

Chapter 1

Why Do Plants Need Defenses?

1.1 Plants as sources of food

All organisms need food to survive. To be more precise, they require a variety of chemical elements—the most important of which are carbon, nitrogen, and oxygen—to provide the building blocks for growth and development. This in turn requires a supply of energy, the only external supply of which comes from the sun. Plants are able to capture the energy from sunlight and convert it into chemical energy, thereby providing the means of financing the formation of carbohydrate from atmospheric CO₂ and water. This autotrophic ability of plants comes at a price. Because most organisms are not autotrophic, they must obtain their energy and building blocks for growth and development from consuming other organisms, including plants. In fact, plants are a direct source of food for an array of organisms that include invertebrates, vertebrates, fungi, bacteria, and even other plants.

The popularity of plants as food sources for so many organisms begs the question “what do plants offer other organisms by way of nutrition?” Clearly, plant tissues will provide a source of carbon and nitrogen, much of which will be in the form of carbohydrates, lipids, and proteins. They will also contain macroelements such as phosphorus, sulfur, calcium, and potassium, as well as various microelements such as iron, manganese, and zinc. However, the relative proportions of these components will vary depending on species. Moreover, different plant parts can have very different compositions (Figure 1.1). For example, fruits and phloem sap can be rich sources of carbohydrates, while seeds are usually good sources of fat. Some parts of the plant, such as bark, offer little in the way of nutrients, since they are composed largely of dead cells, with lignified walls. Nitrogen and protein content also varies between different parts of the plant, but in general, plants contain less nitrogen and protein than most of the organisms that use them as a food source. Typically, the total nitrogen content of plants is between 2 and 4% of their dry weight, while the nitrogen content of animals amounts to 8–14% of their dry bodyweight (Figure 1.2). The amount of nitrogen in insects is even greater than this and can be in the order of 30–40% of their dry weight (Southwood, 1973).

As indicated above, plants are used as food sources by a variety of organisms. Before we proceed further, it is worth considering the mechanisms used by these organisms to obtain the nutrients locked up in plant tissues.

