix atmospheric nitrogen or synthesize it (Higashi *et al.* 1992, Moriya *et al.* 1999). Some termites also support methanogenic bacteria in their guts and are thus able to eliminate excess carbon by methane production (Higashi *et al.* 1992, Brauman *et al.* 1992). Overall, the symbioses that termites have evolved with microbes are essential for maintaining their own C:N stoichiometry. Symbionts at large provide herbivores with essential nutrients, particularly nitrogen that is so critical for growth and reproduction. Notably, symbiotic relationships with microorganisms appear to have provided the opportunity for insects to

exploit and diversify on nutrient-poor resources that are otherwise very difficult to exploit (see Chapter 6 on Mutualism).

Evolutionary shift in body nutrient composition: Another way that herbivores have partially reduced their chronic demand for nitrogen is to evolve a lower dependence on nitrogen for the construction of body constituents, and thus reduce the stoichiometric mismatch with their plant diet (Fagan *et al.* 2002). At the level of protein subunits, selection may favor amino acids with lower nitrogen contents. Recent research on the elemental composition of bacterial and yeast proteins has shown that shifts in protein composition can evolve in response to elemental shortages (Baudouin-Cornu *et al.* 2001). At the tissue level, selection might, for example, reduce the ratio of protein to chitin in insect cuticle that typically ranges from 1:1 to 4:1 (Chapman 1998). At the whole-body level, selection might alter the relative allocation to muscle, cuticle, fat body and other tissues, all of which differ in nitrogen content (Fagan *et al.* 2002). That herbivorous bugs and beetles have thinner cuticles than their predaceous counterparts is in line with this argument (Rees 1986). Selection at all of these levels of organization may explain why insect herbivores have lower nitrogen content (9.6% on average than predators (11.0%)) (Fagan *et al.* 2002, Matsumura *et al.* 2004). Similarly, selective pressures associated with fundamental limitations in nitrogen may have contributed to reductions in body nitrogen content over evolutionary time. Consistent with this hypothesis is the observation that herbivores in the more derived orders of insects (Lepidoptera and Diptera) contain 15–25% less nitrogen than do those in more basal lineages (Orthoptera and Hemiptera) (Fagan *et al.* 2002). In this context, half of the body mass of rigid grasshoppers is proteinaceous cuticle, which is far more than that for flexible caterpillars (Bernays 1986). Thus, nitrogen conservation may have played a role in the evolution of holometaboly (complete metamorphosis) with the development of a thin cuticle in the larval stage of advanced insect orders (Bernays 1991).

4.3.3 Mechanical and structural barriers to herbivore attack

Besides being nutritionally inadequate, plants possess a variety of mechanical features and structures that pose physical-chemical barriers to herbivore attack. Included in the repertoire of “mechanical and structural defenses” are general tissue toughness and hardness that deter or prevent feeding (Lucas *et al.* 2000), trichomes (plant hairs) that can deny or reduce herbivore access to feeding and oviposition sites (Myers and Bazely 1991, Andres and Connor 2003) and surface waxes that can make it difficult for herbivores to colonize and maintain their foothold on plant surfaces (Juniper and Southwood 1986, Eigenbrode and Espelie 1995).

Historically, ecologists have referred to “leaf toughness” as a general mechanical defense against insect herbivores, but usually the structural elements conferring tissue resistance are not explored in detail (e.g., Feeny 1970, Coley 1983, Raupp 1985, but see Peeters 2002). In general, young expanding leaves are less tough than are mature leaves and leaf thickness and the amount of cellulose and lignin, the structural components of plants, have been implicated in tissue toughness (Peeters 2002).

