

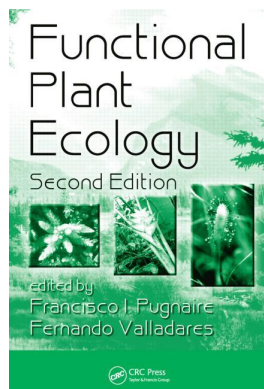
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Publisher: *CRC Press*

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Functiona Plant Ecology

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Plant–Herbivore Interaction: Beyond a Binary Vision

Publication details

<https://www.routledgehandbooks.com/doi/10.1201/9781420007626.ch16>

Elena Baraza, Regino Zamora, Jose' A. Hodar, José M. Gomez

Published online on: 20 Jun 2007

How to cite :- Elena Baraza, Regino Zamora, Jose' A. Hodar, José M. Gomez. 20 Jun 2007, *Plant–Herbivore Interaction: Beyond a Binary Vision* from: *Functiona Plant Ecology* CRC Press

Accessed on: 05 Dec 2023

<https://www.routledgehandbooks.com/doi/10.1201/9781420007626.ch16>

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16 Plant–Herbivore Interaction: Beyond a Binary Vision

*Elena Baraza, Regino Zamora, José A. Hódar,
and José M. Gómez*

CONTENTS

Introduction	482
Plant Traits That Determine Herbivory	482
Probability of Being Found	482
Physical Barriers	483
Quality of Plants as Food	483
Variability of Plants as Food: Theory of Plant Defense	484
Variability of Plants as Food: Effects of Plant Stress	486
Effect on Plant Performance and Populations	486
Herbivory and Plant Performance	486
Factors Affecting Tolerance to Damage	487
Capacity of Compensation	488
Induced Resistance	488
Herbivory and Plant Population Dynamics	489
Herbivory and Plant Distribution	490
Evolutionary Play	490
Plant–Herbivore Coevolution?	490
Cost of Defense	491
Evolution of Plant Tolerance versus Plant Resistance	491
Multispecific Context of Herbivory	491
Effect of Herbivores on Plant–Plant Interaction	492
Affecting Competition between Plants	492
Associations among Plants Sharing Herbivores	493
More than One Herbivore	494
Above and Belowground Multitrophic Interactions	494
Interactions between Herbivores and Pathogens	494
Effect of Herbivores on Mutualism Involving the Host Plant	495
Effect on Pollen-Dispersal System	495
Effect on Plant–Mycorrhiza Interaction	495
Multispecific Interactions	496
Plant–Herbivore Interaction: A Multispecific Vision	498
Case Study 1. Climate Effects on Insect Outbreaks: The Pine Processionary	498
Case Study 2. Conditional Outcomes in Plant–Herbivore Interactions: Neighbors Matter	499

Case Study 3. Ungulates Affect Populations of Both Plants and Other Co-Occurring Herbivores	500
Acknowledgments	501
References	501

INTRODUCTION

Herbivory is currently defined as the interaction that results when an animal consumes the live tissues of a plant (i.e., a heterotroph preying on an autotroph), usually without causing the plant's death (Crawley 1983). It is an antagonistic interaction, in which the animal gets food whereas the plant loses live tissues. This makes herbivory the most basic trophic interaction in the food chain. Herbivory has given rise to the appearance of marvelous phenotypic traits both in plants and animals, has molded the vegetation as well as entire landscapes of virtually all the ecosystems known on earth, and, finally, has determined the success of many species, including our own. Herbivory, thus, deserves firm attention from ecologists.

In the previous version of this chapter, we conducted a review to identify the features that drive current research in plant–herbivore interactions in terrestrial ecosystems (Zamora et al. 1999). In general, the systems traditionally studied were simple pairs (one plant vs. one herbivore of interacting elements), and research on herbivory typically concerns adult plants (woody or herbaceous) affected by defoliation either by insects or vertebrates and analyzing mainly plant chemistry or growth in a simple pair of protagonists. Consequently, herbivory has been viewed mainly as a binary interaction, and the aim of this chapter is to transcend this limited view, examining from a phytocentric perspective the effect of herbivory within a broader ecological framework.

The literature on plant–herbivore interactions in terrestrial ecosystems is vast. The readers can consult many excellent reviews on more specific aspects of plant–herbivore interactions published in such journals as *Annual Review of Ecology, Evolution and Systematics*, *Trends in Ecology and Evolution*, and the minireview section in *Oikos*.

PLANT TRAITS THAT DETERMINE HERBIVORY

In most habitats, plants are abundant, and therefore food quantity is, in principle, not a problem for herbivores. However, plants are not a highly profitable food because they bear compounds of low nutritive value (high content in cellulose and low in proteins) and substances that reduce digestibility, thus hampering the herbivore's nutrient acquisition (Hartley and Jones 1997). Moreover, there are many ways that a plant may avoid herbivores. Some avoidance mechanisms have been extensively studied in early and current plant–animal interaction research, whereas other mechanisms are relatively unexplored (Milchunas and Noy-Meir 2002).

PROBABILITY OF BEING FOUND

As the first step in herbivory, the plant must be found by the herbivore. There are several traits that reduce the plant's probability of being discovered, as for example, remaining inconspicuous within a given habitat, in terms of both morphology and abundance, occupying enemy-free sites, mimicking another well-defended plant (Lev-Yadun and Ne'eman 2004 and references therein) or damaged tissue, completely lacking chemical attraction (odorless), having a short life cycle, and asynchronous timing—that is, the plant produces edible tissues in the period least likely to coincide with herbivore presence or feeding (Chew and Courtney 1991, Aide 1992, Tikkanen and Julkunen-Tiitto 2003).

Another way to escape detection at the individual level includes synchronizing as closely as possible the production of tissues subject to attack (flowers, leaves, or fruit), both within the same plant and among plants of a population. This strategy, termed mass flowering or fruiting, attempts to overwhelm the herbivore's capacity to consume all the tissues available. Plants with mass flower or fruit production benefit from dense populations. In this way, the effect of time is multiplied by the effect of space (Kelly and Sork 2002, Crone and Lesica 2004, Russell and Louda 2004).

Herbivore-free sites could be considered as refuges, providing a degree of physical barrier against the herbivore. Milchunas and Noy-Meir (2002) considered two types of refuges: biotic, when a plant protects a target plant, and geologic. A rock outcrop, mesas, buttes, or islands can act as geological refuges that permitted the subsistence of more palatable species. An intensive literature survey was conducted on studies examining plant-community composition of geologic refuges compared to similar grazed communities reporting increases in diversity inside the refuge (Milchunas and Noy-Meir 2002).

PHYSICAL BARRIERS

After finding a host plant, herbivores must overcome other barriers. Plants have a myriad of structures to repel prospective herbivores (Lucas et al. 2000). These include scales, barbs, thorns, and spines, which are particularly effective against mammals (Grubb 1992, Young et al. 2003), and trichomes, leaf hairs, and similar structures meant to discourage invertebrate approach (Bernays and Chapman 1994, Van Dam and Hare 1998). In the same way, some plants (e.g., *Cariophyllaceae*) have glands that secrete an adhesive to hamper small pests from crawling freely over the plant; these glands, which trap primarily small arthropods, are thought to have given rise to carnivory in plants. Recent studies in conifer stems showed calcium oxalate crystals as a constitutive defense, which in combination with fiber rows provides an effective barrier against small bark-boring insects (Hudgins et al. 2003, Franceschi et al. 2005). In addition, leaf toughness is considered as mechanical defense, since tougher leaves are avoided by herbivores (Lucas et al. 2000, Teaford et al. 2006).

Spines appear more in zones subject to heavy herbivore pressure, and even within an individual plant, parts less accessible to mammal herbivores tend to bear fewer spines than do vulnerable parts (Grubb 1992). Several recent studies had found a direct relation between herbivory and spines density and size (Takada et al. 2001, Young et al. 2003). Furthermore, it has been demonstrated that spines have a negative effect on herbivore performance, reflected by consumption rate (Cooper and Owen-Smith 1986, Milewski et al. 1991, Gowda 1997).

QUALITY OF PLANTS AS FOOD

Herbivores are faced with a poor-quality food resource not only because plants are low in nutrients but also because they produce plant secondary defense compounds that have wide-ranging physiological effects from direct toxicity to digestion impairment (Hartley and Jones 1997). Some of the chemical characteristics that reduce the quality of plants as food are a direct result of its functioning (Coleman and Jones 1991). For instance, the main reason for which the cell wall of higher plants consists mainly of cellulose, hemicellulose, and lignin is the necessity of support for their tissues, to overgrow the neighbors, and transport resources. In fact, these three substances comprise the primary component of the biomass of trees (*c.*90%) and grasses (*c.*65%). However, most herbivore animals cannot directly use this superabundant food resource because they cannot produce the enzymes necessary for decomposing them. Not only do some compounds of primary metabolisms act as digestibility reducers, but also some secondary compounds (e.g., cutins, tannins, and silicate particles—Howe and Westley 1988) increase the large fraction of vegetal tissues consisting of nondigestible vegetal material.