2 Plant Defense

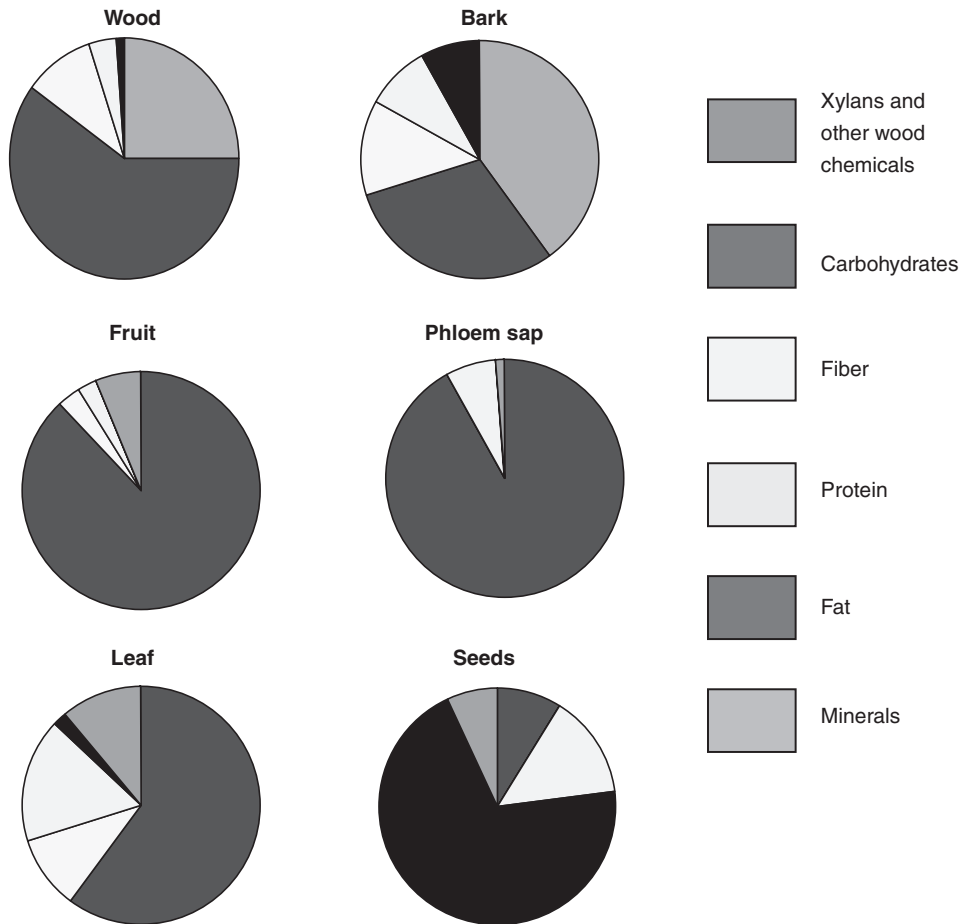


Figure 1.1 Composition of different plant parts that can serve as food for herbivores. (Adapted from Townsend *et al.* (2003), with permission of Blackwell Publishing Ltd.)

1.2 Organisms that use plants as food

1.2.1 Microorganisms

Plants are infected by a wide range of microorganisms. Some of these establish symbiotic associations with plant roots, such as *Rhizobium* bacteria found in nodules on roots of legumes and mycorrhizal fungi, which form intimate associations with the roots of most plant species. Other microorganisms are parasitic on plants and use plants as food sources, causing damage and sometimes plant death, in the process. Some of these microbes, including viruses, protozoa, and some fungi, are biotrophs. These grow and reproduce in nature only on living hosts. Powdery mildew and rust fungi (Figure 1.3a), for example, produce feeding structures called haustoria that invaginate the host plasma membrane, forming an intimate association with the plant cell. Other microbes, mostly fungi and

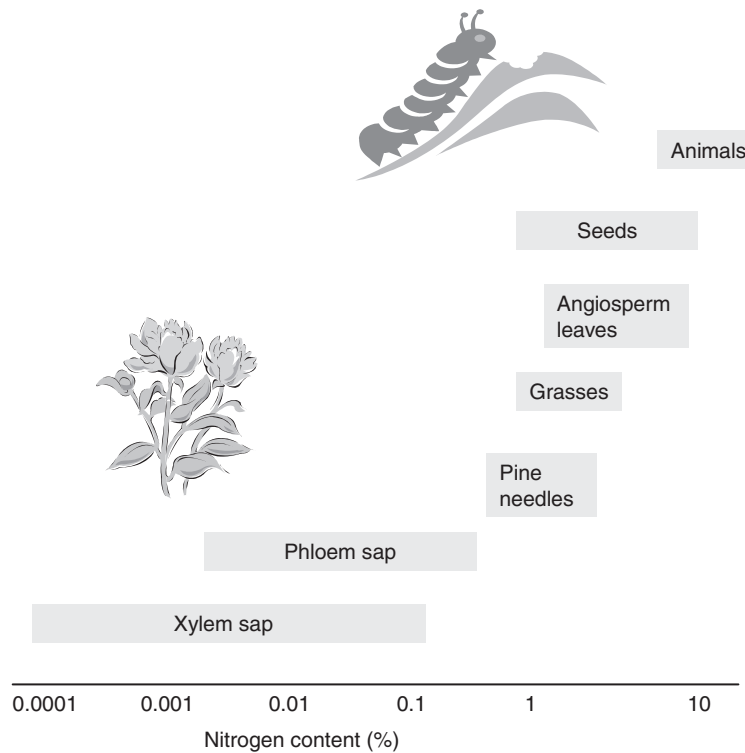


Figure 1.2 Variations in nitrogen concentration (dry weight percentage) of different plant parts compared with that in animals. Xylem and phloem sap concentrations are expressed as nitrogen weight/volume. (Adapted from Mattson (1980), with permission.)

bacteria, are necrotrophic. They secrete enzymes to cause disintegration of plant cells and, either alone or in combination with toxins, often lead to cell and tissue death (Figure 1.3b). The nutrients released in the process are then available for uptake by the pathogen.