Recently, generic “tissue toughness” has been partitioned into two components namely hardness and toughness, both of which can have adverse effects on herbivores (Choong *et al.* 1992, Lucas *et al.* 2000). “Hardness” deters the initial cracking (splitting) of a plant tissue when a herbivore begins to feed, whereas “toughness” results in resistance to crack growth. Thus, a seed coat may be very hard (resist cracking), but be very brittle and therefore not be very tough. The primary source of tissue toughness is the composite cell wall consisting of cellulose microfibrils set in a hemicellulose or lignin matrix, and is roughly proportional to the fraction of plant tissue volume occupied by cell walls. High toughness in plant cells results not from the cell walls themselves, but rather from their plastic ability to collapse. Hardness in plant tissues can be achieved by

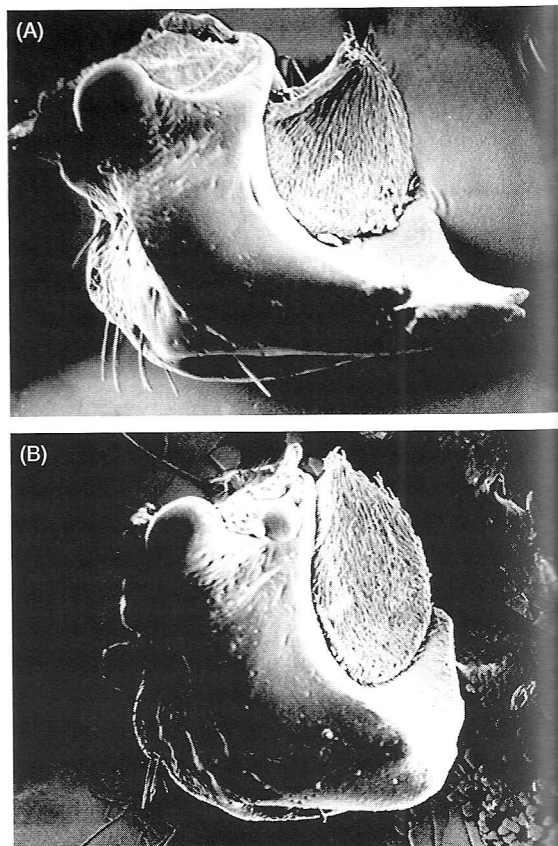


Figure 4.6 Left mandible of an adult willow leaf beetle (*Plagioderma versicolora*) that has fed for one month on (A) tender terminal leaves or (B) tough mature leaves. The incisor of the mandible is completely worn down when beetles feed on tough leaves. From Raupp (1985). Reprinted with permission from Blackwell Publishing.

dense cell walls as in some seed coats or by amorphous silica in leaves, spines or surface structures such as stiff trichomes. Such defenses deter herbivores from contacting plants, but are also responsible for significant abrasion and mandibular wear once feeding has begun (Lucas *et al.* 2000).

For mandibulate herbivores such as lepidopterans and beetles, feeding on “tough leaves” results in reduced consumption and delayed growth, which in some cases can be attributed to increased mandibular wear (Raupp 1985, Stevenson *et al.* 1993, Figure 4.6).

Similarly, leaf-shredding caddisflies can show decreased consumption rates on tough litter types (Motomori *et al.* 2001). In several cases, mandibular wear and impaired growth in stem-boring caterpillars have been linked to the high silica content of their grass host (Pathak *et al.* 1971, Hanifa *et al.* 1974), thus implicating tissue hardness as the underlying mechanism. Even more convincing are studies in which the silica content of the host plant was experimentally increased with adverse effects on the growth and digestion efficiency of grasshoppers, lepidopterans and dipterous stem borers (Moore 1984, Massey *et al.* 2006). Notably, sap-feeding herbivores (aphids) in this study were not affected by elevated silica. Sap-feeders may more easily penetrate the cellular spaces between silica-containing cells and as a consequence are not physically excluded from feeding in the vascular tissue. This may explain why herbivore communities on silica-rich grasses are filtered, largely devoid of many chewing herbivores (e.g., free-living lepidopterans and beetles, but not grasshoppers), and are dominated by sap-feeders such as leafhoppers and planthoppers (Cook and Denno 1994). Recent evidence, however, suggests that sap-feeders too incur mandibular (stylet) wear while feeding in plant tissues (Roitberg *et al.* 2005), but mandibular wear has yet to be compared between chewing and sap-feeding herbivores fed the same diet.