In general, they are quantitative (or chronic) metabolites, which exert their effects according to their concentration within the plant, and do not act instantaneously, but rather gradually depress the growth or fecundity of the herbivore. In addition to reducing digestibility, silicate particles also accelerate tooth wear by the abrasion of mouthparts, contributing to the development of esophageal canker, and may cause fatal urolithiasis due to the formation of calculi in the urinary tracts (McNaughton et al. 1985). Consequently, herbivores generally reject plant parts containing high concentrations of this compound.

Thus, herbivores are limited not by the energy available but by the nutritional quality of plant tissues (White 1993). This is because there are strong stoichiometric differences between the composition of plant and animal tissues; that is, plant matter, compared with animal tissues, is higher in carbon and lower in other essential elements, such as N, P, and S (Sterner and Hessen 1994). As a whole, animal herbivores contain nearly 10 times more nitrogen than do the plants that they eat. Thus, the plant–animal interface is characterized by a marked disparity in the biochemical makeup of consumer and resource. Furthermore, not all mineral nutrients present in vegetable tissues are equally available to herbivores. For instance, such nitrogen sources as proteins can be easily assimilated, whereas several nitrogenous compounds (alkaloids, cyanogenic glycosides) may even be poisonous. In this case, the total nitrogen concentration may not reflect the nutritional values of the plant tissue (Bentley and Johnson 1992).

Consequently, herbivores live in a “green desert” and are critically dependent (especially for female reproduction, Moen et al. 1993) on relatively rare, high-quality plants, or plant organs. Herbivores must, therefore, selectively ingest and assimilate essential limiting minerals. For example, McNaughton (1988) found that the heterogeneous distributions of African ungulates correlated significantly between animal density and levels of minerals such as magnesium, sodium, and phosphorous in vegetation. Similar cases have been found for many different herbivores (insects: Mattson 1980; sea urchins: Renaud et al. 1990; small mammals: Batzli 1983). Despite this dietary selectivity, the chemical composition of herbivore diets is generally unbalanced. The result is that herbivores must consume large quantities of carbon to obtain enough nitrogen and other essential nutrients. The resulting nutritional imbalance can decrease growth efficiency for herbivores, and could filter down from the top of the food chain, causing reduced production at all trophic levels. For example, assimilation efficiency of herbivores is lower (20%–50%) than that of carnivores (nearly 80%, Begon et al. 1990). This nutritional limitation has forced some herbivore species to develop opportunistic feeding strategies to obtain alternative and complementary food nutritionally richer than vegetal tissues (see White 1993 for a thorough revision).

Other types of compounds that reduce the quality of vegetal food are secondary defense compounds. These compounds, accumulated from enzyme catalysis in biosynthesis (Harborne 1997), wield their influence by their sheer presence (qualitative secondary metabolites), striking with immediacy and often inflicting death on the herbivore, many of them acting as inhibitors of tissue digestibility or as poison for herbivores. Normally, these compounds accumulate in tissues unprotected by quantitative substances—new leaves, immature fruits, or flower buds. There is a great variety of secondary defense compounds that, together with the structures of mechanical defense (spines, thorns, barbs, hairs), constitute the main traits that reduce the preference or performance of herbivores, this translating as the resistance of plants (Strauss and Agrawal 1999). The principal chemical compounds of this type are alkaloids, glucosinolates, toxic amino acids, terpenoids, and cyanogenic compounds (e.g., Rosenthal and Berenbaum 1991, Harborne 1997).

VARIABILITY OF PLANTS AS FOOD: THEORY OF PLANT DEFENSE

The herbivores are exposed to temporal and spatial variations in the abundance and quality of their food (Hunter and Price 1992, Danell and Bergström 2002). Variations in abundance

are intimately linked to annual plant phenology, and vegetation response to climatic variations, whereas internal processes are related to the growth, development, and reproduction of the plant, as well as response to environmental variations (Hartley and Jones 1997). For example, it is well established that plant chemical characteristics change in the course of a season in the same plant (Dement and Money 1974, Schultz et al. 1982, Riipi et al. 2002). Moreover, plants may differ in their quality as food for herbivores whether between different species, between individuals of the same species, or between parts of the same plant (Orians and Jones 2001). These variations can be measured as differences in nutritional value, concentration of chemical and physical defenses, as well as morphological characteristics of twigs and tissues (Hartley and Jones 1997, Danell and Bergström 2002). Dissimilarities in environmental growing conditions (Bryant et al. 1983, Coley et al. 1985, Larsson et al. 1985, Walls et al. 2005, MacDonald and Bach 2005), differing histories of relationships with herbivores (Provenza and Malechek 1984), or genetic differences (Graglia et al. 2001, Oiser and Lindroth 2001) provoke this high variability in plant characteristics, creating a nutritional mosaic for herbivores. For example, plant secondary defense compounds exhibit some of the highest diversities seen in nature.

During the last 30 years several theories have tried to explain the pattern of distribution observed in the concentration and distribution of secondary defense compounds in the different plant species. Berenbaum (1995), for instance, lists as many as 12 different theories to account for the allocation of chemical defenses in plants, and a few more hypotheses have been added to this list recently. Many studies have tried to test the most plausible of these theories, uncovering evidences in favor of and against most of them, without a clear prevalence of one above the others (Stamp 2003). Some authors emphasize the risk of herbivory as the main factor determining the quantity and type of defensive compounds in plants. Thus, according to the apparency theory (Feeny 1976, Rhoades and Cates 1976), “apparent” species (long-lived plant species, with a dominant presence in landscapes) have a greater damage probability and thus require a greater investment in defense, favoring digestibility-reducing chemicals (e.g., tannins), whereas less apparent species are defended by toxic chemicals (e.g., alkaloids). Grubb (1992) developed this theory, taking into account the nutritive value of tissues exposed to herbivore damage.

Other authors consider resource availability as the key factor determining the amount and kind of defenses that plants produce. The carbon/nutrient balance theory (Bryant et al. 1983) is based on the idea that the relationship between the availability of carbon and nitrogen in the environment determines the kind and the amount of resources that a plant invests in defense or growth. The growth/differentiation balance hypothesis assumes that the synthesis of defensive compounds is constrained not only by the external availability of resources but also by internal trade-offs in resource allocation between growth and defense (Herms and Mattson 1992). The resource-availability hypothesis (Coley et al. 1985) predicts that differences in toxicity might depend on the costs versus benefits of defending plant parts in a way that low resource availability favors plants with inherently slow growth rates, which in turn favors large investments in anti-herbivore defense. More recent hypotheses attempt to explain allocation patterns in terms of biosynthetic differences between types of defensive compounds sink/source hypothesis (Honkanen and Haukioja 1998), particularly among terpenoids and different classes of phenolics (Muzika and Pregitzer 1992, Haukioja et al. 1998, Koricheva et al. 1998a), and competition between protein and phenolic synthesis for the common precursor, L-phenylalanine (Jones and Hartley 1999). Some authors defend the evolutionary origin of the resistance characteristics on plant. The optimal-defense theory (Rhoades 1979, Hamilton et al. 2001) argues that the evolution of the defenses in a plant is governed mainly by the balance between the metabolic cost of the defense production and the benefit obtained from the reduction of the loss of tissues by herbivory. Assuming a genetic control of plant defense, herbivores represent a selective pressure that favors the

production of secondary defense compounds depending on the cost or benefit for the plant fitness (Hamilton et al. 2001).

None of the above theories of chemical defense have ever been definitively rejected; they all coexist by virtue of supportive evidence in one system or another (Stamp 2003). Only in the case of carbon/nutrient balance hypothesis, several authors consider that the fundamental assumptions have proved to be incorrect (Berenbaum 1995, Koricheva et al. 1998a), considering the use of carbon/nutrient balance hypothesis no longer logically or philosophically justifiable (Hamilton et al. 2001, Koricheva 2002a, Nitao et al. 2002).

