2.4 Classification of Agroecosystems

Depending of the objectives of the farmer, the availability of capital, energy, and technology, and the institutional and infrastructural context, a great diversity of crop and livestock production systems exist. In addition, there are also differences related to historical and geographic factors. The latter primarily result from the climate, the natural vegetation, and the soils of different zones of the world (Chap. 7).

2.4.1 Cropping Systems

Cropping systems can be classified on the basis of a combination of three key characteristics, each of which can be subdivided into two groups:

1. **Life-form of the crop**
   Crops, similar to other plants, can usually be classified into two groups according to their life-form:
   (a) **Annual crops**, for example cereals, require one vegetation period to complete their development and have, accordingly, a short life span. They must, therefore, be sown again every growing season. However, depending on the species and region, more than one harvest per year is possible. For example, in the humid tropics, rice, with a vegetation period of 120 days, can be cultivated three times per year.
   (b) **Perennial crops** have a lifespan of several years and deliver, depending on the species, a harvest in one or more of these years.
2. **Intensity of production**
   (a) In agroecosystems that are subject to **extensive** management, production is essentially based on the natural site conditions, which means that only a limited quantity of materials are imported into the system, and these usually consist of limited quantities of farmyard manure.
   (b) Agroecosystems that are subject to **intensive** management are characterized by the application of technology which includes the use of machines, mineral fertilizers, and pesticides. In such systems, plant production is not based solely on solar energy but also on fossil energy, which is required for operation of machines and for production and transport of fertilizers and pesticides.

   These two forms of land use are not absolute opposites, but are instead connected by a wide range of production intensity. On the one hand, the different transition forms imply the gradual improvement of production methods that has occurred during the development of agriculture over the course of thousands of years. On the other hand, they show the existing differences between production conditions and the potential of farming in the industrial and developing nations.

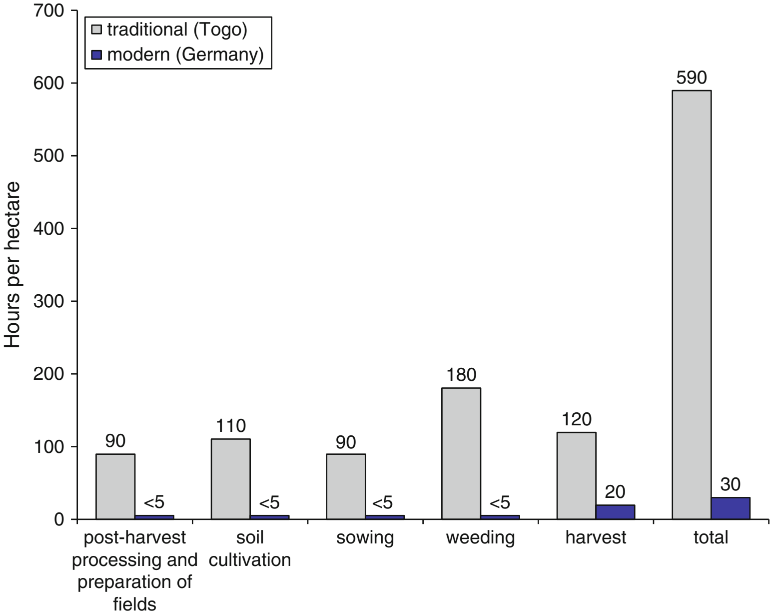

Fig. 2.20 Labour requirements for maize production in Togo and Germany (Based on Koch 1994)

With increasing intensification of agricultural production, the input of human labour usually decreases as the need for manual labour for activities such as soil cultivation, sowing, weeding, and harvesting, decreases. This results in significant differences between the labour required for extensively and intensively managed agroecosystems (Fig. 2.20).

3. **Cropping period**

   (a) In extensive land use, production of crops on the same area is possible for a limited period of time only (usually between 2 and 4 years). Then, the nutrient reserves in the soil no longer deliver satisfactory yields. For regeneration of the soil fertility, an extended fallow period (several years to decades) is therefore necessary, before crop production can start again. Systems in which crop production is interrupted by such a phase are called **rotation systems**.

   (b) By intensification of production, not only an increase in crop yield per field area but also a longer duration of use of the same field, up to permanent use, becomes possible. Thus, in such **permanent systems**, there are no multi-year fallow periods but, at most, seasonally dependent interruptions to production.

A more detailed description of rotation and permanent systems is presented in the following sections. An overview is given in Fig. 2.21.

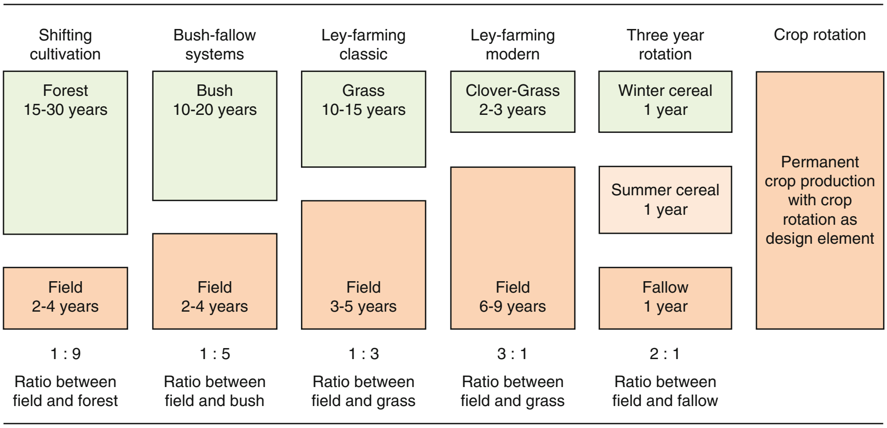

Fig. 2.21 Overview of agricultural rotation and permanent systems

2.4.1.1 Rotation Systems

Production systems with long fallow periods mark not only the beginning of agriculture but are still an important form of crop production in many regions.