Notably, the structural traits of leaves (e.g., blade and cuticle thickness, vein lignification and thickened hypodermis) have also been shown to influence the guild structure of arboreal insect assemblages (Peeters 2002). For example, the density of leaf-chewing herbivores was negatively correlated with a thickened hypodermis and the area of the leaf-vein lignified. In fact, in this extensive study, the functional composition of the herbivore assemblage was better correlated with structural leaf traits than with leaf constituents such as nitrogen and water content. Overall, tissue toughness, hardness and surrogate variables have significant effects on

individual performance, population density and community structure.

Trichomes occur in a diversity of forms, sizes and densities and in part serve to protect plants from herbivore attack, although there is substantial variation in their effectiveness (Myers and Bazely 1991, Peter and Shanower 2001, Hare and Elle 2002, Andres and Connor 2003). In addition to their antiherbivore role, trichomes also insulate leaves from solar radiation, deter evaporation, facilitate water and nutrient absorption, or function in salt excretion (Gutschick 1999). Overall, trichomes affect insect herbivores by influencing oviposition, altering herbivore movement, reducing growth and fecundity, and by influencing interactions with natural enemies (Haddad and Hicks 2000, Andres and Connor 2003, Kennedy 2003). Simply, trichomes can be divided into two general types, namely non-glandular and glandular (Levin 1973, Hare 2005). Multiple trichome types can occur on the same individual plant, the same trichome type can vary in density and size among individuals and populations, and some plant species are dimorphic for trichome type with glandular and non-glandular trichomes occurring in different individuals (Hare and Elle 2002, Kennedy 2003). Non-glandular trichomes physically interfere with feeding and colonization, especially for small insects such as first-instar lime aphids (*Eucallipterus tilliae*) that die because they are denied access to the leaf surface where they reach the phloem (Dixon 1998). When the dense bed of stellate trichomes is removed, the young aphids feed and flourish. Similarly, shaving the dendroid trichomes from mullein (*Verbascum*) leaves promotes colonization by the aphid *Aphis verbascae* (Keenlyside 1989). Other small sap-feeding herbivores such as whiteflies and leafhoppers also fail to colonize or successfully grow on cultivars of crop plants rendered resistant by dense beds of leaf trichomes (Butler *et al.* 1991, Goertzen and Small 1993). Larger herbivores too can be very adversely affected by non-glandular trichomes. For instance, larvae of *Heliconius melpomene* that consume

a number of passion-vine species (*Passiflora*) are excluded from the widespread *Passiflora adenopoda* (Gilbert 1971). The leaves and tendrils of this vine are covered with hooked trichomes. As larvae attempt to feed, their prolegs catch on the trichomes and tear, haemolymph exudes and the larvae quickly desiccate and die (Figure 4.7A and B). Similarly, the growth and survival of the swallowtail butterfly, *Papilio troilus*, and several noctuid moth caterpillars are negatively affected by leaf pubescence, and in some cases reduced performance and survival occur because trichomes are of lower nutritional quality than other leaf tissues (Lambert *et al.* 1992, Haddad and Hicks 2000, Andres and Connor 2003). It should be emphasized that not all herbivores are negatively impacted by trichomes, and in fact some herbivores prefer plants with dense trichomes for oviposition, and if adapted perform better on such plants.