VARIABILITY OF PLANTS AS FOOD: EFFECTS OF PLANT STRESS

There are two contrary theories that seek to explain how the effect of environmental stresses on plant quality as food can affect the preference and performance of herbivores, especially insects. The plant-stress hypothesis (White 1993) predicts that environmental stresses on plants decrease plant resistance to insect herbivory by altering biochemical source–sink relationships and foliar chemistry, to increase the availability of nutrients for herbivores (e.g., soluble amino acids in phloem). Such changes in the nutritional landscape for insects may facilitate insect population outbreaks during periods of moderate stress on host plants. However, not every kind of stress provokes the same response in plants, and there are cases in which stressed plants represent suboptimal food with respect to control plants (e.g., see Mopper and Whitham 1992). According to Mopper and Whitham (1992), sustained environmental stress (poor soils or persistent drought), by causing numerous metabolic changes (e.g., increasing soluble nitrogen availability, reducing secondary compounds), can be beneficial to insects, whereas a brief drought period during insect oviposition may harm herbivore performance. By contrast, Price (1991) stated that some specialized herbivores feed preferentially on vigorous plants or plant modules (plant-vigor hypothesis). It appears that the latter applies especially to insect herbivores most closely associated with plant growth processes, as endophytic gallers and shoot borers (Price 1991, but see Rehill and Schultz 2001). Recent studies also found a better performance of other types of insects in more vigorous plants (Inbar et al. 2001). For example, in the leaf miner *Agromyza nigripes* (Agromyzidae), larva performance (density, survival, and development) was highest on vigorous plants (De Bruyn et al. 2002). In addition, the grass miner *Chromatomyia milii* (Agromyzidae) prefers and performs better on vigorously growing plants not exposed to excess nutrients (Scheirs and De Bruyn 2004) or water stress (Joern and Mole 2005). Many insect species feed specifically on certain plant tissues, which are likely to be differentially affected by stressful conditions. Consequently, the effect of stress on insect performance would vary depending on local plant response to this source of stress (Koricheva et al. 1998b). The revision of diverse studies by Koricheva et al. (1998b) showed that in general, boring and sucking insects performed better on stressed plants, whereas plant stress adversely affected gall-makers and chewing insects. Reduction in performance of chewers was greater on stressed slow-growing plants than on stressed fast growers. Reproductive potential of sucking insects was increased by pollution but reduced by water stress. Furthermore, Huberty and Denno (2004) described consistent positive effects of water stress for borers, negative responses for gall-formers, and inconsistent responses for free-living species and leaf miners.

EFFECT ON PLANT PERFORMANCE AND POPULATIONS

HERBIVORY AND PLANT PERFORMANCE

In natural systems, herbivory is often detrimental to plants as it removes resources through loss of nutrients and photosynthetic area. However, the effects of the herbivory plants are not the simple result of the foraging behavior of the herbivores on vegetation, but also the result

of the different capacities of the plants to react against herbivory (Augustine and McNaughton 1998). A plant may respond to herbivore attack via induced defense, which is important in understanding plant life-history traits (Iwasa 2000). Induced defense takes two basic forms: resistance and tolerance. Tolerance is a plant's ability to reduce the negative effects of consumers (e.g., herbivores, pathogens) on plant fitness (Rosenthal and Kotanen 1994, Stowe et al. 2000), in some cases not only compensating for tissue loss but also overcompensating by increase in plant growth and fitness after herbivory (Strauss and Agrawal 1999). Such responses to herbivory are called induced resistance when they are known to decrease rates of herbivory (Karban and Baldwin 1997). Constitutive resistance is always expressed, whereas induced resistance appears only after an individual has been damaged, serving to reduce additional damage.

Factors Affecting Tolerance to Damage

The tolerance capacity of plants is species-specific and highly dependent on the type of tissue damage, on plant age, and on the amount, pattern, timing, and frequency of herbivory, and the environmental conditions in which the plant is growing.

The impact that herbivory exerts on plant performance is more dependent on the role of the tissue damaged than on the total biomass lost. Although defoliation signifies the loss of photosynthetic tissues, the damage of other tissues such as meristem can have more detrimental effects (Spotswood et al. 2002). Flower and fruit damage implies a greater loss of female reproductive success than does injury to other tissues (Dirzo 1984, Hendrix 1988). This loss may be reflected directly by the diminished number of ovules after herbivore feeding on flowers (Dirzo 1984, Wise and Cummins 2006). Root herbivory is very difficult to investigate and is often a neglected facet of plant–herbivore interaction, despite the fact that below-ground herbivory can have dramatic consequences for plant performance (Prins et al. 1992, Müller-Schärer and Brown 1995, Bebbler et al. 2002, Blossey and Hunt-Joshi 2003).

The impact of herbivory also depends on the age of the plant. Plant tolerance to herbivore damage appears to be high in the cotyledon stage, declines in later seedling stages, but then increases as plants reach the sapling and the reproductive stage (Boege and Marquis 2005). This pattern can change when root damage is analyzed, since seedlings have less root development than do saplings (Stout et al. 2002). Herbivores influence plant mortality primarily at the seed and seedling stages (Harper 1977, Hulme 1996). In this case, herbivory is analogous to predation.

Foliar and stem loss can have a detrimental or stimulatory effect, or no effect at all, on plant growth or reproduction, depending on the intensity and timing of the loss (Maschinski and Whitham 1989, Hester et al. 2004). Even within a modular unit (such as a leaf), the timing of herbivory can have differential effects. For the plant, herbivory losses are more harmful when leaves are young than when leaves are older, especially toward senescence (Harper 1977). Browsing damage to woody plants is also less detrimental at the beginning of the growing season than later (Guillet and Bergström 2006). Moreover, while seedlings may overcompensate for tissue browsed during the dormant season, they may not compensate for tissue lost while a plant is actively growing (Canham et al. 1994, Bergström and Danell 1995).

The frequency of damage is also important for plant tolerance capacity. In saplings of some tree species, the repeated loss of the apical meristem forcibly modifies the architecture of the tree, from tall to dwarf individuals, and retards the timing of the first reproductive season. For example, in the Sierra Nevada, some wild and domestic ungulates feeding on saplings of Scots pine *Pinus sylvestris nevadensis* (Pinaceae) and other tree species develop stunted morphologies due to browsing by Spanish ibex and domestic goats (Zamora et al. 2001).

Capacity of Compensation

Compensation enables damaged plants to maintain their fitness through extra growth and reproduction and may involve a variety of physiological and morphological mechanisms, including increased photosynthesis and altered patterns of resource allocation, differential balance in vegetative and reproductive tissues, changes in nutrient uptake, and altered hormonal balance (see Rosenthal and Kotanen 1994). Several studies have found that compensation follows herbivore attack (Hendrix and Trapp 1989) or experimental clipping (Ehrlén 1992, Obeso and Grubb 1994), and at low levels of herbivory, plants may even overcompensate for damage (Belsky 1986).

Compensation capacity after herbivory is very different between species (Rosenthal and Kotanen 1994, Hawkes and Sullivan 2001). For example, deciduous woody plants tend to have more flexible growth patterns and thus a greater ability for compensatory growth than certain evergreen species such as pines (Vanderklein and Reich 2000, Millard et al. 2001, Hester et al. 2004). Different plant characteristics can be crucial to offset herbivore damage depending on the tissue removed. For example, since browsing damage is more likely to lead to loss of the nutrients stored in foliage or aboveground woody tissues than in trunk or roots, species that store nutrients in the trunk and roots may have more tolerance capacity to browsing damage (Baraza 2004).

Furthermore, many extrinsic factors influence a plant's physiological state and, as a consequence, its ability to compensate for damage (Herms and Mattson 1992). It has long been assumed that a plant's tolerance to herbivory should be greater in low-stress, resource-rich environments, and this assumption has been formalized in what has become known as the compensatory-continuum hypothesis (Maschinski and Whitham 1989). For example, light availability affects the plant's capacity to tolerate herbivory, by determining to a great extent the carbon resources for the synthesis of chemicals and growth, so that, when light is a limiting resource, tolerance diminishes (Lentz and Cipollini 1998, Harmer 1999, Saunders and Puettmann 1999, Baraza et al. 2004). However, resource availability does not affect all species in the same way. Hawkes and Sullivan (2001) in a review by meta-analysis showed that basal meristem monocots in general grew significantly more after herbivory in high resources, while both dicot herbs and woody plants grew significantly more after herbivory in low resources. Wise and Abrahamson (2005) proposed an alternative model, called the limiting-resource model, which specifically identifies the factors that limit plant fitness and the resources that are affected by particular herbivores.

Induced Resistance

Induced plant resistance refers to any active or passive change in the plant after herbivory or infection, which reduces preference, performance, or pathogenicity of the attacker on attack compared with controls (Karban and Baldwin 1997). As in the case of tolerance, resistance induction differs between species and is subject to environmental conditions as well as intensity, timing and pattern of damage (Karban and Baldwin 1997, Nykänen and Koricheva 2003). The common induced-resistance trait analyzed is biochemical change (e.g., increase of toxin or decrease in nutrient value) in the tissues remaining after herbivory (Nykänen and Koricheva 2003). However, there are other types of induced resistance, including heavier mechanical defense (Gómez and Zamora 2002, Young et al. 2003) or changes in morphology that reduce herbivore intake rates (Massei et al. 2000, Martínez and López-Portillo 2003).

Induced plant responses to herbivory have been shown to be a cost-saving strategy (Cipollini 1998, Agrawal et al. 2002). That is, given the costly nature of plant allocation to defense, plant fitness could be enhanced by only allocating to resistance in the presence of herbivory. However, Koricheva (2002b) analyzing diverse studies by meta-analysis detected similar costs of both types of resistance, when constitutive resistance is associated mainly with

metabolically cheap defenses, whereas inductibility evolved primarily in expensive defenses. In addition, cost saving represents only one of many possible reasons why induced resistance may be favored or maintained by selection (reviewed in Agrawal and Karban 1999). For instance, another important but less explored potential benefit of induced resistance may be increased spatial and temporal variability in food quality for herbivores (Shelton 2000).