Shifting Cultivation

Production systems in which short phases of field use alternate with long forest phases are called shifting cultivation or slash-and-burn farming. To establish a 1–4 year phase of crop production, the trees are felled and often burnt. Because the tree roots generally remain in the soil, cultivation of the fields between the remains of the forest vegetation is conducted in the simplest manner, for example with a digging stick. With declining soil fertility, the land is abandoned and left to natural succession, to be used again at a later date. In forested Europe, this form of production was the start of agriculture and was predominant into the early medieval period.

In the tropics, shifting cultivation is still performed by more than 250 million people (Metzger 2003). With increasing population density and the corresponding increasing demand for agricultural products, the forest phases between those of agricultural land use will become shorter. Finally, this leads to overexploitation or nutrient mining of the site, through which the growth of the trees is limited and the forest eventually disappears completely. Often, a cleared site can no longer be used for production because the fertile upper soil layers have been eroded by heavy tropical rainfall (Sect. 4.3.6).

Bush-Fallow Systems

Rotation systems in the form of bush-fallow systems primarily exist in the savanna regions. After a short period of agricultural land use, bush vegetation often becomes

Table 2.1 Types of ley-farming

Unregulated	Irregular alternation between crops and grassland
Regulated	Regular alternation between crops and grassland
Classic	Establishment of grassland after the crop phase by natural succession
Modern	Establishment of grassland after the crop phase by sowing of seed mixtures

established on fallow fields, which serves to regenerate the soil as in shifting cultivation, and is cleared again after a specific period of time.

Ley-Farming

Alternating use of an area as crop field and as grassland (meadow or pasture) is called ley-farming, whereby the grassland serves for soil regeneration. As in many other production systems, a broad range of historical and regional types exist (Table 2.1).

In the early medieval period, from approximately the sixth century onward, ley-farming became established in Central Europe and, in contrast with shifting cultivation, had the advantage that cultivation was not hindered by tree roots. Reforestation of the grassland was generally prevented by grazing.

Basically, one can distinguish between regulated and unregulated ley-farming. In the regulated type, the change in use occurs after a defined number of years. This type of system was usually found in the vicinity of the homestead; crop production was performed for 3–5 consecutive years and then alternated with at least 10 years of grassland use. In the unregulated type, the transition between crop field and grassland occurs irregularly and was typically practised on land distant from the homestead. In this case, grassland use extended from 10 to 40 years and was interrupted by a 1–2-year phase of cereal production.

In many regions of Europe, ley-farming was replaced in the ninth century by three-year rotation (see below), but was continued in marginal regions of production (e.g. the Black Forest, northern Germany, the Alps, and Scandinavia) until today. Whereas in classic ley-farming natural establishment of grasses occurred, the modern type includes sowing (usually of a clover–grass mixture) for production of animal feed. Different types of ley-farming are often among the predominant land-use systems today in the wet–dry tropics, but also in many regions of the temperate latitudes.

2.4.1.2 Permanent Cropping Systems

The population density of Europe increased substantially since approximately the eighth century. This process not only required expansion of agricultural land but also intensification of crop production on existing fields. This occurred through the introduction of a **3-year rotation**, which can be seen as intermediate between

Fig. 2.22 Spelt (*Triticum spelta*)

rotation and permanent systems. In its original form, this system consisted of 2 years of crop production (winter cereals in the 1st year, summer cereals in the 2nd year) and fallow in the 3rd year. The most important cereal crops were barley, rye, and oats. In southwestern Germany, spelt (*Triticum spelta*; Fig. 2.22) was also important. In the nineteenth century, an improved form of the 3-year rotation emerged in which the fallow year was used for the production of feed legumes (primarily clover) or root and tuber crops (primarily potato). The development of permanent cropping without fallow years was also promoted by the increasing availability of fertilizers (compare Sect. 2.3.3).

Because of the need to feed a growing population, permanent systems are also gaining increasing importance in the densely populated regions of the tropics. However, production there often occurs without the possibility of compensating for nutrient losses by sufficient fertilization. As a consequence of this, yields decline. For the savanna regions of West Africa, annual nutrient deficits are estimated to be between 15 and 25 kg nitrogen, up to 2 kg phosphorus, 15–20 kg potassium, and 5 kg magnesium per hectare (Buerkert and Hiernaux 1998).

