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# Grassland Habitats

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Grasslands are plant communities that are based on grasses and herbs, and in which shrubs are rare and trees are absent. Perennial grasses represent the dominant species of grasslands, and make up the largest portion of their biomass, but not necessarily of their species richness. Grasses are often followed by legumes in abundance and herbs from many other plant families. Grassland is the natural vegetation in areas of low or strongly seasonal rainfall (250–1000 mm), but naturally occurring mammalian herbivory (e.g., by elephants) may also effectively suppress establishment of trees. Grasslands naturally encompass a wide range of habitat and vegetation types and span a large latitudinal gradient, from tropical grassland (savannas) to temperate grassland (the prairie in North America and the steppe in Eurasia) to the arctic tundra, totaling about 25% of the earth's land surface. Herbivory in temperate grasslands is dominated by insects, whereas large ungulate herbivores dominate in tropical grasslands. The temperate meadows and pastures are seminatural grasslands growing in essentially deforested areas with a forest climate, and their succession to forests is inhibited by mowing, burning, and human-controlled grazing.

## INSECT COMMUNITIES ON GRASSLANDS

Grasslands are habitats for many insects and may harbor an extraordinarily species-rich community. One temperate old-field grassland may be habitat for more than 1500 insect species, whereas cereal fields, which are monocultures of annual grasses, may contain 900 species. Compared to forests, the structural complexity of the grassland vegetation is obviously simpler, so that the insect diversity is reduced. Similarly, the litter layer of forests is larger and more heterogeneous, with a correspondingly richer decomposer community. Further features of grassland-specific insect communities include the dominance of species adapted to feed on grasses.

Plant and insect communities of grasslands greatly differ depending on climate, soil type, and management practices. Some marked differences are apparent between the plant–insect communities of temperate and tropical habitats. Plant species richness, which determines much of the insect diversity, may be only 10 to 15 species in intensively managed and highly fertilized grasslands, but 50 to 70 in extensively managed and low-input temperate grasslands. In contrast, tropical grasslands may contain over 200 plant species. Chalk-rich temperate grasslands with abundant earthworm populations tend to support the highest faunal biomass (often >100 g fresh mass

per square meter), whereas arid and semiarid steppe and desert soils, dominated by microfauna such as protozoans and nematodes, may have a biomass of only 1 g/m<sup>2</sup>. Tropical grasslands and tundra tend to be somewhere in-between. Termites and ants are dominant groups in tropical and subtropical grasslands, some surface-dwelling predatory arachnids such as scorpions and solifugids are restricted to warm, arid soils, and cold tolerance limits the range of many species in arctic and antarctic conditions. The ways in which insect communities of grasslands are influenced will be the subject of the remainder of this article.

Which insect species attack grasses, and what are the typical plants of grasslands? Ectophages, which feed externally on leaf tissue by chewing, scraping, or sucking, are distinct from endophytic feeders, which include leafminers, gallers, and borers. Grass foliage-chewing insects belong primarily to the Orthoptera, Lepidoptera, Coleoptera (mainly Chrysomelidae and Curculionidae), Hymenoptera (Tenthredinidae), and Phasmida. Of the specialized grass chewers in Great Britain <2% are Coleoptera, 6% Lepidoptera, 6% Hymenoptera, and 41% Orthoptera (the grasshoppers). Specialization on grasses appears to be particularly important in grasshoppers, and their abundance in grasslands is high. Sap-feeders on grasses are Homoptera (Auchenorrhyncha, Sternorrhyncha, Pseudococcidae), Heteroptera (mainly Miridae), and Thysanoptera. The endophagous, mostly stem-boring herbivores belong primarily to the Diptera (mainly Cecidomyiidae, Chloropidae, Agromyzidae), Hymenoptera (Cephalidae, Eurytomidae), Lepidoptera (mainly Pyralidae, Noctuidae), Coleoptera (mainly Cerambycidae, Mordellidae, Chrysomelidae), and mites (Acari).

The number of endophagous insect species associated with grass species can be predicted by (1) the annual-perennial dichotomy (annuals, in contrast to perennials, support almost no endophagous insects); (2) the mean shoot length; and (3) the abundance of the host plant. Annuals have impoverished communities and both shoot length and abundance are positively correlated with insect diversity. Plant height is usually a surrogate for the complexity of the plant architecture and, generally, a well-known predictor of plant-insect ratios. Furthermore, the more widely distributed and abundant a plant is, the more insects it should encounter in its evolutionary history. Annuals, which typically dominate in early-successional habitats, are characterized by a faster relative growth rate than perennials and, therefore, a short exposure time, so that they are a spatiotemporally unpredictable resource for insects.