1.2.2 Parasitic angiosperms

Plants are also parasitized by other plants. Indeed, parasitism among plants seems to have evolved many times during angiosperm evolution. It has been estimated that about 1% of angiosperms, some 3000 species in total, are parasitic on other plants (Parker & Riches, 1993). Parasitic angiosperms are distributed among 17 families, including the Viscaceae and the Cuscutaceae (Table 1.1), and include parasitic plants such as species of *Rhinanthus* and *Orobanch*e (Figure 1.3c and 1.3d). There is considerable diversity in the extent to which parasitic angiosperms rely on the host for growth. Some, such as species of *Rhinanthus*, have functional roots and can therefore take up inorganic nutrients from the soil, while others, such as the mistletoes, have nothing that resembles a root nor functions as one (Hibberd & Jeschke, 2001). There is also considerable variation in the extent to which parasitic plants rely on the host for photoassimilates. Thus, parasitic plants such as *Rhinanthus minor* are able to photosynthesize and can grow with a carbon supply from the host, while others,

4 Plant Defense

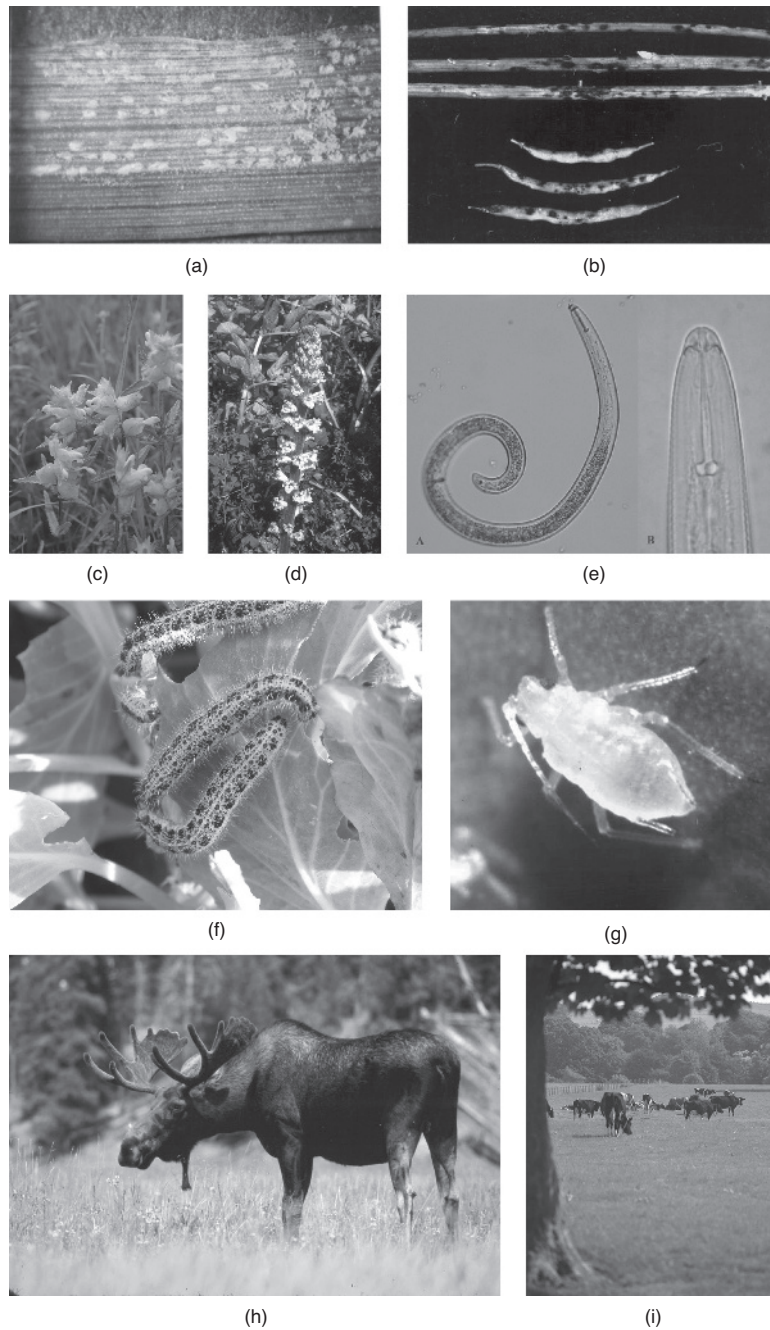


Figure 1.3 (a) Yellow rust (*Puccinia striiformis*) on wheat, (b) *Alternaria brassicae* on pods and stems of oilseed rape (*Brassica napus*), (c) the parasitic angiosperm *Rhinanthus minor*, (d) the parasitic angiosperm *Orobanche crenata*, (e) the plant parasitic nematode *Helicotylenchus*, (f) caterpillar of the large cabbage white butterfly, *Pieris brassicae*, (g) an aphid on a leaf, (h) moose, (i) cows grazing. (Image (c) is the copyright of Glyn Baker and is licensed for reuse under the Creative Commons Licence. Images (d), (e), (f) and (h) are reproduced courtesy of Lytton Musselman, the American Phytopathological Society, Rosemary Collier of the University of Warwick HRI, and the United States Geological Survey, respectively.)

Table 1.1 Main families of parasitic plants

Family	Approximate number of species	Type	Root/shoot
Santalaceae	400	Hemiparasitic	Largely root
Loranthaceae	700	Hemiparasitic	Mostly shoot
Viscaceae	400	Hemiparasitic	Shoot
Rafflesiaceae	500	Holoparasitic	Mostly root
Cuscutaceae	145	Holoparasitic	Shoot
Scrophulariaceae	1500	Hemi/holoparasitic	Root

such as *Cuscuta reflexa*, possess a very low photosynthetic capacity and are unable to grow without a carbohydrate supply from the host (Hibberd & Jeschke, 2001).

1.2.3 Nematodes

