Trophic Dynamics

10

Trophic dynamics govern the movement of carbon, nutrients, and energy among organisms in an ecosystem. This chapter describes the controls over the trophic dynamics of ecosystems.

Introduction

Although terrestrial animals consume a relatively small proportion of net primary production (NPP), they strongly influence energy flow and nutrient cycling in most ecosystems. In earlier chapters, we emphasized the interactions between plants and soil microbes because these two groups directly account for about 95% of the energy transfers in most terrestrial ecosystems. Plants use solar energy to reduce CO_2 to organic matter, most of which senesces, dies, and directly enters the soil, where it is decomposed by bacteria and fungi. Similarly, most nutrient transfers in ecosystems involve absorption by plants and return to the soil in dead organic matter, from which nutrients are released by microbial breakdown. In most ecosystems, the uncertainties in our estimates of primary production and decomposition exceed the total energy transfers from plants to animals. It is perhaps for this reason that many terrestrial ecosystem ecologists have ignored animals in classical studies of production and biogeochemical cycles. Aquatic ecologists, in contrast, have been unable to ignore animals because herbivory accounts for a much larger proportion of the carbon and nutrient transfer than in terrestrial ecosystems (Fig. 10.1; Cyr and Pace 1993). Perhaps for this reason, aquatic ecosystem ecologists have generally led the theoretical developments relating to the roles of trophic dynamics in the functioning of ecosystems.

The factors governing energy and nutrient transfer to animals have important societal implications. Many human populations depend heavily on high-protein animal products for food. The rising human population and its diet shift toward greater consumption of meat places increasing pressure on the world's food supply. An ecologically viable strategy for efficiently providing food to a growing human population requires a good understanding of the ecological principles regulating the efficiency of converting plants into biomass of animals – including people.

A Focal Issue

Intense herbivory, due either to overstocking of domestic animals or to removal of predators from less intensively managed systems, reduces the density and diversity of palatable plants. This is one of the most extensive human impacts on the planet, operating through removal of large predatory fish from most of the world's oceans, removal of predators from lands that are intensively managed for human habitation and use, and extensive stocking of grasslands and savannas with domestic livestock (Fig. 10.2). Why do herbivores eat more of some plant species than others? How do interactions between plants, herbivores,

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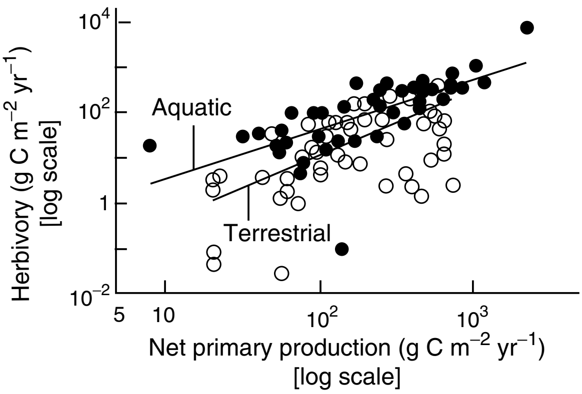

Fig. 10.1 Comparison of rates of primary productivity and herbivory between aquatic and terrestrial ecosystems. Redrawn from Cyr and Pace (1993)

Fig. 10.2 Intensive herbivory reduces the density of palatable plants, altering ecosystem structure. On Australian rangelands, overstocking of cattle can transform grassland savannas to shrublands (Ludwig and Tongway 1995). Photographs by David Tongway

and their predators influence the structure and functioning of ecosystems? What happens to the energy and nutrients that are consumed by an animal? How does human choice of the proportion of meat and plants consumed influence the land base required to meet the food needs of a growing human population? Answers to these questions provide a framework to address some of the most contentious ecological issues facing society.

Overview of Trophic Dynamics

Energy and nutrient transfers define the trophic structure of ecosystems. The simplest way to visualize the energetic interactions among organisms in an ecosystem is to trace the fate of a packet of energy from the time it enters the ecosystem until it leaves (Lindeman 1942). **Trophic transfers** involve the feeding by one organism on another or on dead organic matter. Plants are called **primary producers** or **autotrophs** because they convert CO_2, water, and solar energy into biomass (see Chaps. 5 and 6). **Heterotrophs** are organisms that derive energy by eating live or dead organic matter. Heterotrophs function as part of two major trophic pathways, one based on live plants (the **plant-based trophic system**) and another based on dead organic matter (the **detritus-based trophic system**). The detritus-based trophic system usually accounts for most of the energy transfer through animals in an ecosystem.

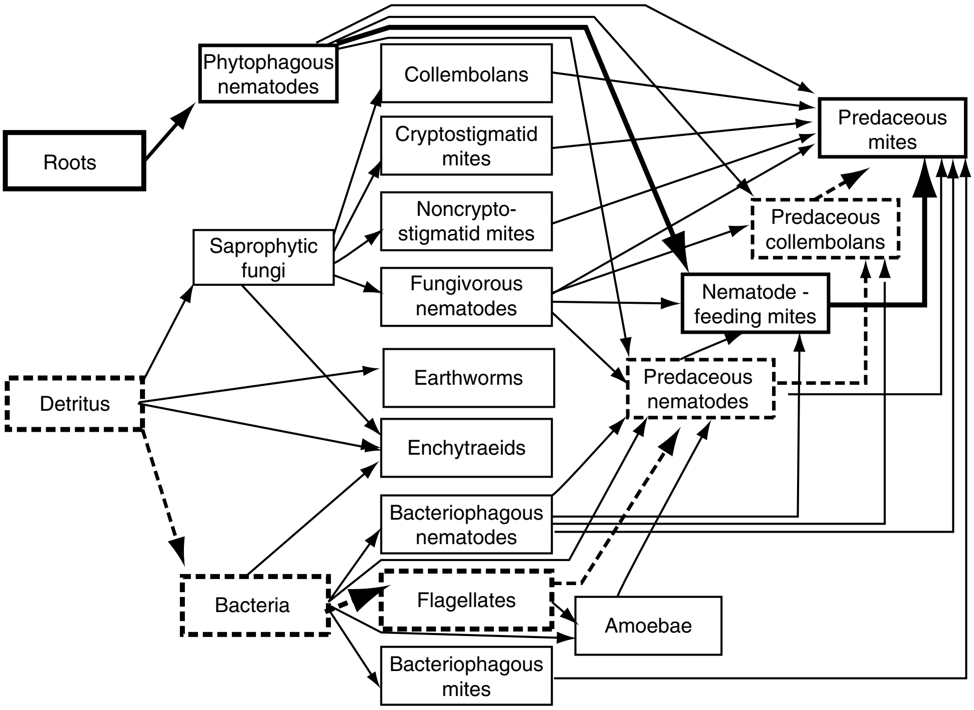

Fig. 10.3 Pattern of energy flow through belowground portions of a grassland food web. Food webs consist of many interconnecting food chains. A plant-based (solid line) and a detritus-based (dashed line) food chain are shown in bold. Modified from Hunt et al. (1987)

Consumers are organisms that eat other live organisms. These include plant-eating **herbivores**, microbe-eating **microbivores**, and animal-eating **carnivores**. A **food chain** is a group of organisms linked together by the process of consumption. Grass, grasshoppers, and birds, for example, form a food chain. Those organisms that obtain their energy with the same number of transfers from plants or detritus belong to the same **trophic level**. Thus in a plant-based trophic system, plants constitute the first trophic level, herbivores the second, primary carnivores the third, secondary carnivores that eat mainly primary carnivores the fourth, etc. (Lindeman 1942; Odum 1959). Similarly, in the detritus-based trophic system, bacteria and fungi directly break down dead soil organic matter and absorb the breakdown products for their own growth and maintenance. These **primary detritivores** are the first trophic level in the detritus-based food chain and are fed on by animals in a series of trophic levels analogous to those in the plant-based trophic system (Fig. 10.3).

Although food chains are an easy way to conceptualize the trophic dynamics of an ecosystem, they are a gross oversimplification for the many organisms that eat more than one kind of food. People, for example, eat food from several trophic levels, including plants (first trophic level), cows (second trophic level), fish (second and often higher trophic levels), and mushrooms (detritivores). Many other mammals and birds also consume both herbivorous and detritus-feeding insects and other animals. The actual energy transfers that occur in all ecosystems are therefore complex **food webs** (Fig. 10.3). We can trace the energy transfers through these food webs only by knowing the contribution of each trophic level to the diet of each animal in the ecosystem. Although food web structures have been partially described for many ecosystems (Pimm 1984), the quantitative patterns of energy flow through food webs are generally poorly known, especially for detritus-based food webs.

Food consists of much more than energy. In fact, animals often select food based as much on protein as on digestible energy content because animals require more nitrogen than do plants (tissue concentrations of 7–14% vs. 0.5–4%; Ayres 1993; Pastor et al. 2006; Barboza et al. 2009). Phosphorus concentrations are also generally higher in animals than plants, so either nitrogen or phosphorus can constrain animal production (Sterner and Elser 2002). Feeding is also strongly influenced by concentrations of plant defensive compounds that are toxic or reduce digestibility. The concentrations of these positive and negative determinants of food quality strongly influence the temporal and spatial patterns of trophic transfer.

The regulation of energy and nutrient flow through food webs is complex and varies considerably among ecosystems. Two theoretical patterns, however, bracket the range of possible controls. (1) The availability of food at the base of the food chain (either plants or detritus) limits the production of upper trophic levels through **bottom-up controls**. In this case, the quantity and quality of food, including the concentrations of nitrogen, phosphorus, and defensive chemicals, determine the amount of food that is eaten and therefore the animal production that can be supported. (2) Alternatively, predators that regulate the abundance of their prey exert **top-down control** on food webs. Most trophic systems exhibit some combination of bottom-up and top-down controls, with the relative importance of these controls varying temporally and spatially (Polis 1999; Allison 2006). In pelagic ecosystems, for example, nutrients, light, and temperature explain much of the geographic and seasonal patterns of production (bottom-up controls), but once a phytoplankton bloom is initiated, zooplankton rapidly grow and reproduce, reducing phytoplankton biomass (top-down controls).