HERBIVORY AND PLANT POPULATION DYNAMICS

It has been demonstrated repeatedly that the performance (growth, reproductive output, and survival) of many plant species is negatively affected by the severe impact inflicted by vertebrate and invertebrate herbivores (Marquis 1992a,b, Guretzky and Louda 1997). Contrasting with this copious literature concerning the effect of herbivores on individual plants, much less empirical information exists on the real effect that these organisms have on the abundance and density of plants (Maron and Crone 2006). Consequently, the importance of herbivory for plant populations remains a controversial issue (Hendrix 1988, Andersen 1989, Crawley 1989, Eriksson and Ehrlén 1992, Marquis 1992a,b, Osem et al. 2004). Although herbivores can theoretically affect plant abundance by arresting recruitment as a consequence of their detrimental effect on plant performance, only a few studies have been able to experimentally demonstrate this effect. Carson and Root (2000) demonstrated that phytophagous insects control the abundance of goldenrod *Solidago altissima* (Asteraceae), whereas Maron and Simms (2001) showed that granivory by rodents affects *Lupinus arboreus* (Fabaceae) recruitment and thereby adult abundance. Unfortunately, the effect of herbivores on plant-population dynamics is usually inferred from their mere effect on some demographic components, such as seed germination, seedling emergence, or juvenile recruitment (Crawley and Long 1995, Louda and Potvin 1995, Hulme 1996, 1997, Curran and Webb 2000, Maron and Gardner 2000, Wenny 2000, Ehrlén 2003).

However, two main nonexclusive reasons suggest that it is not accurate to infer any effect on populations merely from the effects on demographic components. First, incomplete components of the performance of plants, such as seed production or seedling survival, cannot be universally used as a substitute for total performance, since total performance in many plant species represents the integration of the effects occurring during different phases of the life cycle (Ehrlén 2003). Focusing on a single component overlooks important trade-offs between different demographic components (Ehrlén 2002). Indeed, a strong effect of herbivores on a particular component of the life cycle of plants can be counteracted by compensatory effects on other components (Ehrlén 2002, 2003). Second, a significant herbivore effect on host-population dynamics takes place only when the number of propagules entering the adult stage is smaller than the number of deaths by herbivory (i.e., the recruitment rate is lower than the death rate, Harper 1977). Under field conditions, plant recruitment depends on the availability of seeds (seed limitation) as well as on the availability of suitable microsites for seed germination and seedling survival (establishment limitation, Eriksson and Ehrlén 1992, Clark et al. 1998, Edwards and Crawley 1999, Nathan and Müller-Landau 2000). When plant populations are limited mainly by the availability of microsites to germinate and become established, rather than by the production of seeds, an increase in propagule production (performance) due to a release from herbivores does not automatically translate into an increase in plant abundance (Hulme 1998, Turnbull et al. 2000). In this scenario, the outcome of the herbivory interactions can be neutral at the population level irrespective of their outcome at the plant–individual level. Consequently, when no information exists on the extent to which subsequent density-dependent compensation counteracts the effect of seed and seedling reduction caused by herbivores, a common mistake is to assume that a strong herbivore effect on plant performance implies an equally intense effect on plant population dynamics (Louda and Potvin 1995, Edwards and Crawley 1999, Hickman and Hartnett 2002).

HERBIVORY AND PLANT DISTRIBUTION

Several studies have suggested that some herbivores are able to shape the habitat distribution of their host plant (Bruehlheide and Scheidel 1999, Kleijn and Steinger 2002, DeWalt et al. 2004, and references therein). Two pieces of information have been used to support this proposal: the mere existence of habitat-dependence in the activity of herbivores (Boyd 1988, Herrera 1991, 1993, Gómez 1996, Louda and Rodman 1996, Cabin and Marshall 2000, Sipura and Tahvanainen 2000) and the effect of herbivore release in the habitat expansion of invasive plants (enemy-release hypothesis, Keane and Crawley 2002, DeWalt et al. 2004). Under these circumstances, the habitat distribution of many plant species inhabiting heterogeneous landscapes can be a direct consequence of the activity of their major herbivores (Jordano and Herrera 1995, Schupp 1995, Schupp and Fuentes 1995, Louda and Rodman 1996, Cabin and Marshall 2000, Rey and Alcántara 2000, Sipura and Tahvanainen 2000). Despite its crucial importance, the role that herbivores play in shaping the spatial distribution pattern of the plant populations remains unclear, most studies simply reporting the advantage for individual plants of growing close to neighbors or in specific microhabitats (Danell et al. 1991, Hjäältén et al. 1993, Hjäältén and Price 1997, WallisDeVries et al. 1999, Rebollo et al. 2002). More recent works concerning herbivores in affecting local plant distribution have been undertaken. For example, Gómez (2005a) demonstrated that herbivores influence the spatial distribution of two species of *Erysimum* (Brassicaceae), the distribution of which is limited under shrubs when ungulate herbivores are present (see *Case study 3*). Fine et al. (2004) demonstrated that heavy insect herbivory on tropical tree seedlings might be responsible for limiting the local distribution of particular tree species to sites with specific soil conditions.

EVOLUTIONARY PLAY

PLANT–HERBIVORE COEVOLUTION?

A traditional assumption among evolutionary ecologists is that herbivory tends to lead to coevolution (Ehrllich and Raven 1964), implying that there is simultaneous evolution of ecologically interacting populations, which means synchronous reciprocal adaptation. Contrary to this coevolutionary thinking, the theory of sequential evolution (Jermy 1993) states that plants evolve by selective pressures far more imposing than those exerted by herbivores. Thus, according to this idea, plants shape herbivore evolution, not vice versa. Although paired plant–animal coevolution is theoretically possible, such pairing remains unlikely in nature because most plants interact with an array of herbivorous species and vice versa. A plant species must often respond to the selective pressures exerted by a multispecific system (Simms and Rausher 1989, Meyer and Root 1993). The result can be a dilution of all selective pressures, because the pressure of one herbivore species on plant traits is often opposed, constrained, or modified by pressures of other herbivore species. In this context, diffuse coevolution (Janzen 1980) was suggested as alternative to pairwise convolution when selection imposed reciprocally by one species on another is dependent on the presence or absence of other species. In a recent review, Strauss et al. (2005) outlined a quantitative genetic approach for understanding and quantifying diffuse evolution, taking it as the more plausible evolutive relationship between plants and herbivores (Rausher 1996, Iwao and Rausher 1997, Agrawal 2000a, Rausher 2001).

For a herbivore to be said to select plant traits, a heritability base of the variability of those proposed defensive traits in plants and correlation between the trait (and the damage, of course) and plant fitness must be demonstrated. A genetic basis of the individual variation in damage has been recently shown as stronger than previously thought, since the relative

contribution of plant genotype with respect to environmental variability to determine resistance traits seems to be important in many of the studied systems (Agrawal and Van Zandt 2003). Increased fitness in defended plants when the herbivore is present has been demonstrated for plant-induced resistance to herbivory (Agrawal 1998). However, there are still doubts about the herbivore's role in the evolution of some plant-resistance traits, which could represent a secondary phenomenon that fortuitously benefits the plant (Tuomi et al. 1990). In fact, most of the traits currently related to herbivory would have evolved in a world without animals as a result of abiotic selection for vegetative growth and survival. For example, sclerophyllous leaves may be an adaptive mechanism related to water and nutrient conservation (Turner 1994). Even secondary compounds may now act exclusively as a defense against herbivores, since it has been demonstrated that they play a role in pollination and seed dispersal, pathogen interactions, allelopathic processes, and protection against ultraviolet rays (Bennett and Wallsgrove 1994, Waterman and Mole 1994, Close et al. 2003).

COST OF DEFENSE

The idea that adaptation is costly is a deeply entrenched principle in evolutionary biology. In an evolutionary context, the incremental fitness benefit associated with genotypes conferring greater defense on plants is accompanied by a forfeit in fitness associated with reallocation of resources away from other fitness-enhancing functions (Fritz and Simms 1992). This means that defense has a cost. Costs of defense production may arise by many mechanisms, including allocation trade-offs, ecological interactions, and genetic effects such as pleiotropy (Rausher 2001, Heil and Baldwin 2002). The empirical evidence for the existence of such cost is conflicting, suggesting that significant fitness costs of defense arise in some circumstances but not in others, depending on the environment in which they are measured, the resources available to the plant, and the ecological interactions of the community (Rausher 2001, Heil and Baldwin 2002, Strauss et al. 2002, Koricheva 2002b). For example, high resource availability may diminish allocation costs, thereby allowing for both growth and defense (Siemens et al. 2003, Walls et al. 2005, Donaldson et al. 2006).