Nematodes are wormlike in appearance (Figure 1.3e) but are quite distinct from the true worms. Several hundred species are known to feed on living plants, obtaining their food with spears or stylets. Nematode feeding causes only slight mechanical damage to plants. The majority of the damage caused by nematodes appears to be caused by saliva injected into plants during feeding. Nematodes will puncture a cell wall, inject saliva into the cell, and withdraw part of the cell contents. Some nematodes feed rapidly and move on within a few seconds, while others feed more slowly and remain at the puncture for hours or even days. As long as the nematodes are feeding, they will inject saliva intermittently into the cell.

1.2.4 Insects

There are more species of insects than any other class of organisms on earth and nearly half of these, some 400,000 species, feed on plants (Schoonhoven *et al.*, 2005). These herbivorous insects harvest their food in a variety of different ways. Chewing insects possess “toothed” mandibles that cut, crush, and macerate plant tissues. Many feed externally on the plant, while others, such as leaf miners, harvest tissue layers between the upper and lower epidermis of the leaf. Chewing insects include species belonging to the orders Lepidoptera (moths and butterflies) (Figure 1.3f) and Orthoptera (e.g., grasshoppers). Some insects do not remove chunks of plant tissue, but rather suck fluids from the plant using specialized tubular mouthparts. Thus, insects in the order Hemiptera include aphids (Figure 1.3g), which feed on phloem sap. Other members of the Hemiptera, for example, whiteflies, feed on the contents of leaf mesophyll cells. Yet other insects make galls on their plant host. These insects manipulate the host tissues, providing themselves with both shelter and nutrients. A striking feature of relationships between insects and plants is the extent of food specialization among insect herbivores. Some insects, including many lepidopterous larvae, hemipterans, and coleopterans, occur on only one or a few closely related plant species and are termed monophagous. Others, such as the Colorado potato beetle, *Leptinotarsa decemlineata*, are oligophagous; these feed on a number of plant species, all belonging to

6 Plant Defense

Table 1.2 Major categories of dietary specialization in herbivorous mammals, according to Eisenberg (1981)

Category	Diet
Nectarivores	Nectar and pollen
Gumivores	Exudates from trees
Frugivore/omnivore	Pericarp or fleshy outer covering of plant reproductive parts, invertebrates and small vertebrates
Frugivore/granivore	Reproductive parts of plants, including seeds
Frugivore/herbivore	Fleshy fruiting bodies and seeds of plants, storage roots, and some green leafy material
Herbivore/browser	Stems, twigs, buds, and leaves
Herbivore/grazer	Grasses

the same family. Yet other insect herbivores, for example, the aphid *Myzus persicae*, accept many plants belonging to different families. Such insects are polyphagous.