Trophic transfers of energy and nutrients have profound effects on the functioning of ecosystems. They reduce plant biomass, thereby altering all the ecosystem processes that are mediated by plants, including the cycling of water, energy, and nutrients. Consumption of plants and detritus also accelerates the return of nutrients to the environment, although, as we shall see, the effects of herbivory on nutrient cycling depend on initial nutrient availability (Pastor et al. 2006).

Controls Over Energy Flow through Ecosystems

Bottom-Up Controls

Plant production places an upper limit to the energy flow through both plant-based and detritus-based webs. The energy consumed by animals in the plant-based trophic system, on average, cannot exceed the energy that initially enters the ecosystem through primary production. This constitutes a fundamental constraint on the animal production that an ecosystem can support. When all terrestrial ecosystems are compared, herbivore biomass and production tends to increase with increasing primary production (Fig. 10.4). The relationship between primary production and herbivore biomass is particularly strong, when comparisons are made among similar types of ecosystems. In the grasslands of Argentina, for example, the biomass of mammalian herbivores increases with increasing aboveground production along a gradient of water availability in both natural and managed grasslands (Fig. 10.5; Osterheld et al. 1992). In the Serengeti grasslands of Africa, the large herds of ungulates also acquire most of their food in the more productive grasslands (Sinclair 1979; McNaughton 1985). Similarly, productive forests generally have greater insect herbivory than do unproductive forests. When forests are fertilized to increase their production, this usually increases feeding by herbivores (Niemelä et al. 2001).

The world's large fisheries depend on the strong relationship between primary production and animal production, particularly in the coastal zone where the upwelling of nutrient-rich bottom waters supports a high productivity of phytoplankton, zooplankton, and fish (see Chap. 6). At the opposite extreme, productivity is low in the central gyres of tropical oceans that are isolated from nutrient-rich bottom waters and in **oligotrophic** (nutrient-poor) lakes on the Canadian Shield, whose soils were scraped away by Pleistocene glaciers.

Subsidies can supplement secondary production above levels that could be supported by NPP. Most of the energetic base for headwater streams in forests, for example, comes from inputs of

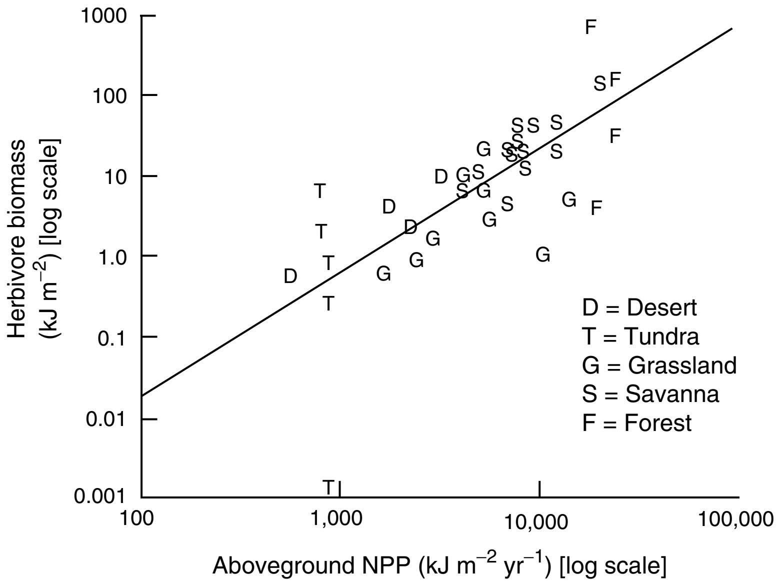

Fig. 10.4 Log–log relationship between aboveground net primary production (NPP) and herbivore biomass. One gram of ash-free biomass is equivalent to 20 kJ of energy. Production and biomass of aboveground herbivores correlates with aboveground NPP across a wide range of ecosystems. Redrawn from McNaughton et al. (1989)

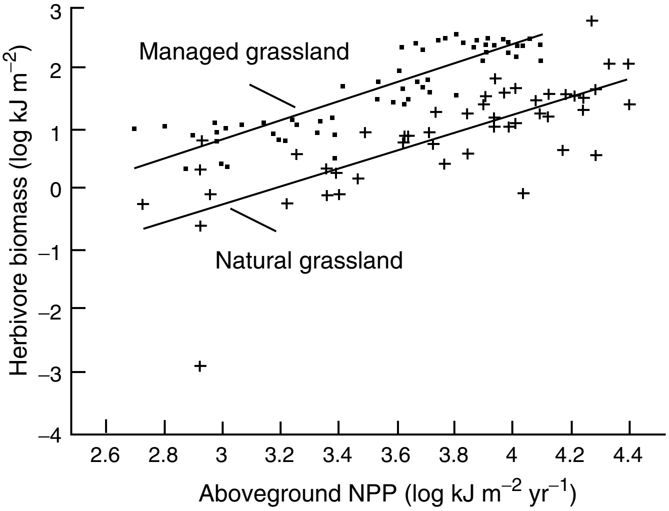

Fig. 10.5 Log–log relationship between mammalian herbivore biomass and aboveground plant production in natural and managed grazing systems of South America. Herbivore biomass increased with increasing NPP. Animal biomass on the managed grassland was 10-fold greater than on the natural grassland at a given level of plant production because managers control predation, parasitism, and disease and provide supplemental drinking water and minerals in managed systems. This difference in herbivore biomass between managed and unmanaged systems indicates that NPP is not the only constraint on animal production. Redrawn from Osterheld et al. (1992)

terrestrial litter. This **allochthonous** input (i.e., an input from outside the stream ecosystem) constitutes a subsidy that, together with **autochthonous production** (i.e., production occurring within the stream), provides the energy that supports aquatic food webs (see Chap. 7). At a finer scale, filter-feeding invertebrates in stream riffles derive most of their energy from algal production in upstream pools (Finlay et al. 2002). Terrestrial food webs near the ocean, rivers, and lakes are often subsidized by inputs of aquatic energy, for example when birds or bears feed on fish, or spiders feed on marine detritus (Polis and Hurd 1996; Milner et al. 2007). High-intensity agricultural production is strongly subsidized by human inputs of nutrients, water, and fossil fuels (Schlesinger 2000).

Biome differences in herbivory reflect differences in NPP, nutrient balance, and plant allocation to structural and chemical defenses. The most dramatic differences in herbivory among ecosystem types are consequences of variation in plant allocation to physical support. Lakes, the ocean, and many rivers and streams are dominated by phytoplankton that allocate most of their energy to cytoplasm rather than to structural support. Most phytoplankton are readily digested by zooplankton, so animals eat a large proportion of primary production and convert it into animal biomass. Even among phytoplankton, chlorophytes (naked green algae) are generally consumed more readily than phytoplankton that produce a protective outer coating, such as diatoms, dinoflagellates, and chrysophytes. At the opposite extreme, forests have a substantial proportion of production allocated to cellulose- and lignin-rich woody tissue that cannot be directly digested by animals. Some animals, however, like ruminants (e.g., cows), caecal digesters (e.g., rabbits), and some insects (e.g., termites) with symbiotic gut microbes are capable of cellulose breakdown. These animals can assimilate some of the energy released by this microbial breakdown of cell walls. Consequently, the fraction on NPP consumed by animals is much lower in forests, where plants allocate much of their biomass to structural material (Barboza et al. 2009; Craine 2009).

Among terrestrial ecosystems, there is a 1,000-fold variation in the quantity of plant biomass consumed by herbivores (McNaughton et al. 1989). Herbivores consume the least biomass per unit land area in unproductive ecosystems such as tundra (Fig. 10.6a). However, the energy consumed by herbivores is quite variable within and among biomes. Consumption by herbivores shows a much stronger relationship with production of edible tissue (e.g., leaves; Fig. 10.6b) than with total aboveground NPP (Fig. 10.6a) because the woody support structures produced by many plants contribute relatively little to herbivore consumption.

Plant chemical and physical defenses reduce the proportion of energy transferred to herbivores. It has been argued that predation rather than food availability must limit the abundance of herbivores because the world is covered by green biomass that has not been eaten by animals (Hairston et al. 1960). Not all green biomass, however, is digestible enough to serve as food. Ruminants and insects, for example, need plant biomass with at least a 1% nitrogen concentration to gain weight, with even higher requirements for reproducing animals (Craine 2009). In low-nutrient habitats, plants have not only low nitrogen and phosphorus concentrations but also high concentrations of chemical defenses (Bryant and Kuropat 1980; Pastor et al. 2006). In Africa, for example, fertile grasslands support higher diversity and production of herbivores than do the less fertile grasslands. The same pattern is seen in tropical forests, where higher levels of chemical defense and lower levels of insect herbivory occur on infertile than on fertile soils (McKey et al. 1978). Three factors govern the allocation to defense in plants: (1) genetic potential, (2) the environment in which a plant grows, and (3) the seasonal program of allocation.