Grasses (which are monocots) are hosts of many specialized endophagous insects and a multitude of ectophagous insects, a pattern that shows no principal difference from that of dicots. Host-plant preferences of oligophagous grass feeders often differ between grass species. Even more, variability among the many commercially available strains of the perennial ryegrass *Lolium perenne* to frit fly (the stem-boring chloropid fly *Oscinella frit*) attack is

greater than the variability between many pasture species. Attack of many species, such as frit fly, are negatively correlated with silica content, which presumably influences the females' choice of oviposition site and larval performance. Further, wild biotypes are often better resources than grasses grown from commercially available seeds and support richer insect communities, which may be of importance for sowings with a nature-conservation background.

## GRASSES AS FOOD RESOURCE

Grasses make up the largest portion of the grassland biomass; consequently, the insect communities of grasslands are determined more by the monocotyledonous Poaceae than by the dicotyledonous herb families. Grasses differ from the Dicotyledonae in that their architecture is simple, and the intercalary meristems, which substitute for growth from terminal buds, are protected by hard leaf sheaths. Most grasses lack the variety of secondary compounds that deter herbivory in most dicotyledons. For example, cyanogens and toxic terpenoids are rare, and alkaloids are present in <0.2% of grass species but in 20% of all vascular plants. Grass-feeding insects such as the oligophagous grasshoppers select their pooid-grass host plants in that they simply reject plant tissues enriched with secondary compounds (deterrents), while no phagostimulants characterizing grasses as a group have been found. Grasses are not toxic, but this does not mean that they are little protected from herbivory; just the contrary is true (see below).

Endophytic fungi have been considered acquired chemical defenses in grasses, and the main mechanism is the production of mycotoxins, notably alkaloids. The presence of these seed-borne *Neotyphodium* endophyte fungi may cause dramatic toxicosis to grazing livestock, best known from *L. perenne* and *Festuca arundinacea*. In addition to deterring vertebrate herbivory, these endophytes are also well known for increasing resistance to insect pests, microorganisms, and drought. Endophytes may also alter attack of natural enemies in that they enhance larval development time of the herbivore (the slow growth-high mortality hypothesis) or directly affect immature enemies, e.g., parasitoids feeding on the toxic tissues of their hosts.

Within and among grass species, a considerable chemical and morphological variability may be found. Nutrient availability of grass shoots is greatly determined by the shoots' age. Fresh internodes have high concentrations of the major nutrients (water, protein, minerals) and reduced concentrations of plant-resistance factors (raw fiber, silicate). High levels of plant nitrogen are generally associated with a high assimilation efficiency and density of phytophagous insects.

## HERBIVORE-PLANT INTERACTIONS

Long-term experiments with chemical control to eliminate insect herbivores indicated an average annual yield loss of

15%, and nematode control increased biomass by 12 to 28%. The biomass losses appeared to be mainly the result of frit fly and other stem-boring Diptera, which kill the central grass shoots, root-feeding wireworms (*Agriotes* spp., Elateridae), root-feeding scarabeid grubs, the range caterpillar *Hemileuca oliviae*, armyworms (*Spodoptera* spp.), grass worms (*Crambus* spp.), the Mormon cricket (*Anabrus simplex*), and leatherjackets (*Tipula* spp., in wetter soils). Planthoppers (Auchenorrhyncha), grass bugs (genera *Labops*, *Irbisia*, *Leptopterna*) and grasshoppers (Acrididae), and plant-feeding nematodes may also be important pests. In Sweden, the grass-feeding antler moth *Cerapteryx graminis* may reach densities of 100 to 1500 individuals per square meter; their corresponding effects on grass biomass consequently enhance herb populations. In the years following *C. graminis* outbreaks, shifts from herb dominance to renewed grass dominance show effects of competitive release and the return to competitive exclusion.

In temperate grasslands, the below-ground standing crop of insects is 2 to 10 times greater than the aboveground insect mass, although the effects of below-ground insects remain largely unseen, unless scarabeid beetle larvae or nematodes cause heavy decreases in shoot growth or even kill grass over large areas. In a latitudinal gradient across North American grasslands, root-to-shoot ratios vary from 2:1 to 13:1, with high values in cooler climates; tropical grasslands have even lower ratios (0.2:1 to 2.6:1). As can be expected from these data, the soil fauna is less abundant in tropical savannas and forests compared to temperate ecosystems. Earthworms usually dominate the soil biomass, but in the tropics, termites and ants are particularly important. These below-ground species can be a key in nutrient dynamics determining plant growth and aboveground plant-insect interactions.