1.2.5 Vertebrates

Herbivory is not confined to insects. In fact, it is a common trait among mammals (Figure 1.3h and 1.3i), with roughly half of the 1000 or so genera of mammals including plants in their diet (Danell & Bergström, 2002). While the majority of herbivorous insects are mono- or oligophagous, feeding on a few plant species, vertebrate herbivores tend to be polyphagous and feed on a wider range of plant species. Vertebrate herbivores are larger than their invertebrate counterparts and are thus able to remove a greater amount of plant tissue with each mouthful (Danell & Bergström, 2002). The classification of animals into functional groups is usually achieved using diet composition. Sixteen major categories of dietary specialization in mammals have been proposed (Eisenberg, 1981), and of these, seven refer to herbivores (Table 1.2). Categories range from nectarivores that feed on nectar and pollen to gumivores that feed on exudates from trees. The most dominant group is numerically the frugivores/omnivores, which represent approximately 33% of vertebrate herbivore genera (Table 1.2).

1.3 Impact of infection and herbivory in natural and agricultural ecosystems

1.3.1 Microorganisms

Pathogenic microorganisms can exert a profound effect on the structure and dynamics of individual plant species and plant communities. The extent and type of damage to individual plants is related to the lifestyle of the pathogen, that is, whether it is a biotroph or a necrotroph. Necrotrophs destroy plant tissue and it seems obvious therefore, that loss of leaf tissue, for example, will decrease rates of photosynthesis, thereby reducing plant growth. In contrast, biotrophs do not kill plant tissue, although effects on photosynthesis can

be just as profound. Thus, effects on chloroplast structure and function can lead to dramatic reductions in rates of photosynthesis in plants infected with rust or powdery mildew fungi (Walters & McRoberts, 2006). Photosynthesis can also be affected by other means. In plants infected with vascular wilt pathogens, such as *Verticillium albo-atrum*, blockage of xylem vessels can lead to water stress and partial closure of stomata, thus reducing rates of photosynthesis. Of course, the effects of pathogens on the host plant are not restricted to photosynthesis, and some pathogens, for example, can alter water and nutrient uptake, while others produce toxins, which affect host metabolism. Whatever the mechanism, pathogen infection can lead to greatly reduced plant growth and reproductive output. Thus, *Albugo candida* and *Peronospora parasitica*, both biotrophs, reduce reproductive output in *Capsella bursa-pastoris* (Alexander & Burdon, 1984), while the tobacco leaf curl virus reduces growth and seed production in its host, *Eupatorium chinense*, and is an important cause of plant mortality (Yahara & Oyama, 1993).

Pathogen infection can also lead to plant death. Thus, fungal damping off and root diseases can cause mass mortality of seedlings, especially under humid conditions. Damping off was responsible for 64–95% of seedling deaths of the tropical tree *Platypodium elegans* in the first 3 months after emergence (Augsburger, 1983). Pathogens can also cause death of older plants. In Australia, an epidemic of the root rot pathogen, *Phytophthora cinnamomi*, devastated a dry sclerophyll forest (Weste & Ashton, 1994), while the pathogen *Phacidium infestans* was a significant cause of mortality in 5- to 10-year-old *Pinus sylvestris* (Burdon *et al.*, 1994).

In crop production systems, losses due to pathogens can be substantial. In the period 1996–1998, global crop losses due to pathogens (fungi, bacteria, and viruses) were 12.6%, in spite of crop protection measures (Oerke & Dehne, 2004). Some crops seem to suffer more than others, and between 1996 and 1998, pathogens accounted for losses of 22% in global potato production. Even more devastating can be the spread of a pathogen into a new geographical area. For example, the soybean rust, *Phakopsora pachyrhizi*, was first reported in South America in 2001 (in Paraguay) and by 2003 was detected in most soybean-growing regions of Brazil, with losses estimated at 5% of total soybean production (Yorinori *et al.*, 2005).

1.3.2 Parasitic angiosperms

The diversion of host resources to parasitic plants can have large effects on host growth and reproductive output. Infection of *Poa alpina* with the annual hemiparasite, *R. minor*, reduced host biomass by more than 50% (Seel & Press, 1996), while the phloem-tapping mistletoe, *Tristerix aphyllus*, greatly reduced the production of buds, flowers, and fruits by its cactus host, *Echinopsis chilensis* (Silva & Martínez del Rio, 1996). Death of the host plant can occur, particularly in extreme cases, such as heavy infestation with mistletoe (Aukema, 2003).