1. Ecosystem differences in plant defense are determined most strongly by species composition. Terrestrial and aquatic species vary substantially in the type and quantity of defensive compounds produced. Terrestrial plants and marine kelps adapted to low-nutrient environments generally produce long-lived tissues with high concentrations of **carbon-based defense** compounds (i.e., organic compounds that contain no nitrogen, such as tannins, resins, and essential oils; see Chap. 6). These compounds deter feeding by most herbivores (Coley et al. 1985; Hay and Fenical 1988). Tissue loss to herbivores is often similar (1–10%) to the annual allocation to reproduction (i.e., the allocation that most directly determines fitness), suggesting that natural selection for chemical defenses against herbivores must be strong. When genotypes of a species are compared, for example, those individuals that allocate most strongly to defense grow most slowly (Fig. 10.7),

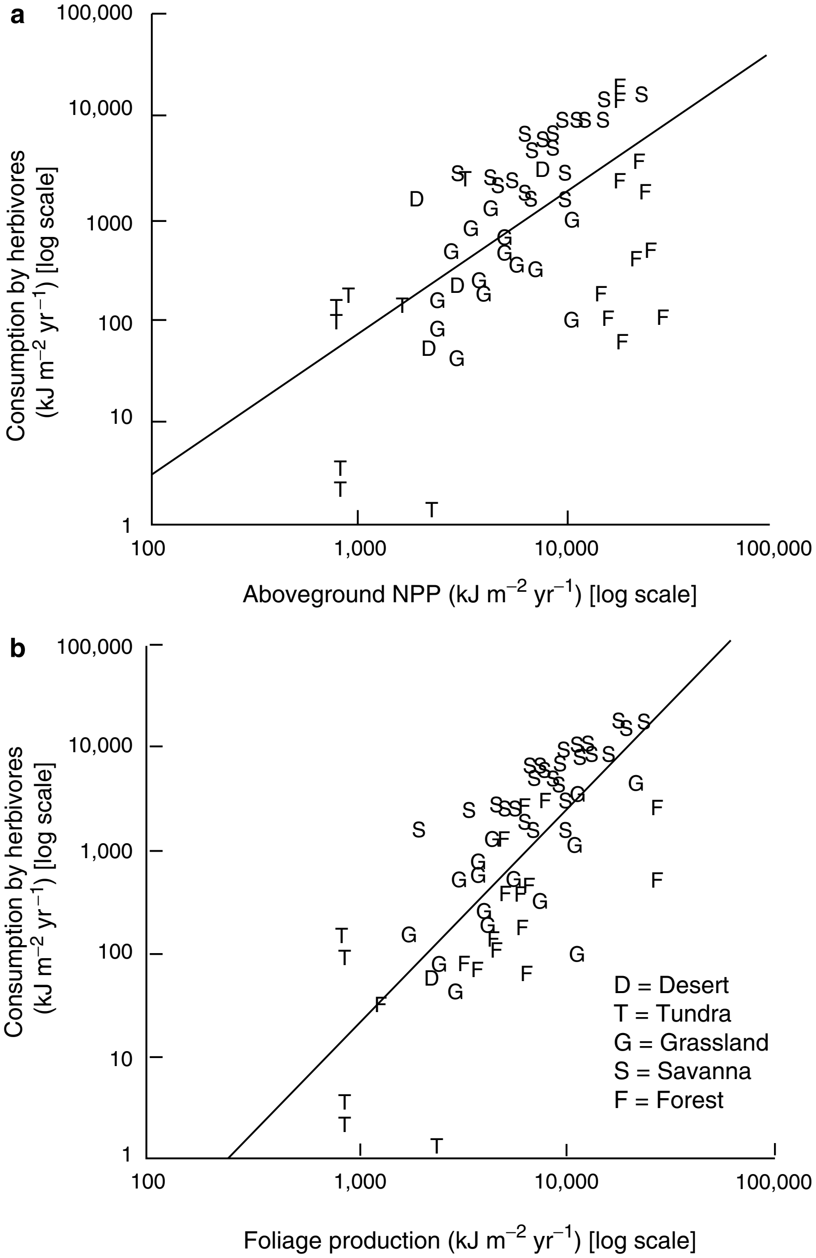

Fig. 10.6 Log–log relationship between (**a**) aboveground NPP or (**b**) foliage production and consumption by herbivores. One gram of ash-free biomass is equivalent to 20 kJ of energy. Consumption by herbivores is more closely related to foliage production than to total aboveground NPP because much of the aboveground NPP is inedible by most herbivores. Redrawn from McNaughton et al. (1989)

suggesting a tradeoff between allocation to growth vs. defense (Coley 1986). Plant species typical of high-nitrogen environments, particularly nitrogen-fixing species, often produce **nitrogen-based defenses** (i.e., organic compounds containing nitrogen, such as alkaloids) that are toxic in relatively small quantities to generalist herbivores. Nitrogen-based defenses are well developed, for example, in terrestrial legumes and freshwater cyanobacteria. Other types of defenses include sulfur-containing defenses, accumulation of selenium or silica,

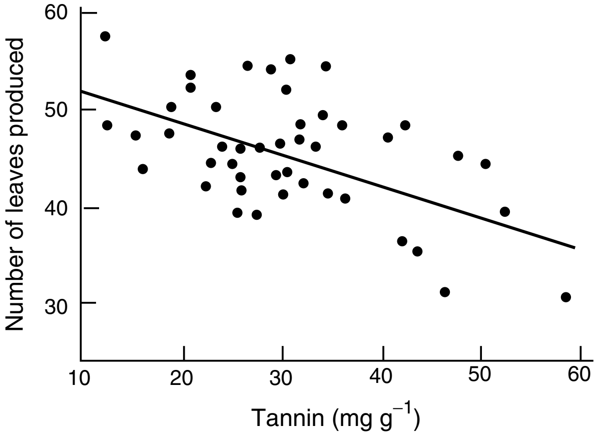

Fig. 10.7 Relationship between rate of leaf production (an index of growth rate) and leaf tannin concentration in the tropical tree *Cecropia peltata*. The graph shows a negative relationship between investment in defense and growth rate. Redrawn from Coley (1986)

and physical defenses like thorns (Boyd 2004). Reproductive tissues which have high value to the plant and constitute a modest proportion of total production are often protected by nitrogen- or sulfur-based toxic compounds (Zangerl and Berenbaum 2006).

2. Any plant is less palatable when grown in infertile than in fertile soils, due to a lower protein content and a higher level of carbon-based defenses (Ayres 1993). Under conditions of low nutrient availability, growth is constrained more strongly than is photosynthesis, so carbon tends to accumulate (see Chap. 6; Bryant et al. 1983). Under these circumstances, carbon allocated to chemical defense may have only modest negative effects on growth rate.
3. In a given environment, plants vary seasonally in their allocation to defense, with allocation to growth occurring when conditions are favorable and allocation to tissue differentiation and defense when conditions deteriorate (Lorio 1986; Herms and Mattson 1992). Newly expanding leaves, especially those that expand rapidly, are poorly defended and are particularly vulnerable to herbivory (Kursar and Coley 2003).

The first two causes of variation in allocation to plant defense (genetics and environment) lead to high levels of plant defense on infertile soils. Plant defenses are either directly toxic, or reduce the availability of limiting resources to herbivores during ingestion or digestion (Barboza et al. 2009). Tannins, for example, bind with proteins, reducing N availability to herbivores; alkaloids can act as neurotoxins; and thorns reduce the feeding rate of mammals.

The balance of nitrogen, phosphorus, and digestible energy influence the efficiency with which these resources support animal production (Sterner and Elser 2002). Nonliving materials have a wide range of ratios of carbon to nitrogen to phosphorus. Living protoplasm, however, is much more constrained in these ratios because of the fundamental similarity of biochemical processes in all living cells (Reiners 1986; Sterner and Elser 2002). In general, phosphorus concentration is more variable than nitrogen in both plants and animals. Just as observed in plants (see Chap. 8) and microbes (see Chap. 9), animal production is constrained by the resource (nitrogen, phosphorus, digestible energy) that is most limiting in its food, and animals strengthen the coupling of nitrogen and phosphorus cycles by preferential acquisition of the most limiting element. For example, animals extract nitrogen most efficiently from low-nitrogen food through selective foraging, high rates of nitrogen absorption from the gut, or reduced rates of loss. Similarly, animals extract phosphorus most efficiently from low-phosphorus food. Elements that are less limiting are extracted from food less efficiently and are preferentially released to the environment. These **stoichiometric relationships** (element ratios) are important determinants of element cycling rates in all ecosystems (Sterner and Elser 2002), as discussed earlier and again in this chapter.

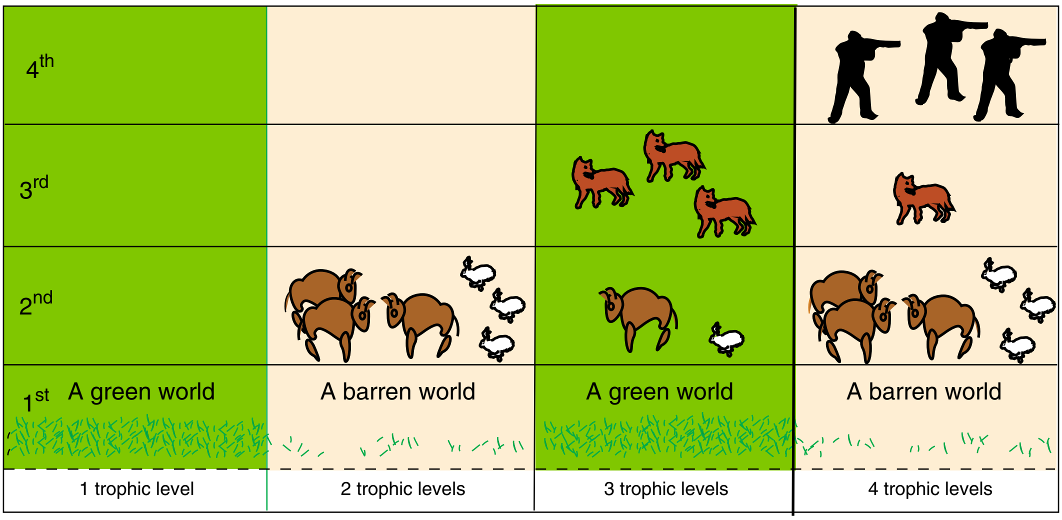

Fig. 10.8 Effect of food chain length on primary producer biomass in situations where trophic cascades operate. Plant biomass is abundant where there are odd numbers of trophic levels (1, 3, 5, etc.) because these have a low biomass of herbivores; plant biomass is reduced where there are even numbers of trophic levels (2, 4, 6, etc.) because these have a large biomass of herbivores

Top-Down Controls

Consumption by predators often alters the abundance of organisms across more than one link in a food web (trophic cascade; Pace et al. 1999). A predator, for example, may reduce the density of its prey, which releases the prey's prey from consumer control (Carpenter et al. 1985; Pace et al. 1999; Beschta and Ripple 2009; Schmitz 2009). Trophic cascades cause an alternation among trophic levels in biomass of organisms (Power 1990). In many streams, for example, if only algae are present, they grow until their biomass becomes nutrient-limited, producing a "green" surface (Fig. 10.8). If there are two trophic levels (plants and herbivores), the herbivores graze the plants to a low biomass level, leaving a barren surface with sparse, fast-growing algae. With three trophic levels, the secondary consumer reduces the biomass and grazing pressure of herbivores, which again allows algae to achieve a high biomass. Algal biomass is generally low when there is an even number (2, 4, etc.) of trophic levels. An odd number of trophic levels in a trophic cascade reduces the biomass of herbivores and releases the algae, producing a "green" world (Fretwell 1977).