The exudates from glandular trichomes can deter, mire or poison insect herbivores (Ranger and Hower 2001, Andres and Connor 2003, Kennedy 2003). Small herbivores such as aphids and leafhoppers become entrapped and die in the sticky exudates produced by glandular trichomes on their host plants (Dixon 1998, Kennedy 2003, Figure 4.7C, D and E). However, the exudates of glandular trichomes also contain toxins, which in the case of tomato confer resistance to a variety of herbivores including aphids, whiteflies, lepidopterans and dipteran leaf miners. Although the physical deterrence of non-glandular trichomes is clear, it is often difficult to isolate the effects of mechanical defense, allelochemistry and nutrition when glandular trichomes are involved because the battery of "plant defenses" is so intimately intertwined.

Scaling up to herbivore communities, an extensive study of the insect guilds on manzanita (*Arctostaphylos* species) showed that leaf pubescence has both community-wide and guild-specific effects on folivorous insects because of its selective effects on free-living, but not concealed, feeding guilds (Andres and Connor 2003). Feeding by herbivores can also induce the production of trichomes on the

new growth of their host plants, with adverse consequences not only for the inducer, but also for the community of other herbivores feeding on the plant (Baur *et al.* 1991, Agrawal 1998, 1999, 2000a, Traw and Dawson 2002). Induced defenses at large will be dealt with in a forthcoming section of this chapter.

Leaves of some plant species also bear other surface structures that deter herbivore attack. For example, protrusions on the stipules and meristems of *Passiflora* bear an amazing resemblance to the eggs of *Heliconius* butterflies, the primary herbivores on these plants (Benson *et al.* 1975, Williams and Gilbert 1981, Figure 4.8). So-called "egg mimics" significantly reduce the number of potential oviposition sites because adult butterflies avoid placing eggs in their presence. Selection has apparently favored oviposition site scrutiny in these visually oriented butterflies because upon hatching larvae are very cannibalistic and consume other nearby eggs.

In contrast to plants with trichome-laden surfaces, many plants have leaves rendered slippery by the surface waxes that provide protection from desiccation and pathogen invasion (Eigenbrode and Espelie 1995, Eigenbrode *et al.* 2000, Rutledge *et al.* 2003). Such waxes often pose problems of attachment for many herbivores. For example, glossy varieties of cabbage (*Brassica oleracea*) deter foraging and feeding by larvae of the diamondback moth (*Plutella xylostella*), caterpillars of the imported cabbage butterfly (*Pieris rapae*) and cabbage aphids (*Brevicoryne brassicae*), whereas other herbivores such as flea beetles (*Phyllotreta cruciferae*) are able to maintain a foothold. In the cabbage system, complex interactions among the structure of surface waxes and the tarsal morphology of insects combine to influence attachment (Eigenbrode and Jetter 2002). Similar effects have been documented in natural systems, whereby young leaves of some *Eucalyptus* species possess a waxy bloom that precludes attachment and feeding by beetles (Edwards 1982). Overall, the distribution and abundance of leaf