Parasitic plants can exert a considerable impact on plant communities (Press & Phoenix, 2005). Thus, *Rhinanthus* species have been shown to reduce total productivity in European grasslands by between 8 and 73% (Davies *et al.*, 1997), while dwarf mistletoes can reduce volume growth of Douglas fir by up to 65% (Mathiasen *et al.*, 1990).

Striga is a genus of root hemiparasite with some 35 species, most of which are of no agricultural importance. However, those species that parasitize crop plants can be

8 Plant Defense

devastating. Yield losses in cereals infected by *Striga* can reach 100%, and fields can be so heavily infested that they are abandoned by farmers (Berner *et al.*, 1995). Some 40 million hectares of cereals are thought to be severely infested with *Striga* spp. in West Africa, and the Food and Agriculture Organization (FAO) estimates that annual yield losses in the savannah regions alone account for US\$7 billion (Berner *et al.*, 1995).

1.3.3 Nematodes

Nematode infestation can lead to substantial reductions in plant growth. In clover, the stem nematode, *Ditylenchus dipsaci*, reduced establishment from seeds and led to a 30% reduction in shoot growth (Cook *et al.*, 1992), while the potato cyst nematodes, *Globodera pallida* and *Globodera rostochiensis*, reduced growth of potato roots within 1 day following inoculation onto root tips (Arnitzen *et al.*, 1994). Nematodes have also been linked to plant deaths. Thus, pathogenic nematodes have been identified as the probable cause of die-out of the dune grass, *Ammophila breviligulata*, on the mid-Atlantic coast of the USA (Seliskar, 1995), while the pine wood nematode, *Bursaphelenchus xylophilus*, was responsible for the deaths of some quarter of a million mature pine trees in a single location in Japan (Numata, 1989).

1.3.4 Insects

Given the existence of more than 300,000 species of herbivorous insects (Schoonhoven *et al.*, 2005), it is surprising that there is not more evidence of plant devastation. In fact, complete defoliation of vegetation occurs only sporadically. Some plants can compensate or overcompensate for sizeable amounts of damage, but even so, insect herbivory will reduce plant fitness (reproductive capacity) (Bigger & Marvier, 1998). We deal with the reasons for plant survival against such odds in later chapters. In the meantime, it is worth noting that some 10% of all annually produced biomass is consumed by insect herbivores (Barbosa & Schultz, 1987; Coupe & Cahill, 2003).

The extent of plant loss, however, is dependent on a number of factors, including vegetation type, timing of herbivory, and locality. Thus, herbivore pressure is likely to be greater in tropical dry forests than in temperate forests (Coley & Barone, 1996), with the result that rates of herbivory are significantly greater in forests in tropical regions than those in temperate zones (Coley & Aide, 1991; Figure 1.4). Variation in the damage caused by herbivory also exists between different species of plants. Thus, up to 50% of foliage production by Australian *Eucalyptus* trees can be lost as a result of insect herbivory, while other plant species, for example, *Juniperus* and *Rhododendron*, exhibit little damage from insects (Schoonhoven *et al.*, 2005). Considerable variation in damage resulting from insect herbivory also exists within the same genus. In a study of herbivory among different *Piper* species, some suffered little damage from insects, while other species lost up to 25% of their leaf area (Marquis, 1991; Figure 1.5).

Insect herbivory affects many plant parts, including leaves, roots, and seeds. Perhaps the most obvious signs of insect herbivory are seen on leaves. It is estimated that rates of defoliation caused by insects lie within the range 5–15% of leaf area per year (Landsburg & Ohmart, 1989), although this is thought to be an underestimate (Crawley, 1997). Less obvious to the observer is perhaps root herbivory, although this is more likely to have an impact on plant dynamics than leaf herbivory (Crawley, 1997). Whatever plant part

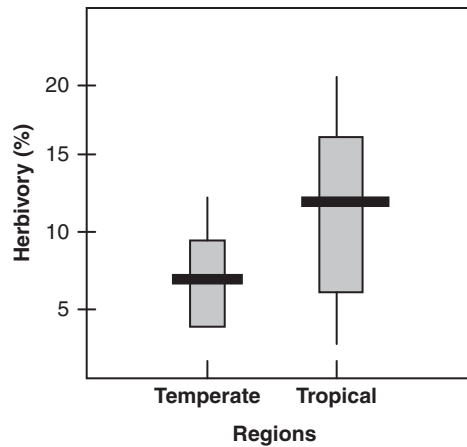


Figure 1.4 Rates of herbivory in temperate and tropical forests. Plots indicate mean \pm SD and range. (From Schoonhoven *et al.* (2005), with permission of Oxford University Press.)