Trophic cascades have been demonstrated in a wide range of ecosystems, ranging from the open ocean to tropical rainforests and microbial food webs (Pace et al. 1999; Schmitz et al. 2000; Borer et al. 2005; Beschta and Ripple 2009). Trophic cascades generally result from strong interactions between individual species and are therefore best documented at the level of species rather than ecosystems (Paine 1980; Polis 1999). Because of the species-specific nature of trophic cascades, they are most likely to emerge at the ecosystem scale when a single species dominates a trophic level, for example when *Daphnia* is the dominant herbivore or a minnow-eating fish is the dominant carnivore in a lake (Polis 1999). Similarly, removal of wolves in the western U.S. caused population explosions of elk and other ungulates, which overbrowsed their food supply. Wolf reintroductions reversed this effect through both predation and ungulate avoidance of areas with high predation risk (Frank 2008; Beschta and Ripple 2009).

Eutrophication of fresh waters often leads to strong species dominance, thereby providing conditions where trophic cascades can emerge (Pace et al. 1999). Trophic cascades have important practical implications; introduction of minnow-eating fish, under the right circumstances,

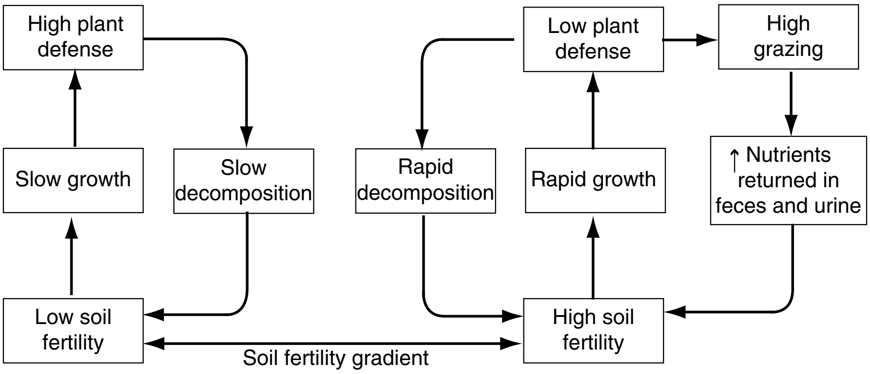

Fig. 10.9 Feedbacks by which grazing and plant defense magnify differences among sites in soil fertility. In infertile soils, herbivory selects for plant defenses, which reduce litter quality, decomposition, and nutrient supply rate. In fertile soils, herbivory speeds the return of available nutrients to the soil. Based on Chapin (1991b)

can release populations of zooplankton grazers, which graze down algal blooms and increase water clarity. Trophic cascades that involve invertebrate herbivores and homeothermic vertebrate predators are particularly strong (Schmitz et al. 2000; Borer et al. 2005). Unfortunately, unanticipated species interactions often become important when trophic dynamics are altered, leading to unexpected responses to species introductions or removal (Kitchell 1992). Manipulation of trophic cascades to address management issues therefore requires a sophisticated understanding and careful testing of the ecology of the species involved and the factors governing their interactions.

Trophic Effects on Nutrient Cycling

Herbivores enhance the productivity of productive ecosystems and reduce the productivity of unproductive ones (Frank 2006; Pastor et al. 2006). Dominance by plants with well-developed defenses in low-nutrient environments tends to reduce the frequency of herbivory in these ecosystems because herbivores select against patches in the landscape where plant palatability is low (see Chap. 13; Frank 2006). Herbivores in these environments (like the plants themselves) efficiently retain and recycle nitrogen and phosphorus and therefore produce feces with very low nutrient concentrations (Barboza et al. 2009), promoting nutrient immobilization by soil microbes. Herbivores indirectly reduce nutrient cycling in these environments by preferentially eating poorly defended plant species, leading to an increase in the abundance of well-defended plants that produce litter with low nutrient concentrations and high concentrations of plant defenses. The toxicity of many plant species to soil microbes causes reductions in decomposition rates (see Chap. 7) and further reduces soil fertility in low-nutrient environments (Fig. 10.9; Pastor et al. 1988; Northup et al. 1995; Pastor et al. 2006).

Herbivores are more abundant in fertile environments, where plants are more productive and more palatable. Their feeding speeds the turnover of plant biomass and the return of available nutrients to the soil as feces and urine. This short circuits decomposition and nitrogen mineralization and enhances plant production (Ruess and McNaughton 1987; Frank 2006; Pastor et al. 2006). Tissue nitrogen concentrations of about 1.5% appear to separate those infertile ecosystems where herbivory drives a decline in nutrient cycling from those more fertile ecosystems where herbivory enhances nutrient cycling (Pastor et al. 2006).

Plants in fertile environments are often well adapted to herbivory. Fertile grasslands are often more productive when moderately grazed than in the absence of grazers (McNaughton 1979; Milchunas and Lauenroth 1993; Hobbs 1996).

Grazing in many managed ecosystems, however, exceeds that which would occur naturally (Figs. 10.2 and 10.5) because people control animal densities through stocking rates and predator control. High levels of grazing, whether natural or managed, can reduce production and plant cover and increase soil erosion, leading to a decline in soil fertility and the productive potential of an ecosystem (Milchunas and Lauenroth 1993).

Ecological Efficiencies

Trophic Efficiency and Energy Flow

Energy loss with each trophic transfer limits the production of higher trophic levels. Not all of the biomass that is produced at one trophic level is consumed at the next level. Moreover, only some of the consumed biomass is digested and assimilated, and only some of the assimilated energy is converted into animal production (Fig. 10.10). Consequently, a relatively small fraction (generally <1–25%) of the energy available as food at one trophic level is converted into production at the next link in a food chain. This has profound consequences for the trophic structure of ecosystems because each link in the food chain has less energy available to it than did the preceding trophic link. In any plant-based trophic system, plants process the largest quantity of energy, with progressively less energy processed by herbivores, primary carnivores, secondary carnivores, etc. This leads inevitably to an **energy pyramid** (Fig. 10.11; Elton 1927) in which the production at each trophic link ($Prod_n$) depends on the production at the preceding trophic level ($Prod_{n-1}$) and the **trophic efficiency** (E_{troph}) with which the production of the prey ($Prod_{n-1}$) is converted into production of consumers ($Prod_n$).

$$Prod_n = Prod_{n-1} \times E_{troph} = Prod_{n-1} \times \left(\frac{Prod_n}{Prod_{n-1}} \right) \tag{10.1}$$

The trophic efficiency of each link in a food chain can be broken down into three ecological efficiencies (Fig. 10.10) related to the efficiencies of consumption ($E_{consump}$), assimilation (E_{assim}), and production (E_{prod}; Lindeman 1942; Odum 1959; Kozlovsky 1968).

$$E_{troph} = E_{consump} \times E_{assim} \times E_{prod} \tag{10.2}$$

In terrestrial ecosystems, the distribution of biomass among trophic levels can be visualized as a **biomass pyramid** that is similar in structure to the energy pyramid, with greatest biomass in primary producers and progressively less biomass in higher trophic levels (Fig. 10.11). This occurs for at least two reasons. First, as described earlier, the energy pyramid results in less energy available at each successive trophic link. Second, the large allocation to structural tissue and chemical defense in many terrestrial plants minimizes the proportion of plant production that can be converted to secondary production. The decrease in biomass with successive links is most pronounced in forests, where the dominant plants are long lived and produce a large proportion of biomass that is inedible or out of reach of ground-based herbivores. Biomass pyramids are less broad in grasslands where plants have a lower allocation to woody structures, and there is a relatively large biomass of herbivores and higher trophic levels.

In contrast to terrestrial ecosystems, freshwater and marine pelagic ecosystems have *less* biomass of primary producers than of higher trophic levels, leading to an **inverted biomass pyramid** (Fig. 10.11). This difference in trophic structure between terrestrial and pelagic ecosystems reflects the relative turnover rate of biomass among trophic levels. Phytoplankton in aquatic ecosystems have less structure and are more edible than their terrestrial counterparts. They are therefore rapidly grazed, and their biomass does not accumulate. Fish turn over more slowly and accumulate a larger biomass. In summary, terrestrial ecosystems are characterized by large, long-lived

$$\text{Consumption efficiency } (E_{\text{consump}}) = \frac{I_n}{Prod_{n\text{-}1}}$$

$$\text{Assimilation efficiency } (E_{\text{assim}}) = \frac{A_n}{I_n}$$

$$\text{Production efficiency } (E_{\text{prod}}) = \frac{Prod_n}{A_n}$$

$$\text{Trophic efficiency } (E_{\text{troph}}) = (E_{\text{consump}}) \times (E_{\text{assim}}) \times (E_{\text{prod}}) = \frac{Prod_n}{Prod_{n\text{-}1}}$$

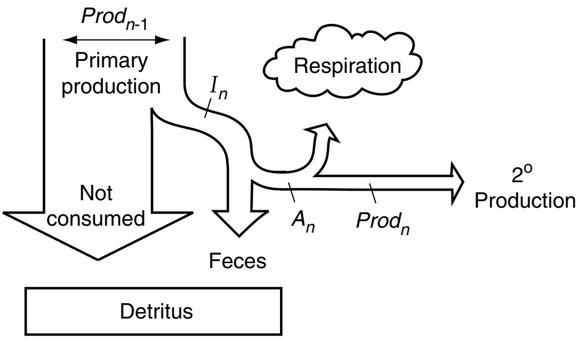

Fig. 10.10 Components of trophic efficiency, which is the product of consumption efficiency, assimilation efficiency, and production efficiency. Production efficiency is the proportion of primary production that is ingested (I_n) by animals. Assimilation efficiency is the proportion of ingested food (I_n) that is assimilated into the blood stream (A_n). Production efficiency is the proportion of assimilated energy (A_n) that is converted to animal production ($Prod_n$). Most primary production is not consumed by animals and passes directly to the soil as detritus. Of the plant material consumed by herbivores, most is transferred to the soils as feces. Of the material assimilated by animals, most supports the energetic demands of growth and maintenance (respiration), and the remainder is converted to new animal biomass (secondary production)

plants, leading to a large plant biomass and relatively small biomass of higher trophic levels. Aquatic ecosystems, in contrast, are characterized by rapidly reproducing phytoplankton that are smaller and more short lived than higher trophic levels (Fig. 10.12).