Permanent Arable Cropping

Worldwide, permanent crop production is predominantly performed in the form of **one-crop systems**, which means the exclusive production of a single crop species in a field. In agricultural land use that is increasingly oriented toward intensification and yield maximization, specific crop species are also grown on the same field for several years in a row. Such **monocultures** are only possible with autotolerant plants. These are plants for which repeated, consecutive production in the same field does not lead to declines in yield. This is true for maize and many other important food plants, including rye and potatoes. In contrast, autointolerant species cannot be repeatedly grown on the same field without interruption, because otherwise yield losses result. This also often happens when an adequate supply of nutrients is not ensured. Species that are autointolerant include sugar beet, oats, wheat, pea, and rapeseed. The causes of this phenomenon, which is also termed soil sickness, are unknown in many cases. For some species (e.g. rapeseed) the reduction in yield is primarily the result of an increased incidence of plant diseases.

For other species, for example alfalfa and some rice varieties, allelopathic effects have been demonstrated (Sect. 4.4.2).

A proved and tested principle of permanent crop production is **crop rotation**, which means a temporal sequence of production of different crop species (mostly one-crop cultivation) in the same field. Crop rotation not only contributes to conservation or improvement of soil fertility (Sect. 4.3.5.3) but are also to a measure of weed management (Sect. 5.1.3) and pest management (Sect. 5.2.3.1), because the population development of weeds or pests can be affected by the change in crop species. In crop rotation, a distinction is made between cereals and leaf crops. The latter are all species other than cereals, for example rapeseed, root and tuber crops (potato, beet, field vegetables), and legumes, but also green and silage maize and fodder grasses. Production of cereals (C) and leaf crops (L) can be designed in different ways. Common systems include simple rotation (C – L – C – L) and double rotation (L – L – C – C). The seasonally dependent temporal gaps between the respective main crops can be filled with the production of **cover crops** which can serve as green manure or animal fodder. Green manure plants are grown to biologically bind nutrients (primarily nitrogen) left in the soil by previous crops, thus protecting them from leaching. Examples of cover crops include legumes, for example lupines and clover species, grasses, and different Brassicaceae (mustard family), for example white/yellow mustard (*Sinapis alba*), radish (*Raphanus sativus*), and field mustard or turnip (*Brassica rapa*). Another cover crop species is the lacy phacelia (*Phacelia tanacetifolia*), which is a member of the Hydrophyllaceae (waterleaf family). It was introduced to Europe from California and also serves as a feeding resource for bees. Summer and winter cover crops are distinguished, depending on the sowing date. In contrast with one-crop systems, **intercropping** involves at least two crop species grown simultaneously in the same field. They are grown in alternate rows or wide strips but often also without a planned order. A particular type of intercropping is the establishment of underseeds (undersown crops). This is done by sowing a plant species into the stand of a main crop. Underseeds used in cereals include clover and grass species which serve as animal fodder.

Whereas in the industrialized nations large one-crop systems predominate, intercropping is a traditional type of land use in many regions of the tropics and continues to be of importance today. Examples include the mixed cropping of maize, beans (*Phaseolus* species), and squash in Central America and the mixed cropping of cereals (sorghum, pearl millet) and legumes, for example cowpea, pigeon pea (*Cajanus cajan*), and/or peanuts in the savanna regions of Africa.

Intercropping enables a better utilization of nutrients and water from the soil, e.g., by growing shallow and deep-rooted crops together. In addition, intercropping can contribute to the suppression of weed growth and to reduced pest incidence (Sect. 5.2.4.5). Overall, intercropping serves to minimize the risk of losing the entire harvest. Even when one of the cultivated crops fails, the other may still produce a yield.

Because of improved resource utilization in intercropping, the yield per unit area is often higher than that from the same area with only one crop. Whether, and to what extent, intercropping furnishes better yields than one-crop cultivation can be

Table 2.2 Example of calculation of the land equivalent ratio (*LER*)

	Yield (t/ha)		
Crop	Intercropping (E_M)	Sole cropping (E_R)	LER partial
A	5.1	8.9	5.1/8.9 = 0.57
B	1.9	3.9	1.9/3.9 = 0.49
C	0.6	2.8	0.6/2.8 = 0.21
LER total	–	–	$\sum \frac{E_{Mi}}{E_{Ri}} = 1.27$

evaluated with the **Land Equivalent Ratio (LER)**. This ratio is calculated by comparing the yields of two or more crop species from intercropping with the yields produced with the same species in sole cultivation. LER is calculated by use of formula:

$$\text{LER} = \sum E_{\text{Mi}} / E_{\text{Ri}}$$

where E_M is the yield of one crop from intercropping and E_R is the yield of the same species from the one-crop system. For every crop, i, represented in the intercropping, the relationship between E_M and E_R is calculated. The resulting partial LER values are summed to produce the total LER value. A value >1.0 means there is a yield advantage from intercropping. In the example given in Table 2.2, the LER total value is 1.27, which means the area required in sole cropping to achieve the same yield of the three crops as is produced by intercropping would have to be 27% larger than in intercropping.

Perennial Crops

Permanent agricultural crops include all crop species with more than one year periods of use. These are perennial field crops, for example asparagus (*Asparagus officinalis*), hops (*Humulus lupulus*), and artichoke (*Cynara scolymus*), and the variety of shrub and tree crops used in agricultural production, for example grapes (*Vitis vinifera*) and tree fruit species.

Plantations (from Latin *plantare* = to plant) are typical permanent cropping systems. In the original sense this term referred to large scale agricultural enterprises in the tropics and subtropics in which plant products were usually grown in monocultures and produced for the world market (Table 2.3).