Grasses are well adapted to herbivory and, in general, tolerate grazing better than herb species; therefore enhanced grazing pressure increases the fraction of grasses in pastures. The high resistance, tolerance, and compensatory ability of grasses are the result of (1) the generally high silicate content, lignification of vascular bundles, and additional sclerenchyma in mature leaves that make foliage hard to chew and digest; (2) the rapid induction of dormant buds that develop into lateral shoots following defoliation or destruction of apical meristems, which is based on the below-ground nutrient reserves; (3) the location of meristematic zones that are in many instances near the ground and not at the top of the plant, where they would be better accessible to grazers; and (4) the compensatory photosynthesis and growth stimulation by bovine saliva, which may also play a role. However, the concept of a herbivore-optimization curve or even grass-grazer mutualisms overestimates the compensatory abilities of grasses and grasslands.

Grazing causes much sprouting from dormant buds and converts tall canopies into shorter and denser grazing lawns. Heavily grazed pooid populations are smaller and have higher silicate concentrations, exhibiting ecotypic variation as a

result of different grazing histories. The mitigation of predation by the highly silicified grasses is presumably not confined to mammals, because the mandibles of many grass-chewing insects are adapted to biting and grinding and are analogous to the teeth of grazing mammals. Although the evolution of siliceous grass leaves appears to be driven by many stress factors (including drought and fungal attack), both mammal and insect herbivory may have been important factors.

## CONSERVATION OF SPECIES-RICH GRASSLANDS

Insect diversity in grassland ecosystems can be best predicted by floral diversity or related characteristics of vegetation structure, especially biomass and structural heterogeneity of the plant community. Species richness of butterflies, wild bees, phytophagous beetles, true bugs, etc., was found to be positively related to the species richness of plants. However, age of the habitat as well as fragment size is known to disproportionately enhance the number of species in higher trophic levels. The fraction of specialized predators and parasitoids increases greatly with area and age of grasslands, although the plant species richness may respond little.

Intermediate levels of vegetation disturbance, caused by ants, rodents, foxes, rabbits, sheep, and other mammals, significantly increase species richness of vegetation with consequent effects on the insect community. For example, gaps reduce the likelihood of competitive exclusion in a plant community when space is monopolized by a few dominant species. The openings are rapidly exploited by seedlings. Rotational management also may enhance grassland heterogeneity, creating a mosaic of old and young, tall and short, early and late successional patches.

Mineral or organic fertilization of meadows or rangeland increases biomass and may also enhance palatability of the nitrogen-rich foliage, resulting in higher insect densities. But the main result of continued grassland fertilization is a steady reduction in plant species richness with a corresponding loss of insect species.

Grasslands established by sowing are colonized in the beginning by relatively few insects. As these grasslands age, communities become more species rich in both plants and insects, and the biotic interactions, such as between predators and their prey or parasitoids and their hosts, increase. Ants and subterranean insects are absent on newly created fields because establishment of nests and populations needs time, and their highest densities occur in mature grasslands. Percentage of macroptery (i.e., those with full wings) in dimorphic insects such as grass-feeding planthoppers is high in early successional habitats, whereas brachypterous (short-winged) species dominate in persistent habitats.

The destruction and fragmentation of habitats has become one of the major threats to biodiversity. Not all insect species are equally affected by habitat fragmentation: species of higher trophic levels, rare species, species with specific habitat requirements, species with greatly fluctuating populations, and species

with poor dispersal abilities are expected to be more prone to extinction. For example, butterfly communities on calcareous grasslands show positive species–area relationships, and the most specialized and endangered butterflies profit most from large grassland fragments. For a few butterflies, morphological characters associated with flight ability have been shown to change with isolation of limestone habitat fragments. This indicates that habitat fragmentation in simple, human-dominated landscapes may also have evolutionary consequences for the life-history traits within populations. As a result of changes in community structure, interspecific interactions such as plant–pollinator interactions may be disrupted. Grasses are wind-pollinated, but most herbs, such as the many legume species that typically play a major role in nutrient-poor or extensively managed grasslands, depend on insect pollination. Populations of pollinating bees need nectar and pollen resources as well as suitable nesting sites. Both may be limiting in small grassland fragments, and so very small plant patches usually receive fewer pollinator visits. Plant ecologists have found clear evidence that pollination efficiency, gene flow by pollen dispersal, and seed set are reduced in small calcareous grasslands. Habitat fragmentation is known to also affect specialized populations of higher trophic levels, for example, in a plant–herbivore–parasitoid food chain. Communities of monophagous butterflies show a steeper increase with the area of grasslands than communities of plants. Theoretical models and empirical evidence show that specialized parasitoids (and predators) suffer even more, so that food chain length tends to be shortened and herbivores tend to become released from possible control of their natural enemies.