Regardless of the biomass distribution among trophic levels, there must always be more energy flow through the base of a trophic chain than at higher trophic levels. It is the *energy pyramid* rather than the biomass pyramid that describes the fundamental energetic relationships among trophic levels because energy is lost at each trophic transfer, so there must always be a decline in energy available at each successive trophic level. Trophic efficiencies with respect to nitrogen and phosphorus are discussed later.

Consumption Efficiency

Consumption efficiency is determined primarily by food quality and secondarily by predation. Consumption efficiency (E_{consump}) is the proportion of the production at one trophic level ($Prod_{n-1}$) that is ingested by the next trophic level (I_n; Fig. 10.10).

$$E_{consump} = \frac{I_n}{Prod_{n-1}} \qquad (10.3)$$

Unconsumed material eventually enters the detritus-based food chain as dead organic matter. On average, the quantity of food consumed by a given trophic level must be less than the production of the preceding trophic level, or the prey will be driven to extinction. There are, however, often short time periods when the consumption by one

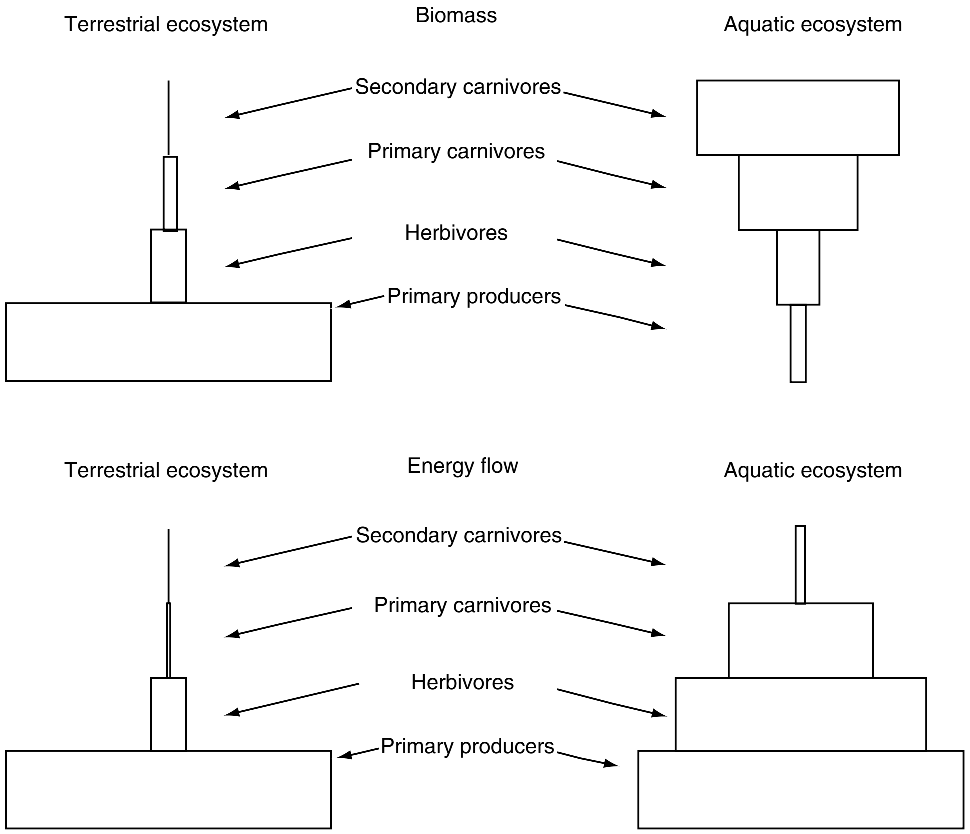

Fig. 10.11 Pyramids of biomass and energy in a terrestrial and an aquatic food chain. The width of each box is proportional to its biomass or energy content. Pyramids of energy are structurally similar in terrestrial and aquatic food chains because energy is lost at each trophic transfer. Biomass pyramids differ between terrestrial and aquatic food chains because most plant biomass (phytoplankton) is eaten in aquatic ecosystems, but not on land

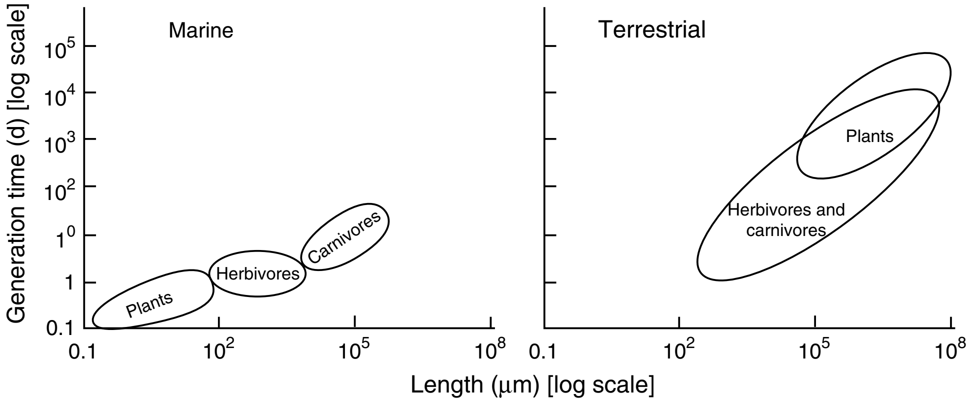

Fig. 10.12 Body size and generation time for organisms in the ocean and on land of dominant plants, herbivores, and carnivores. In the ocean, the dominant plants (pico- and nano-plankton) are generally smaller than the herbivores that feed on them, whereas on land, the dominant plants are often as large or larger than their herbivores. Redrawn from Steele (1991)

Table 10.1 Consumption efficiency of the herbivore trophic level in selected ecosystem types[a]

Ecosystem type	Consumption efficiency (% of aboveground NPP)
Ocean	60–99
Managed rangelands	30–45
African grasslands	28–60
Herbaceous old fields (1–7 year)	5–15
Herbaceous old fields (30 year)	1.1
Mature deciduous forests	1.5–2.5

[a] Data from Wiegert and Owen (1971) and Detling (1988). Terrestrial estimates emphasize consumption by aboveground herbivores and may not accurately reflect the total ecosystem-scale consumption efficiency

trophic level exceeds that in the preceding level. Vertebrate herbivores, for example, consume plants during winter, when there is no plant production. This is, however, offset by other seasons when plants produce more biomass than animals can consume. Situations where consumption efficiency is greater than 100% for prolonged periods lead to dramatic ecosystem changes (Fig. 10.2). If predator control, for example, leads to a large deer population that consumes more plant biomass than is produced, this will reduce plant biomass and alter plant species composition in ways that profoundly affect all ecosystem processes (see Chap. 12; Pastor et al. 1988; Kielland and Bryant 1998; Paine 2000). Similarly, insect outbreaks can substantially reduce the biomass and productivity of their host plants (Allen et al. 2006; Raffa et al. 2008). Sometimes trophic imbalances occur naturally. Some herbivores, such as beavers, typically overexploit their local food supply and move to new areas when their food is depleted. In snowshoe hare or lemming cycles, cyclic variations in herbivore abundance alter the balance between top-down and bottom-up controls.

The proportion of aboveground NPP consumed by herbivores varies at least 100-fold among ecosystems, from less than 1% to greater than 40% (Table 10.1), due primarily to differences in plant allocation to woody structures and chemical defense. Herbivore consumption efficiency is generally lowest in forests (<1–5%), where chemically defended woody biomass accounts for much of the production, and much of the biomass is out of reach of ground-dwelling herbivores. Herbivore aboveground consumption efficiencies are higher in grasslands (10–60%), where most aboveground material is non-woody, and highest (generally >40%) in pelagic aquatic ecosystems, where most phytoplankton biomass is cell contents rather than cell walls. In these ecosystems, more phytoplankton biomass is often consumed by herbivores than dies and decomposes; this pattern contributes to inverted biomass pyramids (Fig. 10.11). In grasslands, aboveground consumption efficiencies are generally greater for ecosystems dominated by large mammals (25–50%) than those dominated by insects and small mammals (5–15%; Detling 1988). The toxic nature of some plant tissues (due to presence of plant defenses) and inaccessibility of other tissues (e.g., roots to aboveground herbivores) constrain the herbivore consumption efficiency of terrestrial ecosystems. Nematodes, which are important belowground herbivores, consume 5–15% of belowground NPP in grasslands (Detling 1988). The highest aboveground consumption efficiencies in terrestrial ecosystems, ~90%, are on **grazing lawns**, such as those found in some African savannas (McNaughton 1985) and arctic wetlands (Jefferies 1988). These highly productive grasslands are maintained as a lawn of short grass by repeated herbivore grazing. Nutrient inputs in urine and feces from these herbivores promote rapid recycling of nutrients and the high productivity of these grasslands (Fig. 10.9; Ruess et al. 1989).

Consumption efficiencies of carnivores are subject to the same general constraints as herbivores, but carnivores are less constrained by the quality of their food. Consequently, efficiencies are often higher than those of herbivores, ranging from 5% to 100%. Vertebrate predators that feed on vertebrate prey, for example, often have a consumption efficiency greater than 50%, indicating that more of their prey is eaten than enters the soil pool as detritus. Invertebrate carnivores often have a lower consumption efficiency (5–25%) than vertebrate carnivores. Consumption efficiency of a trophic level at the ecosystem scale must integrate vertebrate and invertebrate consumption, including animals that feed below ground, but these efficiencies are not well documented at the ecosystem scale.

More often, consumption efficiency is documented for a single large herbivore in an ecosystem where it is abundant.