This type of operation was first established by the Europeans in their colonies and was inseparably connected with slavery from the beginning of the seventeenth century to the end of the nineteenth century.

Plantations are used in the production of:

- perennial field crops, for example sugar cane, sisal (*Agave sisalana*; Fig. 2.23), and pineapple;

Table 2.3 Important crop species of the tropics that are primarily produced in plantations for the world market

Species	Length of economic use period (years)	Main producers
Sugar cane	6–8	Brazil, India
Oil palm	50	Indonesia, Malaysia
Banana	20	India, Brazil
Coconut	80	Philippines, Indonesia
Pineapple	6–13	Thailand, Philippines
Rubber tree	30–40	Thailand, Indonesia
Coffee	30–100	Brazil, Columbia
Tea	50	India, China
Sisal	6–20	Brazil, Tanzania

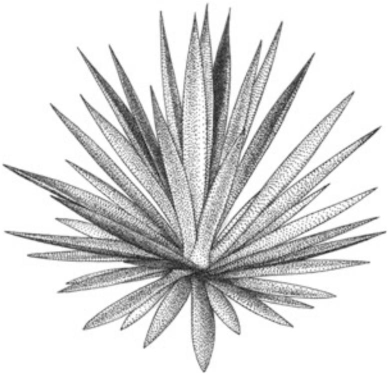

Fig. 2.23 Sisal (*Agave sisalana*)

- shrub crops, for example coffee, tea (*Camellia sinensis*; Fig. 2.24), and cacao (*Theobroma cacao*; Fig. 2.25);
- herbaceous perennials, for example the banana (*Musa* × *paradisiaca*); and
- tree crops, for example oil palm, coconut palm (*Cocos nucifera*), and rubber tree (*Hevea brasiliensis*), and various fruit and spice trees, e.g. cloves (*Syzygium aromaticum*) and nutmeg (*Myristica fragans*).

Agroforestry systems are also permanent systems producing trees or other woody plants and agricultural crops together on the same plot. By combining such species, the diversity of products gained from the system can be increased and, in addition, various ecological functions are better fulfilled than in sole arable cropping systems. Woody plants provide better protection of the soil from wind and water erosion (Sect. 4.3.6) than annual plants and increase the biodiversity of the system. Their root systems reach greater depths than those of most arable crop species, which means that water and nutrients from deeper soil layers can be used. The organic material in tree litter reaches the soil's surface where it is decomposed by soil organisms, so the inorganic components of this "nutrient pump" become available to plants. Overall, the need for external fertilizers is thus reduced. The

Fig. 2.24 Tea (*Camellia sinensis*)

Fig. 2.25 Cacao (*Theobroma cacao*) is a cauliflorous tree species. Cauliflory refers to woody plants which flower and fruit from their main stems or branches as opposed to the ends of the twigs

root systems of woody plants also affect the soil structure and, thus, the rate of infiltration of precipitation and the water balance of the soil.

In addition to the positive effects mentioned above, woody plants can also have negative effects on the other plants of an agroforestry system, primarily as a result of competition for light, nutrients, and/or water. Therefore, for every system it is necessary to investigate which perennial and annual species are best suited for cultivation together, to achieve complementary effects. Factors such as sowing and planting dates of the species also affect the ecological interactions.

A particular form of agroforestry are **home gardens**, in which crops are integrated in natural tree stands. They are primarily found in Southeast Asia and serve to produce fruit trees, rattan palms, medicinal plants, and vegetables. Another type is the so-called agro-silvopastoral system (Latin *silva* = forest, and *pastor* = shepherd), in which forestry and agricultural uses are complemented by a livestock component.

2.5 Livestock Systems

In addition to, and sometimes in combination with cropping systems, a large variety of livestock production systems exist around the globe. Important factors involved in livestock production include the animal species and the type of product, the climatic conditions in the region of production, the type of land use, and the type and origin of feeding resources.

In consideration of these and with additional criteria, for example socio-economic conditions, several system classifications have been proposed. Among these, the classification scheme based on Seré and Steinfeld (1996) has become most widely accepted and is also used in the following discussion. Further information is provided by Steinfeld et al. (2006) and Robinson et al. (2011).

As shown in Fig. 2.26, this classification first distinguishes two main categories, i.e., solely livestock systems and mixed farming systems. These groups are then broken down into different categories considering animal type, land use, and climate.

2.5.1 Solely Livestock Production Systems

This group includes the two most extreme types of livestock production, ranging from old traditional systems using large areas of natural grassland to systems of intensive livestock production with high animal densities in factory farming systems with low space requirements.

2.5.1.1 Landless Livestock Systems

These systems are largely independent of climate and are defined as livestock systems in which more than 90% of the dry matter fed to animals is introduced from outside the farm, and in which annual average stocking is above ten livestock units (LU) per hectare of agricultural land. (In this context, a livestock unit is one individual for cattle or eight individuals for sheep or goats.)