EVOLUTION OF PLANT TOLERANCE VERSUS PLANT RESISTANCE

The joint evolution of plant tolerance and resistance to herbivores has attracted substantial theoretical attention over the last decade (Rosenthal and Kotanen 1994, Strauss and Agrawal 1999, Mauricio 2000, Stowe et al. 2000, Tiffin 2000a, Fornoni et al. 2003, 2004a,b). Resistance and tolerance have been considered for years as incompatible strategies of resistance against herbivores. However, Leimu and Koricheva (2006), reviewing the empirical evidence for tolerance-resistance trade-offs by means of meta-analysis, found that conditions under which a negative association between resistance and tolerance occurs and, thus, the evolution of multiple resistance strategies in plants is constrained, are much more restrictive than previously assumed. Mixed defense strategies, with resistance and tolerance, both maintained at intermediate levels, are possible when the cost of each defense rises disproportionately with its effectiveness (Fornoni et al. 2004a,b), and strongly negative genetic correlations between resistance and tolerance can promote polymorphism in each (Tiffin 2000b).

MULTISPECIFIC CONTEXT OF HERBIVORY

Herbivory has traditionally been viewed as a binary interaction focusing on a simple pair of interacting elements (one plant vs. one herbivore; see previous edition of this chapter). This species-to-species view of plant-herbivore interactions has been progressively challenged by

an increasing body of studies showing that plant–herbivore interactions are strongly affected in a predictable way by the community context (Björkman and Hambäck 2003, Strauss and Irwin 2004). Plants compete against other plants for substrate and nutrients at the same time as they may be simultaneously eaten by many herbivores and pollinated by many species of floral visitors. The importance of the community context becomes apparent with the observation that the strength and even the sign of the interaction between two species may change in the presence of others by the action of the so-called *indirect effects* (Strauss 1991, Strauss and Irwin 2004). Under these circumstances, scenarios in which only two or three species interact generally offer an overly simplistic and even inappropriate view of what in fact occurs in nature. In this section, we provide examples of multispecies systems in plant–herbivore interaction. A useful approach to the study of the enormous complexity of ecological communities is the “community modules” proposed by Holt (1997), involving a small number of species (3–6) linked in a specified structure of interactions. Most ecological studies on herbivory venture beyond the paired species traditionally analyzed in these types of subsystems (see later).

EFFECT OF HERBIVORES ON PLANT–PLANT INTERACTION

Affecting Competition between Plants

Competition from plant neighbors and herbivory are two factors that determine the growth, survival, and reproduction of plant individuals, and subsequently the abundance of plant populations (Harper 1977, Crawley 1983, Gurevitch et al. 2000). Herbivory influences the effect of competitive interactions between plants and vice versa.

Herbivores can impair the competitive abilities of their host plants (Harper 1977, Edwards 1989, Figure 16.1, *left*). The selective consumption of individual plants can result in a hierarchy of sizes within a given plant population and thereby increase the likelihood of asymmetrical competition between the plants (Weiner 1993). McEvoy et al. (1993) showed that herbivory on ragwort *Senecio jacobaea* (Asteraceae) by the beetle *Longitarsus jacobaea* (Chrysomelidae) intensifies the competition of the plant with other species, speeding the ragwort’s elimination, which would otherwise come about slowly. Moreover, herbivory by livestock can alter competition between plants. *Cirsium obalatum* (Asteraceae) and *Veratrum lobelianum* (Liliaceae), two large unpalatable native perennial herbs, had strong positive effects on the growth of two more palatable species, *Anthoxanthum odoratum* and *Phleum alpinum* (Poaceae) and no effects on unpalatable species *Luzula pseudosudetica* (Juncaceae) when livestock were present. Contrarily, inside exclosures they had no effect on palatable species and had competitive effects on *L. pseudosudetica* (Callaway et al. 2005).

Herbivory can also produce apparent competition among plants that share herbivores (Figure 16.1, *center*). An increase in density of one plant species results in a decrease in density

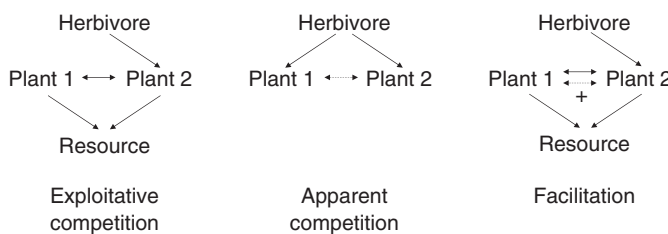


FIGURE 16.1 Schematic representation of the modules referring to more than one plant interacting with one herbivore. Solid arrows mean direct effects, whereas dotted arrows refer to indirect effects. All effects are negative except those marked with “+.”

of another, not because they compete for the same resources, but because they are consumed by the same herbivore (Huntly 1991). For example, Rand (2003) found that the presence of *Salicornia* when insect herbivores are excluded has no effect on *Atriplex* (both Chenopodiaceae). Meanwhile, when herbivores appeared, the presence of *Salicornia* resulted in a pronounced decrease in plant survivorship and fruit production of *Atriplex*. Thus, shared herbivory resulted in a strong apparent competitive effect of *Salicornia* on *Atriplex*.

Competition between plants can affect their relationship with their herbivores. Competition may limit resource availability for plants and, in turn, this may influence the resistance to herbivores of plants (van Dam and Baldwin 1998, Agrawal 2000b). In addition, competition and herbivory produce additive effects for plant growth (e.g., Fowler and Rausher 1985, Mutikainen and Walls 1995, Reader and Bonser 1998, Erneberg 1999, but see Fowler 2002, Agrawal 2004, Haag et al. 2004), decreasing the herbivore tolerance when plants compete for limited resources. Moreover, intraspecific competitive interactions with herbivory can affect components of fitness and mating system (Steets et al. 2006).

Associations among Plants Sharing Herbivores

The probability that a plant will be attacked by a herbivore depends not only on the characteristics of the individual plant, but also on the quality and abundance of the neighbors. A plant species may have a positive net effect on another species by deterring the amount of herbivory that would otherwise be inflicted on the other species (Figure 16.1c, right). For example, palatable plants in a matrix of unpalatable vegetation may remain undetected by the herbivore and thereby escape consumption. Moreover, neighboring plants may affect the local resource abundance to polyphagous herbivores in ways that reduce the attack rate or the time herbivores remain on their host plant. These processes are called associational resistance, associational defense, associational refuge, or plant-defense guilds (Tahvanainen and Root 1972, Pfister and Hay 1988, Holmes and Jepson-Innes 1989, Hjäältén et al. 1993, Hambäck et al. 2000). For example, Russell and Louda (2005) found a marked decline in head weevil (*Rhinocyllus conicus*, Curculionidae) attack of wavyleaf thistle (*Cirsium undulatum*, Asteraceae) flower heads in the presence of successful flowering by an alternate, newly adopted native host plant, the platte thistle (*Cirsium canescens*, Asteraceae).

Conversely, when the herbivore selects within the patch, the result of the association of a palatable plant with unpalatable ones can shift to greater consumption or damage of the edible species, which was preferred by the herbivore. Moreover, an unpalatable plant surrounded by palatable plants can be damaged by the herbivore attracted by its neighbors. These processes are called associational susceptibility, associational damage, or shared doom (Atsatt and O'Dowd 1976, McNaughton 1978, Karban 1997). For instance, White and Whitham (2000) found strong indications for associational susceptibility of cottonwoods (*Populus angustifolia*–*Populus fremontii*, Salicaceae) to cankerworms (*Alsophila pometaria*, Geometridae) when growing under the most preferred species (*Acer negundo*, Aceraceae), since it was colonized by two- to threefold more cankerworms, and suffered two- to threefold greater defoliation than cottonwoods growing in the open or under mature cottonwoods.

Facilitation can also result from physical protection provided by nurse plants. There is a considerable number of studies that demonstrate a grazing protection component of woody and perennial plants harboring other species growing under them (Milchunas and Noy-Meir 2002, and references therein), enhancing community diversity (Olf et al. 1999, Callaway et al. 2000, Rebollo et al. 2002). Shrubs can protect saplings against herbivores (Callaway 1995, García and Obeso 2003) facilitating the regeneration of palatable tree species that would be untenable without shrub presence (Rousset and Lépart 1999, Meiners and Martinkovic 2002, Smit et al. 2006) The advantage of facilitation increases parallel to herbivore pressure (Bertness and Callaway 1994, Baraza et al. 2006), to the point that in some situations the

only seedlings and juvenile trees that survive remain within the islands formed by spiny shrubbery. Beyond these protectorates, natural regeneration can be completely arrested by strong herbivore pressure.

MORE THAN ONE HERBIVORE

Interspecific relationships between two herbivorous species can range from mutually competitive to mutually beneficial (Crawley 1983, Strauss 1991). When one plant becomes the host of several different herbivore species, it is difficult to understand the result of an interacting pair of species without taking into account the effect of the other herbivores.