The consumption efficiency of a trophic level depends on its biomass and food intake, which are influenced by the quantity and quality of available food (bottom-up controls) and predation controls on consumer biomass (top-down controls). Bottom-up and top-down controls often interact. Rising atmospheric CO_2 concentration, for example, reduces leaf nitrogen concentration and increases the concentration of digestibility-reducing tannins (Ayres 1993). A caterpillar must therefore eat more food over a longer time period to meet its energetic requirements for development, extending the time that it is vulnerable to predators and parasites (Lindroth 1996). Bottom- up controls related to NPP and food quality often explain ecosystem differences in average consumer biomass and consumption, with greater consumer biomass in more productive ecosystems (Figs. 10.4 and 10.5). Predation and weather, however, explain much of the interannual variation in consumer biomass and the quantity of food consumed.

People have substantially altered the trophic dynamics of ecosystems through their effects on consumer biomass. Stocking of lakes with salmonids, for example, increases predation on smaller fish. Removal of fish can have a variety of trophic effects, depending on the trophic level of the target fish. Overfishing of herbivorous fish in coral reefs, for example, allows macroalgae to escape grazing pressure and overgrow the corals, killing them in places. On land, stocking of cattle at densities higher than can be supported by primary production causes overgrazing and a decrease in plant biomass; this has led to the loss of productive capacity in many arid lands (Fig. 10.2; Schlesinger et al. 1990). The consequences of human impacts on trophic systems are highly variable, but they often have profound effects on trophic levels up and down the food chain, as well as on the target species (Pauly and Christensen 1995; Pauly et al. 2005).

The bottom-up controls over consumption efficiency can be described in terms of the factors regulating food intake. Consumption by individual animals depends on the time available for eating, the time spent looking for food, the proportion of food that is eaten, and the rate at which food is consumed and digested. Each of these four determinants of consumption has important ecological, physiological, morphological, and behavioral controls that differ among animal species (Barboza et al. 2009).

Animals do many things other than eating, including predator avoidance, digestion, reproduction, and sleeping. In addition, unfavorable conditions often restrict the time available for foraging, especially for **poikilothermic** animals such as insects, amphibians, and reptiles, whose body temperature depends on the environment. Because of this constraint, desert rodents feed primarily at night; bears hibernate most of the winter; and mosquitoes feed most actively under conditions of low wind, moderate temperatures, and high humidity. **Activity budgets** describe the proportion of the time that an animal spends in various activities. Activity budgets differ among species, seasons, and habitats, but many animals spend a relatively small proportion of their time consuming food. Changes in climate or predator risk that influence activity budgets of an animal can profoundly alter food intake and therefore the energy available for animal production and maintenance. These effects can propagate through food webs. Reintroduction of wolves in Yellowstone National Park in the western U.S., for example, caused elk to concentrate their activity in less productive ecosystems, shifting the landscape patterns of consumption and soil carbon turnover (Frank 2008; Beschta and Ripple 2009).

Animals must find their food before they eat it. Most predators such as wolves spend more time looking for food than ingesting it. Other animals, including most herbivores, search for favorable habitats within a landscape, then spend most of their time ingesting food. Animals generally consume food faster than they can digest it, so some of the time spent in other activities simultaneously contributes to digestion of food.

Once an animal finds its food, it generally consumes only some of it. Many herbivores, for example, select only the youngest leaves of certain plant species and avoid other plant species, older leaves, stems, and roots. Similarly, carnivores may eat only certain parts of an animal and leave behind parts such as skin and large bones.

This selectivity places an upper limit on consumption efficiency. Many animals become more selective as food availability increases. Lions and bears, for example, eat less of their prey when food is abundant. Gypsy moths and snowshoe hares also preferentially feed on certain plant species, given the opportunity, but will feed on almost any plant during population outbreaks, after palatable species have been depleted.

Selectivity also depends on the nutritional demands of an animal. Caribou and reindeer, for example, have a gut flora that is adapted to digest lichens, which are avoided by most other herbivores. These animals eat lichens in winter when low temperatures impose a high energy demand for **homeothermy** (maintenance of a constant body temperature). Lichens have a high content of digestible energy but little protein. In summer, however, when these animals have a high protein requirement for growth and lactation, they increase the proportion of nitrogen-rich vascular plant species in their diet (Klein 1982). Other herbivores may select plant species to minimize the accumulation of plant toxins. Moose or snowshoe hares in the boreal forest, for example, can consume only a certain amount of particular plant species before accumulation of plant toxins has detrimental physiological effects (Bryant and Kuropat 1980; Feng et al. 2009). They therefore tend to avoid plant species with high levels of toxic **secondary metabolites**, that is, compounds that are not essential for normal growth and development. Selectivity by herbivores also depends on the community context. Mammalian generalist herbivores preferentially select plant species when they are uncommon because rare species are consumed too infrequently to reach a threshold of toxicity. Selectivity by these generalist browsers therefore tends to eliminate rare plant species and reduce plant diversity (Feng et al. 2009).

Selectivity differs among animal species. Some grazers, like wildebeest in African savannas, are almost like lawnmowers. They follow the pulse of grass growth that occurs after rains and consume most plants that they encounter. Other animals, like impala, select leaves of relatively high nitrogen and low fiber content, especially in the dry season. Among mammals, there is a continuum from large-bodied **generalist herbivores**, which are relatively nonselective, to small-bodied **specialist herbivores**, which are highly specific in their food requirements (Barboza et al. 2009). Similar patterns are seen among freshwater zooplankton; large-bodied cladocerans like *Daphnia* are generalist filter feeders, whereas same-sized or smaller copepods are more selective (Thorp and Covich 2001). Specialization is even more pronounced among terrestrial insects. Some tropical insects, for example, eat only one part of a single plant species. The abundance of specialist insects could contribute to the high diversity of tropical forests, by preventing any one plant species from becoming extremely abundant.

Assimilation Efficiency

Assimilation efficiency depends on both the quality of the food and the physiology of the consumer. Assimilation efficiency (E_{assim}) is the proportion of ingested energy (I_{n}) that is digested and assimilated (A_{n}) into the bloodstream (Fig. 10.10).

$$E_{assim} = \frac{A_n}{I_n} \tag{10.4}$$

Unassimilated material returns to the soil as feces, a component of the detrital input to ecosystems.

Assimilation efficiencies are often higher (5–80%) than consumption efficiencies (0.1–50%). Carnivores feeding on vertebrates tend to have higher assimilation efficiencies (about 80%) than do terrestrial herbivores (5–20%) because carnivores eat food that has less structural material and is more digestible than in terrestrial plants. Carnivores that kill large prey can avoid eating indigestible parts such as bones, whereas most terrestrial herbivores consume low-quality cell walls in combination with high-quality cell contents. Among herbivores, species that feed on seeds, which have high concentrations of digestible, energy-rich storage reserves, have a higher assimilation efficiency than those feeding on leaves. Leaf-feeding herbivores, in turn, have higher assimilation efficiencies than those feeding on wood, which has higher concentrations of cellulose and lignin. Many aquatic herbivores have particularly high assimilation efficiency (up to 80%) because of the low allocation to structure in many phytoplankton and other aquatic plants. Even in aquatic ecosystems, however, herbivores that feed on well-defended species have low assimilation efficiencies. Assimilation efficiencies of herbivores feeding on cyanobacteria, for example, can be as low as 20%.

The physiological properties of a consumer strongly influence assimilation efficiency. Ruminants, which carry a vat of cellulose-digesting microbes (the rumen), have a higher assimilation efficiency (about 50%) than do most nonruminant herbivores (Barboza et al. 2009). One reason for the high assimilation efficiency of ruminants is the greater processing time than in nonruminants of similar size, giving more time for microbial breakdown of food. Homeotherms typically have higher assimilation efficiencies than do poikilotherms due to the warmer, more constant gut temperature, which promotes digestion and assimilation. Homeotherms therefore have an advantage over poikilotherms in both consumption and assimilation efficiency.

Production Efficiency

Production efficiency is determined primarily by animal metabolism. Production efficiency (E_{prod}) is the proportion of assimilated energy (A_n) that is converted to animal production ($Prod_n$; Fig. 10.10). Production efficiency includes both growth of individuals and reproduction to produce new individuals.

$$E_{prod} = \frac{Prod_n}{A_n} \tag{10.5}$$

Assimilated energy that is not incorporated into production is lost to the environment as respiratory heat. Production efficiencies for individual animals vary 50-fold from less than 1% to greater than 50% (Table 10.2) and differ most dramatically between homeotherms (E_{prod} 1–3%) and poikilotherms (E_{prod} 10–50%). Homeotherms expend most of their assimilated energy maintaining a relatively constant body temperature. This high constant body temperature makes their activity less dependent on environmental temperature and increases their capacity to catch prey and avoid predation, but makes homeotherms extremely inefficient in producing new animal biomass. Among homeotherms, production efficiency decreases with decreasing body size because a small size results in a high surface/volume ratio and therefore a high rate of heat loss from the warm animal to the cold environment. In contrast, the production efficiency of poikilotherms is relatively high (about 25%) and tends to decrease with increasing body size. Some large-bodied animals, such as tuna, that belong to groups usually considered poikilotherms are partially homeothermic. Among poikilotherms, production efficiency is lowest in fish and social insects (about 10%), intermediate in noninsect invertebrates (about 25%), and highest in nonsocial insects (about 40%; Table 10.2). Production efficiency often decreases with increasing age because of changes in allocation to maintenance, growth, and reproduction.

Table 10.2 Production efficiency of selected animals[a]

Animal type	Production efficiency (% of assimilation)
Homeotherms	
Birds	1.3
Small mammals	1.5
Large mammals	3.1
Poikilotherms	
Fish and social insects	9.8
Nonsocial insects	40.7
Herbivores	38.8
Carnivores	55.6
Detritus-based insects	47.0
Noninsect invertebrates	25.0
Herbivores	20.9
Carnivores	27.6
Detritus-based invertebrates	36.2

[a] Data from Humphreys (1979)

Note that belowground NPP, including exudates and transfers to mycorrhizae, is large, poorly quantified, and usually ignored in estimating trophic efficiencies. Our views of trophic efficiencies may change considerably as our understanding of belowground trophic dynamics improves. Fine roots, mycorrhizae, and exudates, for example, turn over quickly and may support high belowground consumption and assimilation efficiencies for herbivores such as nematodes that specialize on these carbon sources (Detling et al. 1980).

