2. Next, perennial, herbaceous plants become established and gradually displace the annuals. Plant species diversity is highest in this phase.
3. In the third phase, woody plants begin to become established (shrub or bush phase). With increasing shade, the herbaceous species are displaced and the plant stand becomes more species poor.
4. In the final stage, trees are dominant and a closed forest develops.

The development of such a community can vary substantially in terms of species composition and the duration of different stages of development, depending on the site. Detailed predictions of the course of succession are therefore hardly possible. The development of agricultural fallow land is primarily determined by three groups of factors. These are:

- previous cultivation, the effect of which is largely determined by the last cultivated crops and agricultural practices, for example fertilization, soil cultivation, and use of herbicides. These factors significantly affect the growing conditions of the plants, and the seed bank found in the soil.
- natural site conditions, which are primarily determined by the climate, soil properties, the exposure, and slope. Generally, drier and cooler site conditions mean that succession proceeds more slowly.
- the vegetation in the direct and more distant vicinity of the site. The frequency of individual plant species, their distance from potential sites of colonization, and the dispersal ability of their seeds affect species composition, especially in early stages of succession. The presence of shrubs which spread through vegetative stolons can accelerate the encroachment of scrub on to fallow land.

Not only plant communities but also animal communities undergo succession. For example, flower-rich, herbaceous plant stands, which develop in the first years on agricultural fallow land are correlated with the presence of butterflies and wild bees. In addition, they provide resources for specific antagonists of pests of cultivated plants (Sect. 5.2.4.5).

The intentional establishment of agricultural fallow land, as a component of the cultural landscape, can contribute to conservation of the species diversity of typical field flora and fauna.

3.5 Flows of Energy and Material

Energy and organic and inorganic materials are continuously transported and transformed within the compartments of an ecosystem, and between different ecosystems. These processes are carried out by organisms and as a result of abiotic factors, for example water and wind.

Table 3.2 The ecological efficiencies which determine the portion of net primary productivity that is used by consumers for production of biomass within an ecosystem

Utilization efficiency in different ecosystems	
Forests	2–7%
Cropping systems[a]	9–21%
Grasslands	5–60%
Oceans	40–99%
Assimilation efficiency of different consumers	
Wood-eaters (xylophages)	15%
Grass and leaf-eaters (herbivores)	30–50%
Seed-eaters (granivores)	70–80%
Predators	70–90%
Detritivores	20–40%
Production efficiency of different consumers	
Mammals and birds	1–3%
Insects and other invertebrates	10–55%

Based on Whitaker (1975), Wiegert and Owen (1971), Humphreys (1979) and other sources

[a] Yield losses of the most important food crops worldwide attributed to phytophages (Based on Oerke et al. 1994)

3.5.1 Energy Flows Through Food Webs

The energy flows in ecosystems proceed via food chains and food webs. Of the total energy fixed by photosynthesis in a plant, representing **gross primary production (GPP)**, only a portion is converted into biomass, representing **net primary productivity (NPP)**. The difference between GPP and NPP is the portion of energy that is needed by the plant for the maintenance of metabolic processes; this is released as heat. Primary production is measured in grams of carbon (C) or grams of biomass (fresh or dry weight) per unit area per year.

The NPP of natural vegetation types on Earth varies within a broad range. In different terrestrial ecosystems, NPP can range from just a few g C m^{-2} year^{-1} in deserts to approximately 2,000 g C m^{-2} year^{-1} in tropical rain forests. The reasons for this are not only the differences in the yearly radiation received from the sun by the different latitudes on Earth (Sect. 4.1), but also such other factors as water and nutrient availability to plants. The proportion of NPP utilized in the production of biomass by the various organisms within the consumer food web is determined by different ecological efficiencies:

- The **utilization efficiency** is the proportion of NPP of a plant stand that is taken up by phytophagous consumers as food. This efficiency varies significantly among different ecosystems (Table 3.2). In a forest, this value is almost 7% (the differences between temperate and tropical latitudes is slight) and is primarily consumed by insects. In grassland ecosystems, utilization efficiencies range from 5 to 60%. The highest values for terrestrial ecosystems are found in the African savannas, for which grazing mammals are mostly responsible. Of the

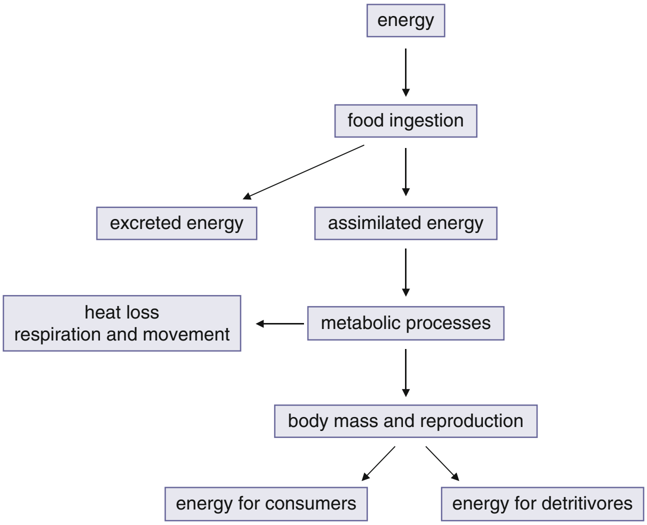

Fig. 3.11 Pathways of energy within a trophic level

globally most important crops in agroecosystems, between 9 and 21% are consumed by phytophagous pests.