is used by insects as food, herbivory can have a sizeable impact on plant growth. For example, to study the effect of insect herbivory on tree growth in a eucalyptus forest, trees were sprayed with insecticide for several years (Morrow & LaMarche, 1978). Tree growth was substantially greater in sprayed trees, which had reduced insect loads, compared to unsprayed trees, which harbored greater insect numbers. Interestingly, while defoliating insects exerted little impact on acorn production by oaks (*Quercus robur*), the exclusion of sucking insects by spraying with insecticide increased acorn production consistently (Crawley, 1985).

Feeding by different types of insect herbivore can affect plant fitness more or less independently. For example, in *Lupinus arboreus*, the bush lupin, there was no statistical interaction between above ground and below ground herbivory, and both types had significant

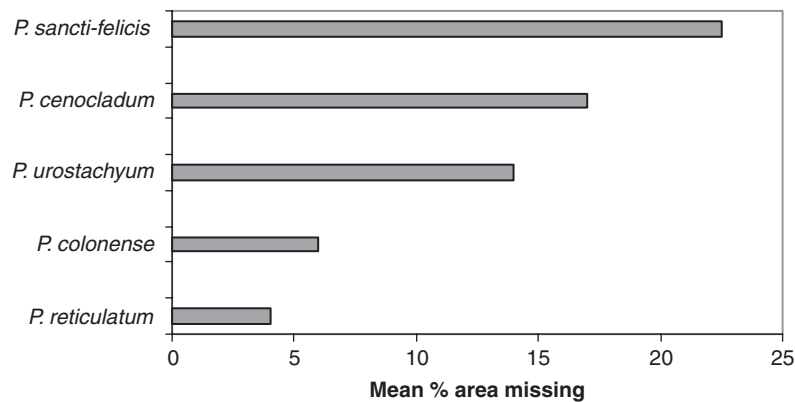


Figure 1.5 Rates of herbivory for different species of *Piper*. The data represent the mean percentage area missing for individual *Piper* species for a minimum of 50 freshly abscised leaves per species. (From Schoonhoven *et al.* (2005), with permission of Oxford University Press.)

10 Plant Defense

cumulative effects on plant fitness. When bush lupin plants were protected from chronic above ground herbivory, seed output over a 3-year period increased by 78%, while suppression of below ground herbivory increased mean seed production by 31%. Interestingly, root herbivory was associated with a greater risk of plant mortality (Maron, 1998).

Plants in agricultural ecosystems often suffer more damage as a result of insect herbivory than their natural counterparts. As a result, considerable quantities of insecticide are used to control insect pests. Nevertheless, it is estimated that some 15% of global crop production is lost annually to insect damage, despite the use of insecticides. It is estimated that some 9000 species of insects attack agricultural crops worldwide, although only about 450 of these are considered as serious pests (Pimentel, 1991). Most insect pests are specialist feeders, with 75–80% of lepidopterous pests being monophagous or oligophagous (Barbosa, 1993).

1.3.5 Vertebrates

As mentioned above, because of their size, vertebrate herbivores are likely to remove more plant tissue per mouthful than their invertebrate counterparts. However, invertebrate herbivores are probably ten times more abundant than vertebrate herbivores (Peters, 1983). Herbivores are estimated to remove about 10% of net primary production in terrestrial environments (Crawley, 1983), and indeed, if we look at the Nylsvley savanna in southern Africa, for example, vertebrate grazers and browsers are estimated to remove 6% and invertebrate herbivores (grasshoppers and caterpillars) are estimated to remove 5% of the above ground primary production (Figure 1.6). The amount of vegetation removed by vertebrate herbivores depends greatly on habitat and the herbivore. For example, although in arctic areas, vertebrate herbivores remove between 5 and 10% of net primary production (Mulder, 1999), lemmings and geese can remove as much as 90% (Cargill & Jefferies, 1984), while muskoxen remove only 1–2% of vegetation (Bliss, 1986). Their greater body