Food Chain Length

Production interacts with other factors to determine length of food chains and trophic structure of communities. Both the NPP and the inefficiencies of energy transfer at each trophic link constrain the amount of energy that is available at successive trophic levels and could therefore influence the number of trophic levels that an ecosystem can support. The least productive ecosystems, for example, may have only plants and herbivores, whereas more productive habitats might also support multiple levels of carnivores (Fretwell 1977; Oksanen 1990). Detritus-based food chains also tend to be longer in more productive ecosystems (Moore and de Ruiter 2000). In some aquatic ecosystems, however, the trend can go in the opposite direction. Oligotrophic habitats can support inverted biomass pyramids in which large long-lived fish are more conspicuous than the phytoplankton and invertebrate populations that support them. When ecosystems are compared across broad productivity gradients, there is no simple relationship between NPP and the number of trophic levels (Pimm 1982; Post et al. 2000). Other factors such as environmental variability and the physical structure of the environment often have greater impact on the number of trophic levels than does the energy available at the base of the food chain (Post et al. 2000).

Seasonal and Interannual Patterns

In terrestrial ecosystems, production by one trophic level seldom coincides in time with consumption by the next. The temporal relationship between predator and prey is highly variable, but some common patterns emerge. Plants and their insect predators often use similar temperature and photoperiodic cues to initiate spring growth. However, insects cannot afford to emerge before their food, so there is often a brief window in spring when plants are relatively free of invertebrate herbivory (Fig. 10.13). After insect emergence, there is often a brief window before leaves become too tough or toxic for insects to feed (Feeny 1970; Ayres and MacLean 1987). In contrast to insects, homeotherm herbivores continue to consume food during the cold season, when plants are dormant. In addition, many herbivores migrate seasonally in response to seasonal variation in food quality and environment (Frank 2006; Pastor et al. 2006). These are, however, only three of many highly specific seasonal patterns of interaction between plants and their herbivores. Predation by higher trophic levels often focuses at times when prey are most vulnerable, such as when vertebrates are giving birth to young, when salmon are migrating, or when insects are moving actively in search of food. Again, the specific patterns are quite diverse and depend on the biology of predator and prey. The important point is that production by one trophic level and consumption by the next are seldom equal at any time in the annual cycle.

Predator–prey interactions also vary among years, in part because predators and prey often differ in their responses to interannual variation in weather or long-term trends in climate. Long-term warming and drying trends in the western U.S., for example, have contributed to an extensive outbreak of the mountain pine beetle due to increased

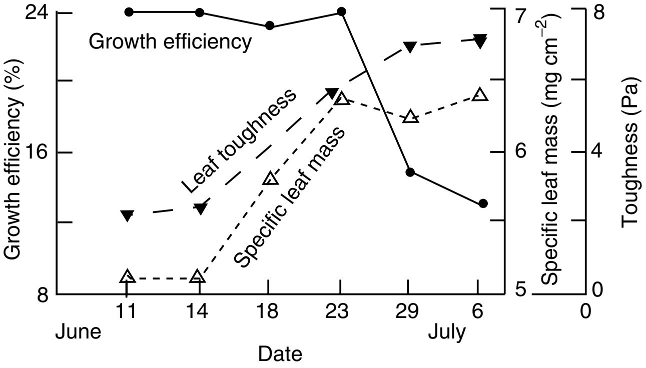

Fig. 10.13 Seasonal pattern of specific leaf mass and leaf toughness of Finnish birch leaves and of growth efficiency of fourth instar larvae of birch moths. The herbivore grows at maximal efficiency until leaves become tough and mature. After this 2-week window of leaf development, the herbivore grows slowly. Data from Ayres and MacLean (1987)

overwinter survival of the insect and a drought-induced decline in tree resistance (Allen et al. 2006; Raffa et al. 2008). Extensive tree mortality has altered virtually all ecosystem processes and shifted these forests from being a regional carbon sink to a source (Kurz et al. 2008). Predator–prey interactions can also drive population cycles of small mammals (Hanski et al. 1991) that cause changes in their food supply and vegetation-related ecosystem processes (see Chap. 12).

Nutrient Transfers

The *pathway* of nutrients through food chains is usually similar to that of energy. Nitrogen, phosphorus, and other nutrients in plants and animals are either organically bound or are dissolved in the cell contents. Nutrients contained in biomass eaten by animals therefore generally follow the same path through food chains as does energy, from plants to herbivores to primary carnivores to secondary carnivores, etc. At each link in the food chain, nutrients are digested and assimilated by animals, just as energy is digested and assimilated, although the efficiencies may differ substantially. As with energy, nutrient losses occur with each trophic transfer in the form of uneaten food, feces, and urine, so the quantity of nutrients transferred must decline with each successive trophic link. The pyramids of nutrient transfers are therefore similar in shape to those of energy flow, although the quantitative dynamics generally differ.

An important exception to this rule is sodium, which is required by animals for transmission of impulses in nerves and muscles. In contrast to animals, most plants do not require sodium and actively exclude it from roots and leaves, so tissue concentrations are lower in plants than would be expected based on soil solution concentrations (see Chap. 8). Sodium is therefore sometimes limiting to herbivores. Many terrestrial herbivores supplement the sodium and other minerals acquired from food by ingesting soil or salts from **salt licks**, which are mineral-rich springs or outcrops. Minerals may therefore show a different pathway of trophic transfer than do other nutrients.

A larger proportion of the nutrients contained in plant production pass through terrestrial herbivores than is the case for energy. Most terrestrial herbivores selectively feed on young tissues with high concentrations of nutrients and digestible energy and low concentrations of cellulose and lignin. Because of selective herbivory on nutrient-rich tissues, a larger proportion of plant-derived nutrients cycle through plant-based trophic systems than is the case for carbon.

Terrestrial herbivores not only select nutrient-rich tissues; they cycle nutrients more rapidly than do plants. Plants resorb about half the nitrogen and phosphorus from leaves during senescence, so plant litter generally has only half the nitrogen and phosphorus concentrations compared to the live tissue eaten by herbivores (see Chap. 8). For this reason, herbivory on leaves is at least twice as important an avenue for nitrogen and phosphorus cycling in terrestrial ecosystems as it is for biomass and energy. The rate of nutrient turnover by animals depends on the relative limitation by nutrients and energy (Sterner and Elser 2002). Terrestrial grazers excrete nutrients that are in excess of their growth requirements in inorganic form or as simple organics such as urea and uric acid that are quickly hydrolyzed in soils (see Chap. 9). In summary, terrestrial herbivores speed nutrient cycling in at least three ways: (1) by removing plants tissues that are more nutrient-rich than would otherwise return to the soil in litterfall, (2) returning nutrients to the soil faster than they would be recycled by plants, and (3) returning nutrients to the soil in forms that can be directly absorbed by plants (Fig. 10.9).

The ratio of elements required by plants and herbivores determines the nature of element limitation in organisms and the patterns of nutrient cycling in ecosystems. Both freshwater and terrestrial plants require nitrogen and phosphorus in a molar ratio of about 30:1 (Fig. 10.14; see Fig. 8.9; Sterner and Elser 2002). The N:P ratio in herbivorous zooplankton and insects is similar (about 26:1) to that in plants. N:P ratio is, however, quite variable among both plants and animals, reflecting both storage of nitrogen or phosphorus that is accumulated in excess of immediate requirement (see Chap. 8) and differences among organisms in their requirements for

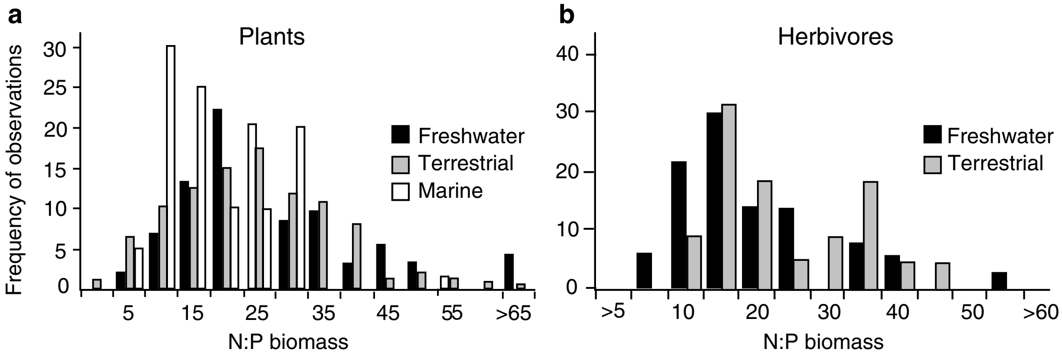

Fig. 10.14 Frequency distribution of N:P molar ratios in freshwater, terrestrial, and marine plants (*left*) and terrestrial and freshwater herbivores (insects and crustaceans, respectively; *right*). Redrawn from Elser et al. (2000)

the two elements. Rapidly growing or actively reproducing zooplankton, for example, have high concentrations of phosphorus-rich ribosomes to support protein synthesis, and therefore a lower N:P ratio (higher phosphorus requirement). Large vertebrates also have a low N:P ratio because their high proportional allocation to bones entails a high phosphorus investment (Sterner and Elser 2002). Fish in an oligotrophic lake, for example, may account for 75% of the water-column phosphorus, and moose antlers may account for 10% of the phosphorus turnover in the boreal forest (Moen et al. 1998; Sterner and Elser 2002).

Given the wide range in N:P ratios of plants and animals, herbivores often confront food resources with a quite different element balance than their own bodies. This imbalance is corrected by efficiently acquiring the most strongly limiting element and returning to the environment a disproportionate share of elements that do not limit their growth. This tends to reinforce the patterns of nutrient limitation in the ecosystem. Differences in N:P ratios among grazers in lakes illustrate the importance of this effect. *Daphnia* is a rapidly growing cladoceran grazer that has a higher phosphorus requirement to support its rapid growth (lower N:P ratio) than more slowly growing copepods. Under conditions of *Daphnia* dominance, grazers accumulate more phosphorus and excrete more nitrogen than when copepods are the dominant grazer; this leads to short-term phosphorus limitation of phytoplankton growth when *Daphnia* dominates and short-term nitrogen limitation when copepods dominate (Sterner and Elser 2002).