Above and Belowground Multitrophic Interactions

Plants are frequently attacked by both above- and belowground arthropod herbivores. Aboveground and belowground herbivores influence each other indirectly via changes in biomass and the nutritional quality of host plants (Blossey and Hunt-Joshi 2003, and references therein). For example, root-feeding herbivores can induce changes in plant secondary chemistry (increase induced defenses), which reduce the performance of the foliage-feeding insect (Bezemer and van Dam 2005). Moreover, belowground herbivores can affect not only secondary metabolisms but also primary plant compounds. In fact, Bezemer et al. (2005) found a significant reduction in offspring production of aphids (*Rhopalosiphum padi*, Aphididae) in the presence of a nematode, probably by a decrease in foliar nitrogen and amino acid concentrations in the preferred host plant *A. odoratum* (Poaceae).

Although belowground decomposers are not directly associated with plant roots, they can influence aboveground plant-defense levels as a result of differences in the availability of nutrients to the plant (Wurst and Jones 2003, Wurst, et al. 2004a). Through decomposition, earthworms can increase nitrogen availability in the soil, resulting in the plant investing more in growth and less in direct defense compounds (Wurst et al. 2006). For example, Wurst et al. (2004b) found a decline in foliar catalpol concentration of *Plantago lanceolata* (Plantaginaceae) in the presence of earthworms (*Aporrectodea caliginos*, Lumbricidae), documenting the potential of decomposers to influence concentrations of plant secondary metabolites.

In the same way, aboveground herbivores can alter subterranean organisms and processes through plant responses. Two principal mechanisms have been proposed by which this occurs—through herbivore effects on patterns of root exudation and carbon allocation and through altering the quality of input of plant litter (Bardgett et al. 1998). Positive effects arise when herbivores promote compensatory plant growth, returning organic matter to the soil as labile fecal material (rather than as recalcitrant plant litter), inducing greater concentrations of nutrients in remaining plant tissues and impairing plant succession, thereby inhibiting the ingress of plant species with poorer litter quality. Negative effects arise through the impairment of plant productivity by tissue removal, induced production of secondary defenses, and promotion of succession by favoring the dominance of unpalatable plant species with poor litter quality. Whether net effects are positive or negative depends on the context (Wardle et al. 2004). In general, positive effects of herbivory on soil biota and soil processes are most common in ecosystems of high soil fertility and high consumption rates, whereas negative effects are most common in unproductive ecosystems with low consumption rates (Bardgett and Wardle 2003).

Interactions between Herbivores and Pathogens

The interaction between herbivores, such as insects, slugs, snails, birds, or mammals, and pathogens (e.g., bacteria, fungi, and viruses) has been studied only recently (Faeth and Wilson 1997). Bowers and Sachi (1991) recorded an increase in disease levels of the rust *Uromyces*

trifolii (Pucciniaceae) on clover (*Trifolium pratense*, Fabaceae) in fenced enclosure plots compared with control plots. This increase results from an increase in host plant density in the enclosures. On the other hand, some studies have reported that macro-herbivores prefer plants bearing micro-herbivores. Molluscs graze more heavily on rust-infested plants than on healthy ones (Ramsell and Paul 1990). Similarly, Ericson and Wennström (1997) have analyzed the interaction between the fungus *Urocystis tridentalis* (Ustilaginales), its host plant *Trientalis europaea* (Primulaceae), and two herbivores (scale insects and voles) in a 2 year experiment. The results indicate that both the scale insects and the voles preferred smut-infested shoots to healthy shoots. Fencing out the voles resulted in a significant boost in host density and a significantly higher disease level. On the contrary, the willow leaf beetle *Plagioderia versicolora* (Chrysomelidae) significantly avoided feeding and oviposition on leaves of the willow hybrid *Salix × cuspidata* (Salicaceae) when they are infected by the rust fungus *Melampsora allii-fragilis* (Uredinales et al. 2005).

The interaction between herbivores and pathogens is not always antagonistic. For example, herbivores can transmit diseases to the host plant, increasing its harmful effect without substantial direct consumption of plant tissue. European elm (*Ulmus* spp., Ulmaceae) forests have declined in the last 20 years because of a parasitic fungus that produces graphiosis. This fungus is transmitted by some species of herbivorous beetles belonging to the family Scolytidae (Gil 1990). The detrimental effect of the beetle increases elm mortality not by direct consumption of cambium, but by acting as vector of the parasite.

EFFECT OF HERBIVORES ON MUTUALISM INVOLVING THE HOST PLANT

Plants are involved in a diverse array of mutualistic interactions, including pollination, seed dispersal, or mycorrhiza symbiosis. Herbivores can influence any of these mutualistic interactions displayed by the host plant.

Effect on Pollen-Dispersal System

By reducing plant resources, herbivory may have direct consequences on the mating system. Resource limitation caused by herbivory can affect flower production (e.g., Lehtilä and Strauss 1997, Mothershead and Marquis 2000), flowering phenology (Juenger and Bergelson 1997), and seed mass and number (e.g., Stephenson 1981, Koptur et al. 1996, Agrawal 2001, Hódar et al. 2003). For example, leaf damage decreases pollen production and performance in *Cucurbita texana* (Cucurbitaceae, Quesada et al. 1995) and produces selective fruit abortion in *Lindera benzoin* (Lauraceae, Niesenbaum 1996).

Leaf damage can reduce the number of simultaneously open flowers on a plant (Strauss et al. 1996, Elle and Hare 2002) and, thus, decrease the potential for pollinators to affect geitonogamy (selfing among flowers on a plant) (Harder and Barrett 1995). Herbivory can also modify flower morphology and reward, which in turn may reduce pollinator visitation (Strauss et al. 1996, Mothershead and Marquis 2000). Moreover, flower consumption by herbivores also affects the pollen-dispersal system indirectly, by altering the visitation rate of pollinators in entomophilous plants (Marquis 1992a).

Effect on Plant–Mycorrhiza Interaction

The relationships among plants, their mycorrhizal fungi, and their herbivores are likely to be complex and can be observed from different standpoints:

1. Herbivore effects on mycorrhiza. Foliage removal by insect herbivores can reduce arbuscular mycorrhizal (AM) colonization levels of herbaceous plants (Gange et al. 2002a), and ectomycorrhizal (ECM) colonization levels in trees (Gehring and

Whitham 2002). Conversely, moderate grazing in tallgrass prairie microcosms seems to improve AM colonization levels (Kula et al. 2005), perhaps because aboveground herbivory may increase the nutrient demand of host plants (Eom et al. 2001). In an experiment with three AM species, Klironomos et al. (2004) found that clipping of *Bromus inermis* (Poaceae) affects certain mycorrhizal characteristics, depending on the fungal species involved. As a result, any mycorrhizal feedback that may occur in response to herbivory is not simple to predict, either (Wamberg et al. 2003).

2. Mycorrhiza effect on herbivores. Both AM and ECM fungi are known to alter plant physiology and chemistry, and, as a result, can affect herbivores that feed on them. Several works have reported resistance to insect herbivory in plants inoculated with mycorrhiza (Gange and West 1994, Borowicz 1997, Gange et al. 2005). However, the interaction between mycorrhizal infection and herbivory is complex, depending on the species not only of herbivore, but also of the fungi and plant (Gehring and Whitham 2002, Gange et al. 2005). In general, changes provoked by AM on plants boosted the growth of specialist chewing as well as specialist and generalist sucking insects, but decreased the growth of generalist chewers (Gange and West 1994, Borowicz 1997, Gange et al. 1999, Goverde et al. 2000, Gange et al. 2002b). The underlying mechanism by which AM fungi affect an insect community has been linked to mycorrhizal-induced changes in plant chemistry, either through changes in secondary metabolites (Gange and West 1994) or alterations in plant-nitrogen content (Gange and Nice 1997, Rieske 2001).
3. Mycorrhiza effect on plant tolerance to herbivores. Mycorrhiza improvement in plant nutrients supplied could also confer a greater capacity for recovering from herbivory (Hokka et al. 2004, Kula et al. 2005). Nevertheless, there is controversy concerning the effect of mycorrhiza on damaged plants, since, on the one hand, symbiosis imposes a cost of carbon that cannot be used for plant growth, and, on the other hand, mycorrhiza contributes necessary nutrients for plant growth (Borowicz 1997). Moreover, plant response to herbivory depends on environmental conditions, mycorrhizal symbiosis becoming more important in the case of high-intensity light and low water and nutrients availability (Gehring and Whitham 1994). In addition, in this case, the plant species is determinant. For example, Allsopp (1998) found that *Lolium* and *Digitaria* (Poaceae), which are pasture species, are better able to maintain an external AMF hyphal network following fairly frequent defoliation, whereas *Themeda* (also Poaceae), a rangeland grass, which is more intolerant of grazing, has a lower capacity for sustaining its hyphal network when defoliated.