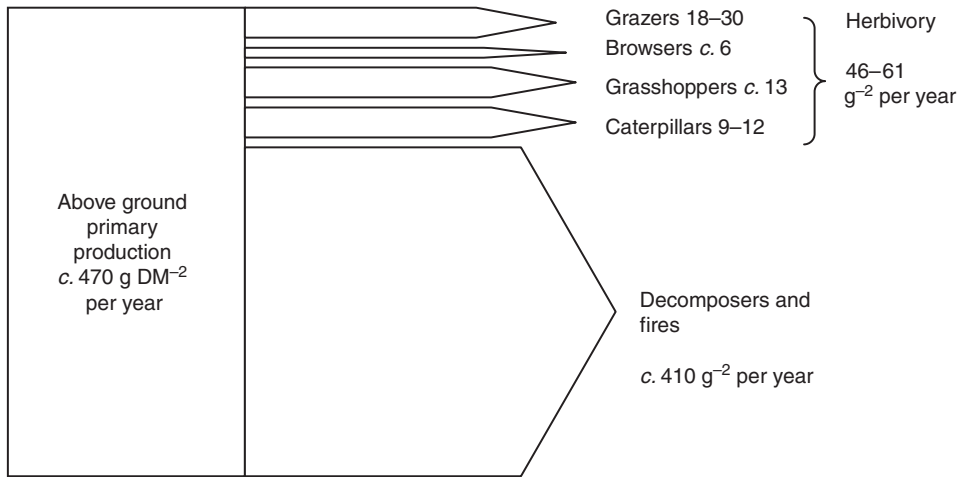


Figure 1.6 Pathways of disappearance of leaf material in the broad-leaved savanna at Nylsvley, South Africa, and their approximate magnitude. (Reproduced from Danell & Bergström (2002), with permission of Blackwell Publishing Ltd.)

size—polyphagy, individual bite size, mobility, and tolerance of starvation—suggests that vertebrate herbivores should exert a more immediate, and in the long term a more profound impact on plant populations than invertebrate herbivores (Danell & Bergström, 2002).

Some plants can tolerate vertebrate herbivory, and there is still debate about whether this tolerance is an evolutionary response to herbivory, and if so, whether grazing or browsing can benefit the plant in terms of increased fitness. The increase in net primary productivity of savanna grasses (McNaughton, 1979) and increased flower production in *Ipomopsis aggregata* (Paige, 1992) following herbivory are examples of the possible increase in plant fitness by vertebrate herbivory. However, vertebrate herbivory can deleteriously affect plant reproductive tissue and fecundity. Thus, simulating rodent damage to bilberry by branch cutting led to negative effects on flower production and berry development (Tolvanen *et al.*, 1993), while sheep grazing on a shrub in the Karoo rangeland in South Africa reduced both flower production and seed size (Milton, 1995). Equally, there are examples where vertebrate herbivory exerts minimal impact on plant fitness, as in the case of ungulate grazing of *Balsamorhiza sagittata* (Asteraceae), a dominant native perennial forb in western Montana, USA. Here, in comparison to insect herbivory, vertebrate grazing had little impact on plant fecundity (Amsberry & Maron, 2006).

Plant size and shape can be altered by herbivory (e.g., removal of the leading shoot or apical bud in woody species), with consequences for interplant competition and effects on other organisms. Even removal of a small amount of plant biomass can have a profound effect on plant shape. Thus, removal of the leading shoot of a tree by vertebrate grazing can alter the architecture of the whole tree for many years.

Although vertebrate herbivory does not often result in plant death, mortality can occur, especially when vertebrates feed on small plants or seedlings (Hulme, 1994), or when older trees are debarked, by, for example, elephants, deer, squirrels, voles, and hares (Danell & Bergström, 2002).

1.4 Conclusions

Plants are attacked by a wide range of organisms, from viruses and bacteria to large vertebrates. These interactions can have a considerable impact on natural plant populations and indeed are thought to represent a major selective force on the evolution of plant structure and function. In crop situations, attack by pathogens and herbivores can result in serious losses in yield and quality. However, as we shall see in the following chapters, plants are not defenseless against such attacks, no matter how large the attacker.

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14 Plant Defense

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