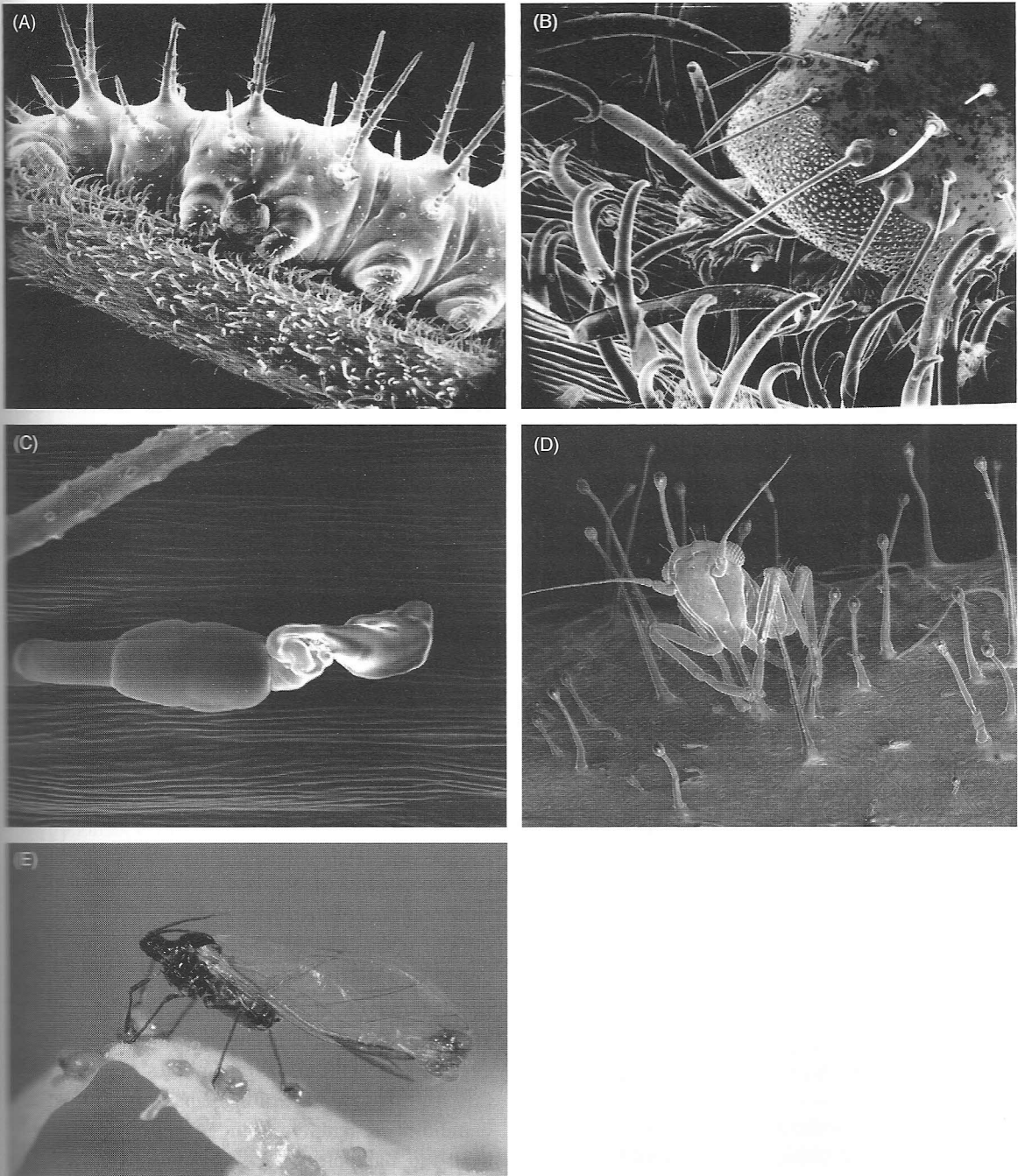


Figure 4.7 (A) Caterpillar of *Heliconius melpomene* caught on the hooked trichomes of *Passiflora adenopoda*. (B) Close-up of trichomes hooked into the caterpillar's proleg. From Gilbert (1971). (C) A glandular trichome of an alfalfa clone resistant to potato leafhopper, *Empoasca fabae* ($\times 1000$), which has released exudates after damage. (D) A nymph of the potato leafhopper entrapped in the latex of its lettuce host plant, *Lactuca sativa*. From Dussourd (1995) © Dr. David Dussourd. (A) and (B) From Gilbert, L. E. 1971. Butterfly-plant coevolution: has *Passiflora adenopoda* won the selectional race with heliconiine butterflies? *Science* 172:585–586. (C) and (D) reprinted with permission from Blackwell Publishing. See color plate section.