MULTISPECIFIC INTERACTIONS

The basic food chain is composed of a plant, its herbivore, and the predator of the herbivore (Figure 16.2). The most widely studied tritrophic systems consist of a plant or a seed, a parasitic herbivore (seed predator, gall-maker, or the like), and parasitoids, although

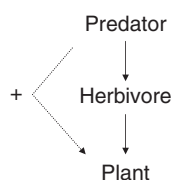


FIGURE 16.2 Schematic representation of a basic food chain.

interest is growing with respect to the types of tritrophic systems, such as those in which insectivorous vertebrates (birds, reptiles, or mammals) intervene in relationship between herbivores and plants (see Tscharntke 1997). For instance, Van Bael et al. (2003) observed that birds decreased local arthropod densities on canopy branches and reduced consequent damage to leaves for three Neotropical tree species. However, this effect of birds on plant damage does not always exert an effect on plant-biomass production (Strong et al. 2000 and references therein).

Parasitism represents a crucial mortality factor for many species of herbivorous insects. For this reason, parasitoids can improve plant performance. Gómez and Zamora (1994) tested the totality of direct and indirect forces in a tritrophic system composed of a guild of three parasitoid species, a single weevil seed predator, and the host plant. When parasitoids were experimentally excluded, the percentage of attacked fruits rose from 20% to 43%, the parasitoids thus enhancing plant reproductive performance. The effect of parasitoids in herbivore population is influenced by characteristics of the host plant. For example, von Zeipel et al. (2006) found an important effect of plant population size on the results of the tritrophic system formed by a perennial plant, *Actaea spicata*, the associated specialist moth seed predator, *Eupithecia immundata*, and a guild of parasitoids. In large plant populations, parasitoids reduced the level of seed predation, thereby enhancing plant fitness. In small populations, usually either a high proportion of seeds was preyed on because of seed predator presence and parasitoid absence or there was no seed predation when the seed predator was absent. Finally, when plant population was of intermediate size, there was intense seed predation, since the seed predator was present but parasitoids were often absent.

Plants are not passive elements in these tritrophic interactions. In response to herbivore damage, several plant species emit volatile chemicals that attract natural enemies (predators and parasitoids), which attack herbivores (Dicke and van Loon 2000 and references therein). Moreover, plants can adaptively react to the chemical information emitted by their neighbors by two types of responses: the induction of a direct defense that makes them resistant to subsequent herbivore attack and an indirect defense that involves the recruitment of carnivorous arthropods as “bodyguards” (Arimura et al. 2000, Dicke et al. 2003).

Multispecific interactions can occur throughout guilds as interactive units, when there are functionally equivalent animals or plants (i.e., from the plant’s or the herbivore’s perspective). Plants may interact with a guild of ecomorphologically similar herbivore species rather than with a particular species. The degree of generalization determines the breadth of the filter of the interaction and the real possibility that the system might be facultative (different species with the same role). For example, Maddox and Root (1990), studying the trophic organization of the herbivorous insect community (more than 100 species distributed among 5 orders) of *Solidago altissima* (Asteraceae), suggest that the functionally similar herbivore groups may constitute selective units more powerful than individual species. This opens the possibility of synergetic responses as opposed to the same blocks of selective pressures (broad-spectrum responses). In this way, Krischik et al. (1991) indicated that nicotine was inhibitory to the growth both of herbivores and of pathogens, suggesting that certain secondary plant chemicals with high toxicity are of a generalized nature and affect multiple species. Adler and Kittelson (2004) determine how different environmental effects influence alkaloid profiles and resistance to multiple herbivores in *Lupinus arboreus* (Leguminosaceae), showing a highly complex response by the different herbivores analyzed. For instance, the density of the leaf galler *Dasineura lupinorum* (Cecidomyiidae) and the fungus *Colletotrichum* spp. (Nectriodaceae) was affected by total alkaloid concentration and alkaloid profiles, whereas the density of apical flies and bud gallers was not affected by any alkaloid measure.

PLANT–HERBIVORE INTERACTION: A MULTISPECIFIC VISION

CASE STUDY 1. CLIMATE EFFECTS ON INSECT OUTBREAKS: THE PINE PROCESSIONARY

The pine processionary moth (*Thaumetopoea pityocampa*, hereafter PPC) is a good example of how climate and plant characteristics interact to provide a given kind of life cycle in a herbivorous insect. PPC is a serious defoliator in the Mediterranean area, which attacks different species of the genus *Pinus* (see e.g., Dajoz 1998). Traditionally, it has been assumed that the incidence of PPC defoliation depended on winter temperatures (Demolin 1969, Hódar et al. 2003). This is due to its particular life cycle; that is, while most arthropods develop as larvae or nymphs during spring and summer, with abundant food and warm temperatures, PPC develops as larvae during winter. For this, larvae of the same egg batch develop together in a communal silk nest that allows them to save heat and continue development (Breuer et al. 1989, Breuer and Devkota 1990, Halperin 1990). However, very low temperatures (−10 to −15°C) can be lethal, and above +30°C larvae cannot stay together in the communal nest. Despite the importance of temperature, it has long been recognized that food quality for larval development is also an important issue in the population dynamics of the PPC. This suggestion is based on the different incidence of defoliation by PPC in the different pine species: while White pine *Pinus pinea* is particularly resistant and defoliation is usually low, others such as Black pine *Pinus nigra* or exotic species are heavily defoliated. In Spain, the more resistant species, such as White pine, inhabit low altitudes, whereas Aleppo pine *Pinus halepensis* and Cluster pine *Pinus pinaster* do so to a lesser degree. On the contrary, Black pine and Scots pine *P. sylvestris*, inhabiting middle or high altitudes in mountains, or introduced species as Canary Island pine *Pinus canariensis* or Monterey pine *Pinus radiata*, are particularly susceptible to PPC attack. Many works have tried to identify the features in pine needles that affect PPC larval development (Schopf and Avtzis 1987, Battisti 1988, Devkota and Schmidt 1990, Tiberi et al. 1999, Petrakis et al. 2001, Hódar et al. 2002, 2004) but none have found conclusive evidence.

The distribution of the pine species in altitude, depending on its palatability, suggests that the most resistant pines, living at lower altitudes with mild winters that enhance PPC development, have acquired constitutive chemical defenses against defoliation. By contrast, pines living at high altitudes, with cold winters that rarely allow the development of PPC larvae (or exotic pines never defoliated by PPC), did not develop these defenses and have a very limited capacity for chemical response (Hódar et al. 2004). When the winter is warm and pines are planted in zones not adequate for their defense, outbreaks of PPC can be frequent. This situation is worsening for two main reasons. The first is the massive forestation with exotic pine species in zones with high PPC incidence, such as *P. radiata* in coastal northern Spain. The second is the increase in temperatures due to climatic change, which is giving PPC the opportunity of thriving in pine woodlands belonging to palatable species, which, until now, were free of PPC attack for climatic reasons. In particular, rising winter temperatures are favoring the progression of PPC in altitude (Hódar et al. 2003, Hódar and Zamora 2004, Battisti et al. 2006) and in latitude (Battisti et al. 2005).

Abundant scientific literature provides analyses of specialized cases of an insect herbivore feeding on a plant depending on nutritional characteristics (see Section “Introduction”). The case of PPC is more complex, because the same insect species feeds on different (but related) pine species with different abilities to tolerate defoliation and because the development of PPC is strongly modulated by the climatic conditions at the pine woodland where PPC lives. The best hosts live where temperatures are inhospitable for PPC. The best temperature for PPC occurs where pines are not a good food, and this interaction between PPC and their food determines the alternation between years of low infestation and years of severe outbreaks.

CASE STUDY 2. CONDITIONAL OUTCOMES IN PLANT–HERBIVORE INTERACTIONS: NEIGHBORS MATTER

Although herbivores try to select more nutritive plants and avoid excessive toxin consumption, other numerous factors influence their foraging behavior, this necessary to be considered when analyzing plant–animal interactions (Provenza et al. 2002). As shown in [Section “Associations among Plants Sharing Herbivores”](#) differences in the palatability of coexisting plant species can affect the interaction of a particular herbivore species with a particular plant. Moreover, other conditions such as climate or herbivore density can alter herbivore foraging behavior. For example, in Sierra Nevada in wet years, only 20% of Scots pine saplings undergo some herbivore attack, while in dry years, with low pasture production, up to 80% of saplings suffer browsing damage (Hódar et al. 1998). In this scenario, herbivore foraging behavior, plant characteristics, the surrounding vegetation palatability, and the environmental conditions could interact to determine the probability of damage to a given plant (Provenza et al. 2002).