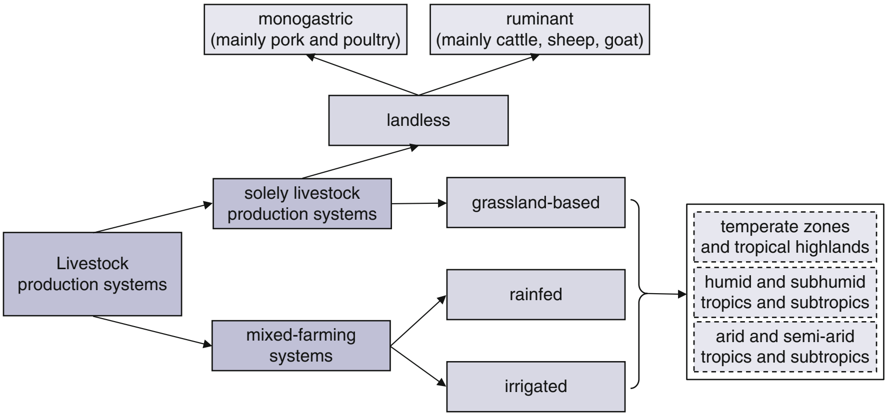

Fig. 2.26 Classification of world livestock production systems (Based on Seré and Steinfeld 1996)

Landless livestock systems can further be subdivided into:

- **Landless monogastric systems** (mainly pigs and poultry) are found predominantly in the industrialized countries of Europe and North America, with approximately half of global landless pork production and landless poultry production each. In pig production, Asia is second, with nearly one third of the world total. The predominant producer of pigs and poultry in Asia is China.
- **Landless ruminant systems** (mainly cattle, sheep, goats) exist in only a few regions of the world. For cattle, they are concentrated in eastern Europe; landless sheep production systems are found in western Asia and northern Africa only.

2.5.1.2 Grassland-Based Systems

Areas used for livestock grazing cover more than a quarter of the global land surface but are inhabited by approximately 4% of the world's human population only. Grassland-based livestock systems produce more than 10% of the dry matter fed to animals and have annual average stocking rates less than ten livestock units per hectare of agricultural land.

Overall, livestock grazing covers a wide range of systems which are defined as follows:

- **Total nomadism**: herders have no permanent place of residence; they move with their animals in a way that normally avoids depleting pastures without regular cultivation.
- **Semi-nomadism**: a permanent place of residence exists; supplementary cultivation is practised, but for long periods of time animal owners travel to distant grazing areas.

- **Transhumance**: herders have a permanent home, and their herds are sent to distant grazing areas, usually on seasonal cycles, e.g. in montane regions the movement between higher pastures in summer and valleys in winter.
- **Partial nomadism**: characterized by farmers who live continuously in permanent settlements and have herds at their disposal that graze in the vicinity.
- **Stationary animal husbandry**: animals remain on the farm or in the village throughout the year.

Solely livestock production on grasslands is of different importance in different climatic regions. Most of the world's large natural grasslands of the temperate zones have conditions suitable for crop production and, therefore, have been developed for arable farming, especially in the North American Prairie, the South American Pampas, and the East European Steppe. The largest areas of natural grassland used for grazing in the temperate zone are found in Central Asia including Mongolia, where 80% of the country is used for extensive grazing.

In the humid and sub-humid tropics, the grassland-based livestock production system is found mostly in the tropical and subtropical lowlands of South America, including the llanos of Colombia and Venezuela and the cattle-ranching lands of the Amazon basin which have developed from cleared and burned rainforest.

In many regions of the arid and semi-arid tropics, extensive grazing systems, usually known as **rangelands**, are the dominant form of land use. Extensive grazing of rangelands for livestock production is called **pastoralism**. In northern Africa and in western Asia, pastoralism is a traditional way of subsistence for an important part of the population. In dry regions, especially, fuel wood is often scarce, leading to an increased role for animals as providers of manure for fuel, in addition to their provision of meat and milk and as a means of transport. In Australia, parts of western United States, and southern Africa, commercial rangeland enterprises are the modern form of land use in dry regions.

2.5.2 Mixed-Farming Systems

Mixed-farming systems are agricultural production systems in which the waste products of one enterprise (residues from crop production) are used by the other enterprise (livestock production) which returns its own waste products (manure) to the first enterprise. In these types of system, more than 10% of the dry matter fed to animals comes from crop by-products or stubble, or more than 10% of the total value of production comes from non-livestock farming activities.

Globally, mixed-farming systems contribute more than half of total meat production, compared with approximately one-third by landless systems and less than 10% by grazing systems.

Mixed systems can combine crops and livestock to different extents, which include on-farm systems with more or less closed ecological cycles, spatially separated systems of between-farm mixing (exchanging resources between different farms within a region), or temporally changing activities and crop–livestock interactions related to seasonal differences (winter/summer or rainy/dry season). In smallholder systems, livestock, in addition to crop production, may provide food and income, draught power for crop production, manure to improve soil fertility, and financial insurance in times of scarcity.

Depending on the water resources available for crop production, mixed systems can be further subdivided into rain-fed and irrigated systems. Most mixed farming systems are rain-fed, and are widespread in semi-arid and sub-humid areas of the tropics and in temperate zones.

Overall, if the land area used for grazing and that used for feed crop production for landless livestock systems are added together, livestock production is the world's largest agricultural sector with the highest proportion of land use.

Driven by human population growth, urbanization, and increased income, the demand for animal-source food products is increasing, especially in the developing countries. In the future, production will increasingly be affected by competition for natural resources, particularly land and water, and competition between human food and animal feed production. Environmental problems of livestock production and potential solutions are raised in Sect. 6.2.2.