- The **assimilation efficiency** represents the portion of the consumed biomass that is available to the consumer as energy source. Thus, it cannot be equated with the quantity of food that reaches the digestive system. Of this, a portion of variable size cannot be used by the organism and is therefore excreted. The assimilation efficiency depends on the quality of the food and the ability of the organism to make the food's energy content available during digestion (Table 3.2). In leaf and grass-eaters, the assimilation efficiency is approximately 30–50%, which means that at least half of the ingested food remains unused. Wood-eating species assimilate only approximately 15% of their food. The assimilation efficiency of seed and fruit-eaters and of secondary consumers (predators) is up to 80%. As in the producers, the assimilated energy is used primarily for two processes—respiration, in which it is released as heat, and production of biomass.
- The **production efficiency** is the proportion of assimilated energy that is available for production of biomass, i.e. for growth and reproduction. Groups of consumers can also be classified on the basis of this efficiency (Table 3.2). Mammals and birds, which must maintain a higher body temperature, can transform 1–2% of assimilated energy into biomass whereas insects and invertebrates can transform 10–55%.

The pathways of distribution of energy within a trophic level are shown in Fig. 3.11. The energy stored within the biomass of dead organisms provides the basis of the detritivore food web.

The energy that flows into the food web via the producers declines from one trophic level to the next. The related transfer efficiency varies with each ecosystem and the associated organisms.

3.5.2 Material Transport Through Water and Wind

In many landscapes, **water** is the most important transport medium for organic and inorganic material. Streams and rivers take up soil and detritus from their watershed. In flood plains, these loads are deposited and not only supply natural ecosystems, for example riparian forests, with nutrients, but also supply agroecosystems. For example, the sediments deposited during the flooding of the Nile had existential importance for the agriculture of Egypt for thousands of years. Removal of natural vegetation by humans increases soil erosion, which also increases the amount of material transported by rivers. The clearing of forests in Central Europe, which began with the spread of agriculture 7,000 years ago, led to filling of stream and river flood plains with fertile soil. In the tropics, because of greater precipitation, the clearing of forests often results in devastating landslides that can destroy entire villages in the valleys. In addition, the rivers transport the removed soil to the ocean, where coral reefs are buried by the sediment and subsequently die. As a result, populations of fish species directly or indirectly dependent on the reefs also decline, which in turn threatens the food supply and livelihoods of many coastal residents.

Material transport through **wind** is also of great importance for many ecosystems. During the Ice Ages, loess, i.e. silt produced by the movements of glaciers on rocks, was formed. On poorly vegetated areas, this material was subject to wind erosion and was, in some cases, deposited in great layers in other locations. Loess forms fertile soils that are among the best agricultural lands in many areas of the world (e.g. China, North America, Central Europe). Today, wind-related transport processes are still important. Over a distance of more than 5,000 km, millions of tons of sand and dust are transported from the Sahara to the Amazon region every year. This is a significant source of nutrients for the rain forest there.

Input of nitrogen from the atmosphere is an (additional) source of nutrients for several ecosystems (Sect. 3.7.4.2).

Ecosystems are not closed entities, but instead are connected with each other through the interactions of species, as well as through the flow of energy and materials.

3.5.3 Flows of Energy and Material in Agroecosystems

With regard to energy and material flows, intensively managed agroecosystems, in particular, have several characteristics distinct from those of natural ecosystems:

- Large proportions of the net primary productivity, i.e. the biomass of the crops, are removed from the system during harvest, which also results in a decline in the nutrient content of the soil.
- To compensate for these losses, fertilizers must be used (Sect. 2.3.3). Mineral fertilizers are imported into the agroecosystem from outside and must be produced and transported using energy, which in turn uses external resources, primarily fossil fuels.
- For the production of crops, further energy is required, specifically for soil cultivation, sowing, harvest, and possibly irrigation. This energy comes from manual labour, the use of animals or the application of machinery and is based on food, feed, or fuel, respectively. Usually, chemicals are also applied to control pests, weeds, and phytopathogens. These substances must also be produced, transported, and distributed. Their residues reach the food webs and ecosystems.
- Only a relatively small portion of the nutrients imported into an agroecosystem as fertilizers is taken up by the crop plants. For example, only approximately one third of the nitrogen applied to the soil in German agriculture is extracted via the plant and animal products. The rest is leached out or escapes as a gas into the atmosphere (Sect. 3.7.4.2). Sixty percent of the nitrogen input into the North and Baltic Seas originates from agriculture.
- Through global trade, agricultural products (e.g. cereals and soybean for animal production) reach other regions where they become a component of the material and energy flows of those ecosystems (e.g. in the form of animal excrement).

Intensively cultivated agroecosystems in particular are characterized by high material and energy flows and to only a limited extent by internal cycles.

3.6 Ecosystem Services

The present and future welfare of people, societies, and economies depend on the various goods and resources provided by nature. Beside the many kinds of plants and animals from agricultural and natural systems that sustain and benefit human life, this also includes a variety of services, often considered as granted and freely available. They are so-called public goods, which cannot be owned and have no markets and prices. Such services are based on natural ecosystem processes and functions, which result in the provision, regeneration, and long-term stability of