Baraza et al. (2006) in an experimental reforestation planted two tree species (a palatable tree and unpalatable one), under four experimental microhabitats: highly palatable shrub, palatable but spiny shrub, unpalatable spiny shrub, and control. The finding was that three factors determine the damage probability of saplings. Palatable species were usually attacked, whereas unpalatable species were only rarely attacked. As surrounding vegetation, highly palatable shrubs can promote high herbivory in the sapling beneath it, whereas an unpalatable shrub reduces the probability of attack (Callaway 1992, Rousset and Lepart 2002, Smit et al. 2006). These two factors can interact in a way that the degree of protection offered by the shrub is greater as its palatability decreases with respect to sapling palatability (Baraza et al. 2006). In addition, herbivore pressure acts as one of the most important and potentially variable factors affecting the degree of sapling protection by shrubs (Baraza et al. 2006). With high herbivore pressure, only unpalatable shrubs can protect palatable saplings, whereas for unpalatable saplings the probability of attack tends to increase when growing near shrubs (Figure 16.3). On the contrary, with low herbivore pressure, shrubs of intermediate palatability

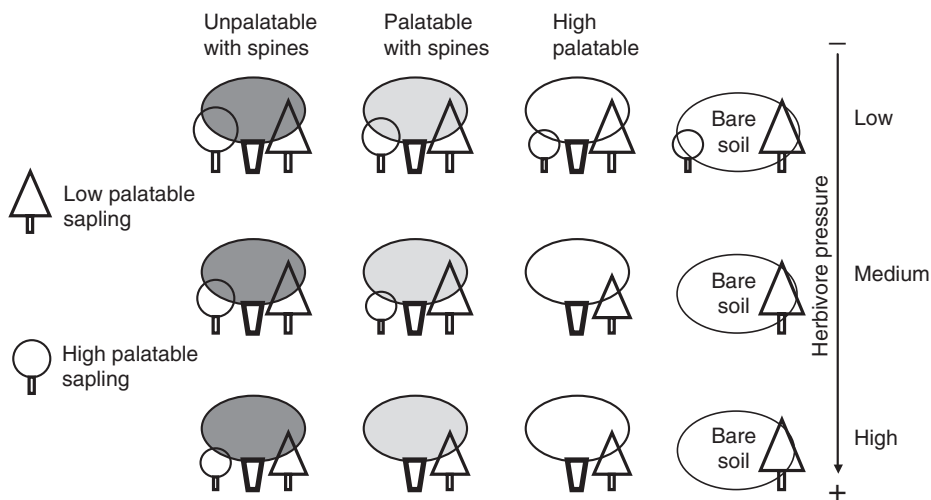


FIGURE 16.3 Sapling damage probability depends on sapling palatability, microhabitat of growth, and herbivore pressure. Smaller sapling figures represent more probability of being eaten and, as a result, less probability of establishment. Probability of damage is higher for palatable saplings than for unpalatable ones in all conditions, while the protective role of shrubs depends on herbivore pressure and the palatability of the shrub. (Reproduced from Baraza, E., Zamora, R., and Hódar, J.A., *Oikos*, 113, 148, 2006. With permission.)

may protect palatable saplings from herbivores, whereas the protective role of unpalatable shrubs increases, and unpalatable saplings are safe in any microhabitat. With intermediate herbivore pressure, palatable saplings decrease their probability of attack by growing under shrubs of intermediate or low palatability, whereas unpalatable saplings start to undergo damage when growing under shrubs (Figure 16.3). These findings show that the quality of a microhabitat for recruitment depends strongly on the degree of herbivore pressure, together with relative palatability of saplings and shrub. Consequently, when herbivory pressure increase, the landscape can change from a high-quality matrix for sapling recruitment to becoming a low-quality matrix where only unpalatable plants constitute available patches for recruitment for palatable species (Callaway et al. 2005, Baraza et al. 2006). These examples show the complexity of plant–herbivore interactions that is affected not only by neighbors (see Section “Associations among Plants Sharing Herbivores”) but also by the environmental context (Baraza et al. 2006). Moreover, this effect of neighbors can determine the consequence of herbivory on vegetation structure (Olf et al. 1999, Calaway et al. 2000, Rebollo et al. 2002).

CASE STUDY 3. UNGULATES AFFECT POPULATIONS OF BOTH PLANTS AND OTHER CO-OCCURRING HERBIVORES

Erysimum mediohispanicum (Cruciferae) is a monocarpic herb found in many montane regions of SE Spain from 1000 to 2000 m a.s.l. Plants usually grow for 2–3 years as vegetative rosettes, then die after producing one (up to eight) reproductive stalk, which can display between a few and several hundred hermaphroditic, slightly protandrous bright yellow. At the SE Spain, reproductive individuals are fed by many different species of herbivores. Several species of sap-suckers (outstanding the bugs *Corimeris denticulatus*, *Eurydema fieberi*, and *Eurydema ornata*, Pentatomidae) feed on the reproductive stalks, both during flowering and fruiting. In addition, stalks are bored into by a weevil species (*Melanobaris erysimi erysimoides*), which consume the inner tissues, whereas another weevil species (*Ceutorhynchus chlorophanus*, both Curculionidae) develops inside the fruits, living on developing seeds. Some floral buds do not open because they are galled by flies (*Dasineura* sp., Cecidomyiidae). However, the main herbivores in the study zones are domestic (sheep) and wild ungulates (Spanish ibex *Capra pyrenaica*, Bovidae). Postdispersed seeds of both species are consumed by woodmice (*Apodemus sylvaticus*, Muridae), several species of birds (*Fringilla coelebs*, *Serinus serinus*, *Carduelis cannabina* [Frigillidae], among others), several species of medium-sized granivorous beetles (*Iberozabrus* sp. [Carabidae], among others) and ants (*Lasius niger*, *Tetramorium caespitum* and probably *Cataglyphis velox* and *Leptothorax tristis*, Formicidae).

Ungulates damage exclusively the inflorescences and infructescences of the plants, cutting them and consuming the flowers/fruits plus the stalks. Damage to plants occurred before they had dispersed the seeds, increasing the potential detrimental effect of herbivory. Indeed, ungulates heavily affect many components of *Erysimum* performance, such as fecundity, seed survival to postdispersal seed predation, seedling emergence, and survival. Consequently, ungulates had a significant detrimental effect on the population dynamics of *Erysimum mediohispanicum* (Gómez 2005a).

The occurrence of ungulates has additional indirect effects in the interaction that plants maintain with invertebrate pollinators and herbivores between. Thus, ungulates deplete the abundance and diversity of pollinators (Gómez 2005b). Plants frequently grazed by ungulates are pollinated by a less diverse assemblage of pollinators than nondamaged plants, presumably because grazing decreases flower size and number. This fact suggests an indirect negative effect of ungulates on plants through a decrease in mutualistic interactions. In addition, ungulates also outcompete all the phytophagous insects co-occurring in the plants, since the

experimental exclusion of ungulates provokes a significant increase in the abundance of predispersal seed predators, sapsuckers, gall-makers, and stem-borers. Most important, different mechanisms account for the increase in the abundance of different herbivores. Thus, predispersal seed predators are affected mainly by density-mediated indirect interactions, the negative effect of ungulates provoked mostly by a decrease in the shared resources, the seeds. However, ungulates have a significant trait-mediated indirect effect on gall-makers, sapsuckers, and stem-borers, as suggested by the change in the per-capita interaction strength between these insects and the plant when ungulates were present. In fact, in addition to decrease abundance, ungulates modify the phenotype of the plants. Damaged plants produced less and smaller flowers, shorter and narrower flowering stalks, and more trichomes. Sapsuckers, stem-borers, and gall-makers are deterred by these phenotypic traits, and thereby, they show a negative preference for damaged plants (Gómez and González-Megías 2007). Ungulates also affect seed-predators and gall-makers directly by incidentally ingesting them while browsing (Gómez and González-Megías 2007). These two species are endophagous, as they are unable to avoid the interaction with ungulates by directly leaving the plant and usually located in the upper part of the plant, the one more likely ingested by ungulates.

Finally, ungulates also affect postdispersal seed predators. Thus, the rate of seed removal by predators increases after experimentally excluding ungulates. Several nonexclusive reasons can account for this result (Gómez 2005a). First, it could be a consequence of exploitative competition occurring between seed predators and ungulates, which means that after removing ungulates seed-predator abundance could increase. Competition between ungulates and granivorous species has been widely reported (Davidson et al. 1984, 1985, Baines et al. 1994, and references therein) and may occur as a consequence of resource removal (flowers, fruits, and seeds) as well as by the negative effect of vegetative tissue removal on flower and fruit production (Meyer 1993, Meyer and Root 1993, Müller-Scharer and Brown 1995). In the studied systems, by consuming flower and fruits, sheep and ibex surely deplete the resources used by granivorous mammals and invertebrates.

In brief, this example illustrates that the assemblage of herbivores living on the same host plant can maintain complex indirect interactions among them. A full and deep understanding of these interactions can help to accurately find out the net effect that herbivores have on the functioning of plant individuals and populations.

ACKNOWLEDGMENTS

We thank the Agencia de Medio Ambiente, Junta de Andalucía, for permitting to conduct field work in the Parque Natural de Sierra Nevada and in the Parque Natural de la Sierra de Baza. Thanks to Blackwell publishing for permission to use [Figure 16.3](#). The research that supported most part of the work shown here was financed by projects AGF99-0618, 1FD97-0743-CO3-02, and REN2002-04041-CO2-01/GLO (to R.Z.) and UGR2002-30P3176 and BOS2003-09045 (to J.M.G.). E.B. is currently supported by a postdoctoral grant from the Fundación Ramón Areces. David Nesbitt read through the English version of the text.

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