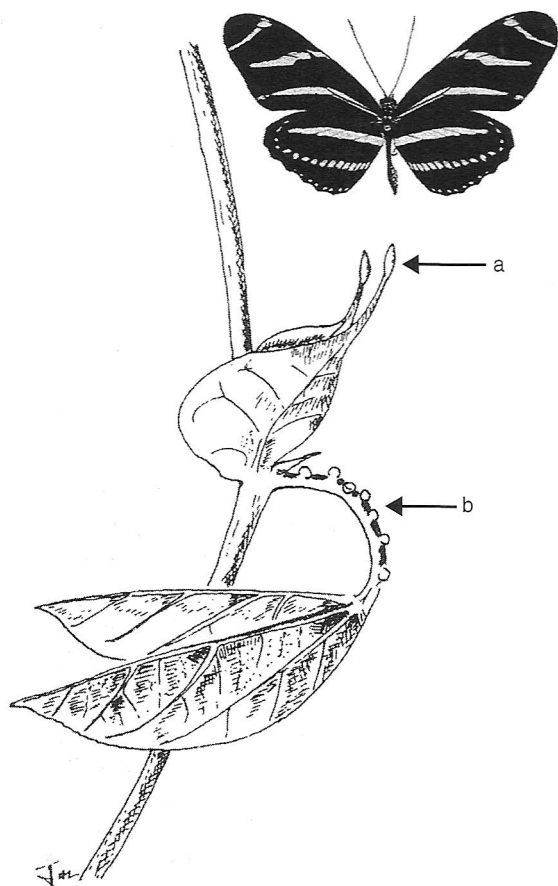


Figure 4.8 Protrusions on the stipules (a) of *Passiflora cyanea* bear a remarkable resemblance to the eggs of *Heliconius* butterflies, the primary herbivores on this group of plants. Adult butterflies avoid placing their eggs in the presence of so-called “egg mimics,” significantly limiting the number of potential oviposition sites and ultimately reducing herbivory. Extrafloral nectaries (b) are sugar-secreting glands that provide carbohydrate resources to ants and other predators that further reduce the density of insect herbivores on *P. cyanea*. Original from Gilbert and Raven (1975); adapted from Strong *et al.* (1984a).

feeding beetles on *Eucalyptus* spp. is related to the waxy bloom on the trees and the attachment abilities of the individual beetle species (Edwards and Wanjura 1991).

Although waxy leaf surfaces and dense trichomes often deter some natural enemies, not all predators and parasitoids are adversely affected (Bottrell *et al.* 1998, Eigenbrode and Jetter 2002, Kennedy 2003, Eigenbrode 2004). For example, some natural enemies are better able to negotiate agricultural crop varieties with reduced surface waxes on their leaves, consume more herbivores and thus exacerbate the direct adverse effect of slippery leaves on herbivores. Likewise, fire ants (*Solenopsis invicta*) are not deterred by soybean plants with dense trichomes and in fact suppress lepidopteran caterpillars better on pubescent varieties than on glabrous ones (Styrsky *et al.* 2006). Thus, to assess the general effect of plant surfaces on the abundance of insect herbivores, one must take into account the direct effects of surface structure on herbivore attachment and the indirect effects of altered foraging by natural enemies.

4.3.4 Herbivore counteradaptations to mechanical plant defenses

Insect herbivores have evolved a number of morphologies and behaviors that allow them to cope in part with the mechanical defenses of plants. Concerning leaf hardness, insights can be gained by comparing the morphology of herbivores that feed on silica-rich grasses with that of forb feeders. For instance, the relative head and associated mandibular mass of grass-feeding grasshoppers and lepidopterans is larger than that for related forb feeders (Bernays 1986), and egg size in the Satyridae and Hesperidae (Lepidoptera) is positively related to the “leaf toughness” of their host grass (Fukuda *et al.* 1984, Nakasuji 1987). Larvae hatching from large eggs have large heads and mandibles which retain their cutting and masticating capability until worn mandibles are renewed at the next molt. Thus, large head and mandible size has apparently allowed some herbivores to exploit grasses, but the price these species have paid for this dietary habit is reduced fecundity. Also, several species of grasshoppers (e.g., the grass-feeding *Chorthippus brunneus*) and

lepidopterans (e.g., the Gypsy moth *Lymantria dispar*) can undergo extra molts during their immature development. Supplemental molting allows individuals to replace worn mandibles, and may allow for the exploitation of hard leaf tissues. Moreover, the mandibles of grass-feeding grasshoppers have “chisel-edged incisors” and a well-developed molar region for grinding, whereas forb-feeders do not (Bernays 1991).