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Chapter 3
Patterns and Processes in Ecosystems

3.1 Biotic Interactions

The different individuals, populations, and species occurring together in a habitat do not exist independently of each other, but instead affect each other unilaterally or reciprocally in numerous relationships. The effects of such interactions have a substantial effect on the different structural and functional characteristics of an ecosystem, for example the number of species present, the sizes of their populations, the temporal development of the communities, and the flows of energy and nutrients.

3.1.1 Food Webs

The fundamental importance of food webs to all species is not only because of the trophic dependency of particular resources, but also because of the possible presence of natural enemies. The latter are also a biotic factor that affects the living conditions and population density of a species. With regard to sources of food, organisms can be subdivided into autotrophs and heterotrophs.

3.1.1.1 Autotrophic Organisms

Species that do not require organic substances as their foodstuffs, but instead have the ability to synthesize organic compounds from carbon dioxide and water, are called **autotrophs**. In ecosystems, they fulfil the function of **producers**. When the organisms obtain the required energy from sunlight, they are called **photoautotrophs** and perform photosynthesis (Sect. 4.1.1). In addition to some bacteria (e.g. cyanobacteria, formerly called blue–green algae), primarily green plants are capable of photosynthesis. **Chemoautotrophic** organisms derive the

K. Martin and J. Sauerborn, *Agroecology*, DOI 10.1007/978-94-007-5917-6_3,

energy needed for the production of organic compounds not from light, but instead by oxidation of inorganic compounds and thus are said to perform chemosynthesis. These organisms include nitrate, sulfur, methane, and iron-bacteria.

3.1.1.2 Heterotrophic Organisms

Animals, fungi, and most bacteria depend on organic compounds produced by other organisms for their nutrition and are called **heterotrophs**. This group includes consumers and detritivores.

Consumers

All species that feed on living organisms are consumers. They include two groups:

First order consumers obtain their food or nutrients from autotrophic organisms. The consumers of plants are:

- **Phytophages** (plant-eating animals), which can be further subdivided on the basis of the plant parts they use (Sect. 4.5.1).
- **Phytopathogens** (agents of plant disease), which primarily include fungi, bacteria, and viruses (Sect. 4.6).
- **Parasitic plants**, which obtain organic compounds and/or nutrients, and water from their host plants (Sect. 4.4.3).

First order consumers cause damage to plants that can lead to losses of fitness and yield (Box 3.1).

Second order consumers feed on heterotrophic organisms and can be divided into three groups:

- **Predators** are defined as organisms that kill other organisms to acquire food. Predation is found primarily among animals, but carnivorous (meat-eating) plants should also be regarded as predators.
- **Parasitoids** are insects (primarily ichneumon wasps; Sect. 5.2.4.1), that lay their eggs in the bodies of arthropods at particular stages of development (egg, larva, pupa, or adult) The parasitoid larvae live in the host's body (endoparasitoids) or attack the host's body from the outside (ectoparasitoids) and feed on its tissues. When the parasitoid has completed its development—after pupation or hatching of the adult (imago)—the host dies. The predatory life strategy of parasitoids is limited to the larval stage. In contrast, the adults are usually flower visitors, feeding on nectar or pollen.
- **Parasites** include groups of animals that live temporarily or permanently on or in the organisms of another animal species to obtain food from them (e.g. mosquitoes, fleas, tapeworms, leeches). In contrast with parasitoids, they do not usually kill their host and are, therefore, not predators.

Box 3.1 Fitness and Yield

For the host plant, attack by phytophages, phytopathogens, and/or parasitic plants is associated with loss of tissue and/or substances (primarily carbohydrates, nitrogen compounds, and water). As a consequence, physiological processes in the plant may be impaired, which can affect the plant's photosynthetic performance, its uptake of water and nutrients, and its use and distribution of photosynthetic products (e.g. as reserves). In reaction to an attack, the plant activates different energy-intensive defence mechanisms (Sect. 4.5.5). Overall, the resulting damage and energy losses can impair growth, development, and, finally, the reproductive success of the plant. **Fitness** serves as a measure of the reproductive success for all organisms. It is defined as the relative contribution of an individual to the offspring of a population. In the spermatophytes (seed-producing plants), this contribution is usually measured as the number of seeds the plant produces over the course of its lifetime. The effect on fitness is thus an objective criterion with which to measure the damage caused by a consumer to a wild plant.

In relation to agricultural crops, the term fitness usually has no meaning because stands of such species are not populations whose individuals reproduce themselves according to natural rules. Rather, their continued existence is determined by humans, for whom **yield** is the crucial factor. "Yield" refers primarily to the quantity and quality of products harvested, which for many species are not the seeds but rather other plant parts (e.g. for leafy vegetables and tubers).