The turnover of nutrients in terrestrial vegetation is quite variable (see Chap. 8). Although herbivory accounts for a smaller proportion of the total nutrient return from plants to the environment in terrestrial than in aquatic ecosystems, it could still have important effects on soil and plant N:P ratios. Elk in Yellowstone Park, U.S., for example, retain substantial phosphorus to support bone and antler growth, excreting nitrogen, and raising the N:P ratios of grazed vegetation (Frank 2008). Stoichiometric analyses provide an exciting theoretical framework for linking the nutrient requirements of organisms to element cycling patterns in ecosystems (Sterner and Elser 2002).

Trophic cascades propagate downward to affect carbon and nutrient turnover in soils. Animals affect soil carbon and nutrient turnover through effects on both the quantity and quality of organic material that enters the soil (Fig. 10.9). Reintroduction of wolves to Yellowstone Park, for example, reduced the abundance of elk and shifted their distribution from productive predator-prone lowland habitats to higher elevations, resulting in reduced herbivory and nitrogen mineralization in lowland sites (Frank 2008; Beschta and Ripple 2009). Grazing by herbivores was more important than hillslope position in governing landscape patterns soil carbon turnover (Frank et al. 2011). Similarly, removal of conspicuous spiders in old fields in the northeastern U.S. increased grasshopper herbivory, altered plant species composition, and increased litter quality and nitrogen mineralization rate, indicating the importance of trophic dynamics for ecosystem biogeochemistry (Schmitz 2009).

Detritus-Based Trophic Systems

Detritus-based trophic systems convert a much larger proportion of available energy into production than do plant-based trophic systems. Decomposer organisms (primarily bacteria and fungi) feed on plant, animal, and microbial detritus, just as herbivores feed on live plants. As in the plant-based trophic system, there is a food chain of animals that feed on these decomposer organisms (Fig. 10.15). The principles governing this energy flow are similar to those in the plant-based food chain.

The rate of input and quality of dead organic matter are the major determinants of the quantity of energy that flows through the detritus-based system. The detritus-based food chain exhibits losses of energy to growth and maintenance respiration and to feces, just as in plant-based food chains (Fig. 10.15). Moreover, each trophic transfer entails the excretion of inorganic N and P, which become available to plants, just as in the plant-based trophic system.

The major structural distinction between plant- and detritus-based systems is that the plant-based system involves a one-way flow of energy, as energy is either transferred up the food chain or is lost from the food chain as respiration, unconsumed production, or feces. In the detritus-based food chain, however, uneaten food, feces, and dead organisms again become substrate for decomposers at the base of the food chain (Fig. 10.15; Heal and MacLean 1975). Energy flow in the detritus-based system therefore has a strong recycling component. Energy is conserved and is available to support detritus-based production until it is respired away or is converted to recalcitrant humic material. Due to the efficient use of carbon that enters the base of the food chain, the detritus-based food

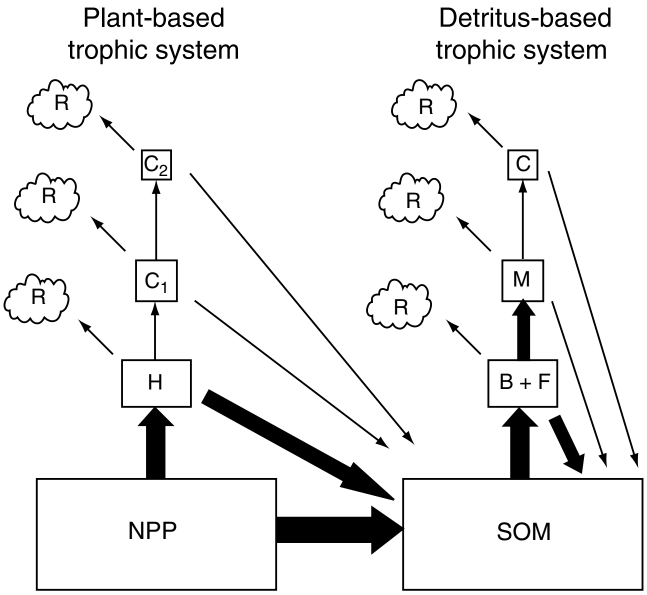

Fig. 10.15 The two basic trophic systems in ecosystems. In the plant-based trophic system, some energy is transferred from live plants to herbivores (H), primary carnivores (C_1), secondary carnivores (C_2), etc. In the detritus-based trophic system, energy is transferred from dead organic matter to bacteria (B) and fungi (F), microbivores (M), carnivores (C), etc. In both trophic systems, energy that is not assimilated at each trophic transfer passes to the detritus pool (as unconsumed organisms or as feces). The major difference between these two trophic systems is that energy passes in a one-directional flow through the plant-based trophic system to herbivores and carnivores or to the detrital pool. In the detritus-based trophic system, however, material that is not consumed returns to the base of the food chain and can recycle multiple times through the food chain before it is respired away or converted to recalcitrant humus. Redrawn from Heal and MacLean (1975)

web accounts for most of the energy flow and supports the greatest animal diversity in ecosystems (Heal and MacLean 1975).

The trophic efficiencies of the detritus-based trophic system are generally higher than in the plant-based trophic system. The consumption efficiency of detritus-based food chains is high because all of the potential "food" is consumed several times until it is eventually respired away. Assimilation efficiency is also high in decomposers (bacteria and fungi) because their digestion is extracellular, so, by definition, all the material that is consumed by decomposers is assimilated. Production efficiencies of decomposers (40–60%; see Chap. 9) and animals in detritus-based food chains (35–45%) are also higher than in plant-based trophic systems (Table 10.2). Together these high trophic efficiencies explain why the detritus-based trophic system accounts for most of the secondary production in ecosystems.

Integrated Food Webs

Food webs blur the trophic position of each species in an ecosystem. In the real world, many animals feed on prey from more than one trophic level, often from both the plant-based and detritus-based trophic systems and at multiple trophic levels within each system (Polis 1991). For this reason it is difficult to assign most organisms to a single trophic level. In pelagic ecosystems, for example, zooplankton select food based on size and shape more than on species identity and consume phytoplankton, detrital particles, and small animals. On land, fungivores feed on a mixture of mycorrhizal fungi that derive their energy from plants and saprophytic fungi that decompose dead organic matter. Bacteria also derive energy from root exudates (a component of NPP) and from dead organic matter. Soil animals that eat bacteria and fungi are therefore part of both the plant-based and detritus-based trophic systems. Root-feeding mites and nematodes fall prey to animals that also eat detritus-based animals (Fig. 10.3). All soil food webs therefore process a mixture of plant and detrital energy and nutrients in ways that are difficult to untangle. Aboveground animals also eat substantial detrital material such as fungi or soil animals. Robins, for example, feed on both earthworms and herbivorous insects. Bears eat plant roots and ants of terrestrial origin (plant-based and largely detritus-based food chains, respectively), and fish from aquatic food webs. Many insects are detrital feeders at the larval stage but as adults drink nectar or blood (plant-based trophic system). About 75% of food webs contain both plant- and detritus-based components (Moore and Hunt 1988), so mixed trophic systems are the rule rather than the exception.

Scavengers such as vultures, hyenas, crabs, and many beetles are technically part of the detritus-based food web, although their consumption, assimilation, and production efficiencies are similar to those of carnivores. Scavengers often kill weakened animals, and many predators feed on prey that have been recently killed by other animals, further blurring the distinction between plant-based and detritus-based food chains.

Parasites, pathogens, and diseases are trophically similar to predators. They derive their energy from host tissues and use the products of these cells for their own growth and reproduction, just like predators. It is difficult in practice, however, to separate the biomass of parasites, pathogens, and diseases from that of their hosts, so the concepts of consumption and assimilation efficiencies are seldom applied to these organisms. Parasites, pathogens, and diseases are therefore often treated as agents of mortality rather than as consumers.

Mutualists also confound the trophic picture. Mycorrhizal fungi can change from being mutualistic to parasitic, depending on environmental conditions and the nutritional status of the host plant (Koide 1991). Under mutualistic conditions, mycorrhizal fungi act as herbivores in transferring carbohydrates from plants to the fungus, whereas nutrient transfer occurs in the opposite direction (detritus-based food chain). The trophic role of these two organisms therefore depends on the constituent of interest. Although the broad outlines of trophic dynamics have a clear conceptual basis, the complexities of nature and our poor understanding of belowground processes often make it difficult to describe these food webs quantitatively.

Summary

Nutrient supply and other factors controlling NPP constrain the energy that is available to higher trophic levels in plant-based trophic systems. These same factors govern the quantity and quality of litter input to the soil and therefore the energy available to the detritus-based trophic system. These factors constitute the bottom-up controls over trophic dynamics. The trophic efficiency with which energy is transferred from one trophic level to the next depends on the efficiencies of consumption, assimilation, and production. Consumption efficiency depends on the interaction of food quantity and quality with predation by higher trophic levels. Consumption efficiency of herbivores is lowest in unproductive habitats dominated by plants that are woody or well-defended. Carnivores generally have higher consumption efficiency than herbivores. Assimilation efficiency is determined primarily by food quality. It is lower in unproductive than in productive habitats and lower for herbivores than for carnivores. In contrast to the other components of trophic efficiency, production efficiency is determined primarily by animal physiology; poikilotherms, for example, have a higher production efficiency than do homeotherms. Most secondary production in terrestrial ecosystems occurs in the detritus-based trophic system. In this system, material that is not consumed or assimilated returns to the base of the food chain and continues to recycle through the food chain until it is respired or converted to recalcitrant humus. Most food webs contain both plant- and detritus-based components. Impacts, including those resulting from human activities, on any link in food webs often propagate to other links in food webs.

Review Questions

1. Describe the pathways of carbon flow in an herbivore-based food chain. How does the efficiency of conversion of food into consumer biomass differ between herbivores and carnivores? What determines the partitioning of assimilated energy between respiration and production?
2. What is the major structural difference between plant-based and detritus-based food chains? Which food chain can support the greatest total production? Why?
3. What are the major structural differences between terrestrial and aquatic food chains? Why do these differences occur?
4. What plant traits determine the amount of herbivory that occurs? What ecological factors influence these plant traits?
5. What are the effects of herbivores on nitrogen cycling?
6. What are the mechanisms by which top predators influence abundance of primary producers in aquatic food chains? How does the number of trophic links affect ecosystem structure?

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