Herbivores also have evolved tarsal morphologies for negotiating trichome-bearing leaf surfaces. Some aphids and mirid bugs, for example the specialist oak-feeding aphid, *Myzocallis scirpigeri*, have tarsal claws modified for grasping trichomes and moving through the densely pubescent leaves (Kennedy 1986, Southwood 1986). Several aphids exploiting host plants with glandular exudates have short tarsi or no tarsi whatsoever, an adaptation which apparently allows them to “tiptoe” through the trichomes (Moran 1986, Bernays 1991). Alternatively, other aphids have solved the problem of accessing the leaf surface by evolving a longer proboscis, which allows them to feed through the dense bed of trichomes (Dixon 1998). Larvae of the Neotropical butterfly, *Mechanitis isthmia*, feed on *Solanum* sp. whose leaves are covered with dense beds of trichomes (Rathcke and Poole 1975, Young and Moffett 1979). Eggs are deposited in masses and upon hatching larvae aggregate on the lower surface of leaves where they collectively spin a “silken scaffolding” over the top of the trichome bed. Subsequently, larvae roam the top of the silken mat where they clip trichomes and safely consume leaf tissue.

Both mandibulate and sap-feeding herbivores have evolved tarsal modifications that allow attachment on waxy leaf surfaces (Bernays 1991). For instance, some chrysomelid beetles, like gecko lizards, are able to hold onto glossy leaf surfaces because of the molecular adhesion provided by thousands of minute setae on their tarsal pads (Stork 1980). Likewise, certain *Empoasca* leafhoppers produce a minute suction cup with their tarsal pads, which provides very effective attachment on smooth leaf surfaces

(Lee *et al.* 1986). Notably, the tarsal adaptation works well on preferred glossy leaf surfaces, but is ineffective on pubescent leaves.

4.3.5 Allelochemical barriers to herbivore attack

The insecticidal properties of plants have been known for several centuries. For instance, water extracts of tobacco (Solanaceae) were used to kill sap-feeding insects in 1690, rotenone (Fabaceae) was used to kill caterpillars in 1848 and pyrethrum (Asteraceae) has been used as an insecticide since 1880 (Ware 1991). Moreover, the active fractions of these botanical insecticides were all isolated prior to 1924 (Matsumura 1985). Despite the long-standing knowledge of the toxic properties of plants by entomologists and natural-product chemists, the role that secondary metabolites (also called secondary chemicals or allelochemicals) play in plant-insect interactions has been realized relatively recently. Brues (1946), Painter (1951), Fraenkel (1959, 1969), Ehrlich and Raven (1964) and Feeny (1968, 1970) were among the first ecologists to promote the importance of allelochemicals as “defenses” against insect herbivores. Since then, the literature documenting the structure, diversity, distribution, concentration, induction, metabolism and antiherbivore properties of allelochemicals has grown enormously (e.g., Rosenthal and Berenbaum 1991, 1992, Tallamy and Raupp 1991, Harborne 1993, Karban and Baldwin 1997, Agrawal *et al.* 1999b, Kessler and Baldwin 2002, Boege and Marquis 2005).

Secondary metabolites are deemed “secondary” because they play little or no known functional role in the primary plant metabolism underlying plant growth and reproduction (Whittaker 1970). Literally thousands of secondary metabolites have been isolated from plants and there is unequivocal and widespread evidence that these compounds serve a defensive function in plants against herbivores and pathogens (Rosenthal and Berenbaum 1991,