Decomposers

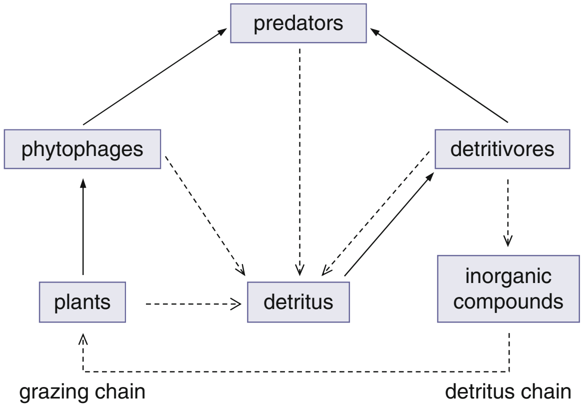
Decomposers are species that, in contrast with consumers, obtain their foodstuffs from the dead remains of organisms. The dead organic matter which results from all organisms at the end of their existence is termed detritus. Two functional groups can be distinguished among the decomposers:

- **Detritivores** utilize organic substances in the same way as consumers and are involved in the decomposition of dead organic material in ecosystems.
- **Reducers** or **mineralizers** transform organic substances into inorganic end products, from which they obtain energy. Mineralization is mostly performed by microorganisms, primarily fungi and bacteria (Sect. 4.3.5.1).

3.1.1.3 Trophic Levels and Food Webs

Producers, first and second-order consumers, and detritivores each represent one distinct **trophic level**. At the same time, they are the links of the **food chain**. Food

Fig. 3.1 Simplified representation of the food chains in ecosystems. The *dashed arrows* show the pathways of non-living materials



chains can be divided into two main types, which are related to each other and are usually found together in terrestrial ecosystems (Fig. 3.1):

1. The **grazing chain** begins with plants and leads, via the phytophages, to the predators.
2. The **detritus chain** is based on the dead organic matter that is produced at all trophic levels. It is consumed by the decomposers, on whom specific predators feed.

The trophic levels consist of numerous species. Most consumers use not only one, but several, species as their food source. Therefore, the trophic relationships between individual species do not form a simple chain, but rather a complex **food web**. As an example, Fig. 3.2 shows a detail of a food web based on rice.

Some species cannot be definitively assigned to a particular trophic level, because their range of foods includes several trophic levels. These species are called **omnivores** and may be, for example, phytophages and predators at the same time (e.g. some birds and small mammals) or may have different feeding strategies at different stages in their development (e.g. many insects with different feeding strategies as larvae and as adults).

3.1.2 Competition

The contest between two (or more) individuals or populations for food, space, or other resources of limited availability, which leads to unilateral or reciprocal negative effects on the participating organisms, is called **competition**. This definition applies to the competition between different species (**interspecific**), and to the competition between individuals of the same species (**intraspecific**).

Fig. 3.2 Detail of the food web of a rice field community in the Philippines. **1** = rice plant (*Oryza sativa*); **2** = yellow rice stemborer (*Scirpophaga incertulas*, Pyralidae), (**a**) adult, (**b**) larva, which lives in the rice stalks; **3** = parasitoid ichneumonid wasp (*Temelucha philippinensis*, Ichneumonidae) which attacks S*ciropophaga*; **4** = ladybird beetle (*Micraspis crocea*, Coccinellidae); **5** = brown planthopper (*Nilaparvata lugens*, Delphacidae), (**a**) adult, (**b**) nymph; **6** = damselflies (Coenagrionidae); **7** = plant bug (*Cytorhinus lividipennis*, Miridae); **8** = big-headed fly (*Pipunculus* sp., Pipunculidae), parasitoid of planthoppers/leafhoppers; **9** = grasshopper (*Acrida* sp., Acrididae); **10** wasp spider (*Argiope* sp., Araneidae); **11** = rice bug (*Leptocorisa* sp., Alydidae) sucks on milk-ripe kernels; **12** = rice farmer

Interspecific competition occurs when three conditions are fulfilled:

1. the species occur in the same habitat,
2. they utilize one or more of the same resources,
3. the availability of these resources is limited.

The intensity of interspecific competition is determined by the quantitative availability of resources and the size of the populations competing with each other.

The effects of interspecific competition are usually asymmetric. In other words, the disadvantages resulting from competition are greater for one of the populations involved than they are for the other. The negative effects are usually evident in the more or less obvious impairment of the development of individuals, which often leads to a reduction in reproduction and, eventually, to lower population growth.

In the extreme case, interspecific competition can become so intense that, over time, access of one species to a resource is completely prevented, or a species becomes locally extinct, because of the other, more competitive species. Such a **competitive exclusion** occurs when populations of two species live in the same habitat and occupy the same ecological niche, with one species reproducing more rapidly than the other. It is hardly possible to determine whether and how often this occurs, or has occurred, in nature. However, competitive exclusion can be observed in some instances when species that have the same pattern of resource use and have evolved in geographic isolation from each other, encounter each other. Such situations are often the result of human activity, for example transport of plant and animals species from one continent to another where they then displace native species from their habitats (Sect. 3.3.3). In many cases, the greater competitive ability of the introduced species can be explained on the basis of their finding more suitable development conditions in their new environments, and because they often encounter fewer natural enemies and diseases than in their original environments.

3.1.3 Mutualism

The term **mutualism** refers to interactions between species that are advantageous to one or both and are not associated with disadvantages for either side. Such “positive” relationships between individuals or populations take many forms and may range from associations promoted by one side that are seldom specific, to associations that are close, or even essential, and very specific. The latter are often referred to as **symbiosis**, whereas the term mutualism is an overall term that includes the full continuum of positive interactions.

Mutualistic relationships are found between very different species. For example, they occur between flowering plants and specific animals that serve as pollinators and seed dispersers and are therefore rewarded by the plant with nectar, pollen, or fruit flesh. Mutualism between bacteria or fungi on the one hand and animals or plants on the other, are also widespread. These include, for example, microorganisms, the mycorrhizae (Box 3.2), which break down cellulose in the digestive tract of some phytophages, and the relationships between nitrogen-fixing bacteria and legumes (Sect. 3.7.4.1). In addition, numerous other more or less mutualistic interactions can occur between two different species of organisms; these are most often related to the acquisition of food, to reproduction, or to protection from enemies.

Box 3.2 Mycorrhiza

The connections between fungi and the roots of higher plants are referred to as mycorrhiza (from the gr. *mykes* = fungi and *rhiza* = root). Such interactions are mutualistic relationships undertaken by more than 80% of plant species and approximately 6,000 species of fungi. The fungi facilitate better supply of nutrients (especially phosphorus) and water to the plant than would be possible with the plant's roots alone. This can partly be explained by the increase in soil space, via the fungi hyphae, available to the plants, and because uptake of nutrients through the hyphae is more effective than the uptake of nutrients by plant roots. The fungi receive all of their organic compound needs from the plants, which provide between 4 and 26% of their photosynthetic products for this purpose (Miller et al. 2002). Two major forms of mycorrhizae can be identified:

The fungal mycelium (mass of branching hyphae) of the **ectomycorrhiza** completely enclose the roots and colonize the root cortex but do not penetrate the root cells. This form is typical of many tree species in the temperate latitudes. The fungi involved are primarily mushrooms of the subdivision Agaricomycotina, which, e.g., include boletus, chanterelle, and fly agaric.

The fungal hyphae of the **endomycorrhiza** penetrate the cells of the root cortex. Such associations are found in many herbaceous species, grasses, and shrubs, but also in tropical tree species. The most common type of endomycorrhiza is the so-called **vesicular-arbuscular mycorrhiza (VAM)**. The name is derived from the structures of the fungal hyphae in the root cells, which may be either tree-like and highly branched (arbuscules) or bubble-like (vesicles). These fungi are representatives of the zygote fungi (Zygomycetae).

Evidence of mycorrhiza, primarily VAM, is also observed for many crop plants (e.g. barley, potato, maize, wheat). The fungi are not only important in the promotion of nutrient uptake but often also reduce the susceptibility of the plant to phytopathogenic fungi and nematodes. Representatives of the Brassicaceae (e.g. cabbage, canola), Chenopodiaceae (e.g. spinach, beet), and many other plant families do not usually have relationships with mycorrhizae fungi.

Species that have mutualistic relationships with one another are usually subject to many effects and factors. It cannot, therefore, be assumed that the partners, irrespective of their relative abundances, always benefit from each other in the same manner. Most mutualistic relationships are not very specific. Thus, for example, in animal–plant interactions such as flower pollination or seed dispersal, strong dependencies rarely emerge between individual species. The closest relationships are formed when the species are fully dependent on each other for their existence. In many cases, such symbioses are based on exchange of chemical compounds between the partners.

In interspecific competition and in most mutualistic associations, the relationships between the species involved are asymmetric, which means that they are not of equal importance to all the species involved.

3.2 Communities

An ecological **community** (also called **biocoenosis**) is an assemblage of species whose populations are in a relationship with each other and thus effect each other unilaterally or reciprocally through feeding relationships, competition, mutualism, or combinations of these interactions. The term "biocoenosis" was first used by the German marine zoologist Karl Möbius in 1877. He introduced the term in his description of oyster banks in the North Sea in his book "*Die Auster und die Austernwirtschaft*" (Möbius 1877).

Most species that coexist in a habitat have a great diversity of relationships with each other. Plants are usually attacked by more or less large numbers of phytophagous species (Sect. 4.5.1), may have mutualistic relationships with pollinators and microorganisms (e.g. mycorrhizae), and may also have relationships with the natural enemies of the phytophages (Sect. 5.2.4.3). They are, in addition, often subject to competition with other plants (Sect. 4.4.1). Predators feed on a particular selection of prey organisms (Sect. 5.2.4.2); most are themselves eaten, and often also have competitors and mutualists. Taken together, these relationships are the biotic factors which, with the abiotic factors, determine the development of populations. So-called indirect effects may also emerge as a result of this. Such effects result when the impact of one species on another further affects the interactions between other species. Examples of this are found in Sect. 5.2.4.

As functionally defined units, communities usually have no definite spatial boundaries. They cannot be defined by a specific site through abiotic characteristics and also cannot be clearly separated from other communities. Habitats in a landscape which can obviously be distinguished on the basis of their vegetation (e.g. forests, meadows, fields), still have relationships among each other through species and their interactions. Animals, through their living requirements, may be closely tied to particular plant stands or to other habitats, but most animal species, in contrast with the plants, are mobile and can change their location. This applies not only to the insects and birds capable of flight, but also to many soil-inhabiting species, for example ground beetles. Even spiders are capable of dispersing and of colonizing different habitats with the help of their silk and the wind. Such circumstances clearly show that **agricultural communities** are not closed units limited to specific cultivated areas, even though these human-established sites are clearly separated from the surrounding vegetation.

Most of the species occurring in agroecosystems, which include a variety of wild plants, phytophages and predators, also exist, at least temporarily, in other habitats of the landscape, from which they colonize the crop stands.