Habitat quality of species-rich grasslands such as the calcareous grasslands mainly depends on the opposing forces of management (see below) and succession. Speed of succession may be related to fragment size because late-successional shrubs and trees often invade from the edge. Abandoned grasslands will often increase in species richness of both plants and insects, but they will certainly decrease on late-successional grasslands (for example after 10–20 years of abandonment), when shrubs and trees become dominant. Many specialized butterflies mainly occur on regularly mown or grazed calcareous grasslands as they appear to rely on warm microclimates and host plants associated with only sparse vegetation (Fig. 1). The rare British butterfly *Hesperia comma* prefers small plants of the grass *Festuca ovina* surrounded by sunny bare ground and nectar resources as oviposition sites. Death of rabbits from the myxomatosis virus appeared to enhance population declines of this butterfly, because the reduced rabbit populations caused less grazing. Ground-nesting species such as solitary bees are also more abundant on regularly mown or grazed grasslands, because the sparse vegetation and open soil provide nesting sites and thereby greatly enhance populations. In contrast, aboveground-nesting solitary bees are enhanced by dense, high, and woody vegetation that offers the necessary plant

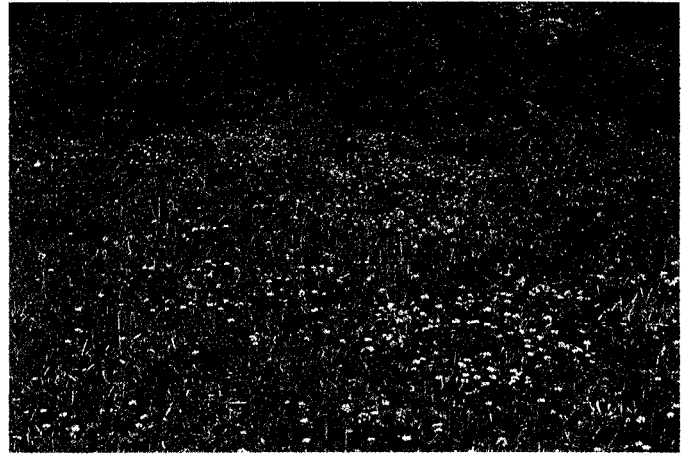


FIGURE 1 Calcareous grasslands belong to the most species-rich habitat types in Central Europe and depend on annual cutting or grazing (near Göttingen, Germany, photograph by Jochen Krauss).

material for nest construction. Altogether, species will profit from early-, mid-, or late-successional stages depending on their life-history traits, and highest overall diversity should be conserved with a mosaic of different successional stages.

## MANAGEMENT OF GRASSLAND

Cutting, grazing, and burning are typical methods of grassland management. As management alters plant growth and vegetation structure profoundly, the community of associated insects will also change. The insects' responses greatly differ between functional and taxonomic groups, and consequently it is often difficult to decide which management strategy is best in the conservation of overall diversity. Closely cut (or grazed) grasslands typically have an impoverished insect fauna. This is partly the result of pronounced vertical stratification of species using different parts of the sward canopy during the growing season (Fig. 2) and has been shown for planthoppers and leafhoppers (Auchenorrhyncha) as well as phytophagous beetles (Coleoptera). In particular, cutting affects flower visitors, pollen feeders, and grass-seed feeders among the gall midges (Cecidomyiidae) and other groups (Miridae, Chloropidae, Thripidae). In general, vegetation height and, therefore, the structural complexity of grasses decrease with intensity of grazing or mowing, and the complexity of plant architecture is a good predictor of insect species richness. The positive correlation between aboveground plant biomass and insect species richness is well established, whereas root feeders and other soil invertebrates are often more abundant at intermediate levels of grazing or mowing (of temperate grassland) than on unaffected patches. When grassland has been left unmanaged for a few years, the hemipterous and coleopterous fauna quickly recovers. With increasing number of mowings per year, which may be best observed in the sometimes extremely often mown urban turf-grass areas, species richness of both plants and insects (e.g., planthoppers

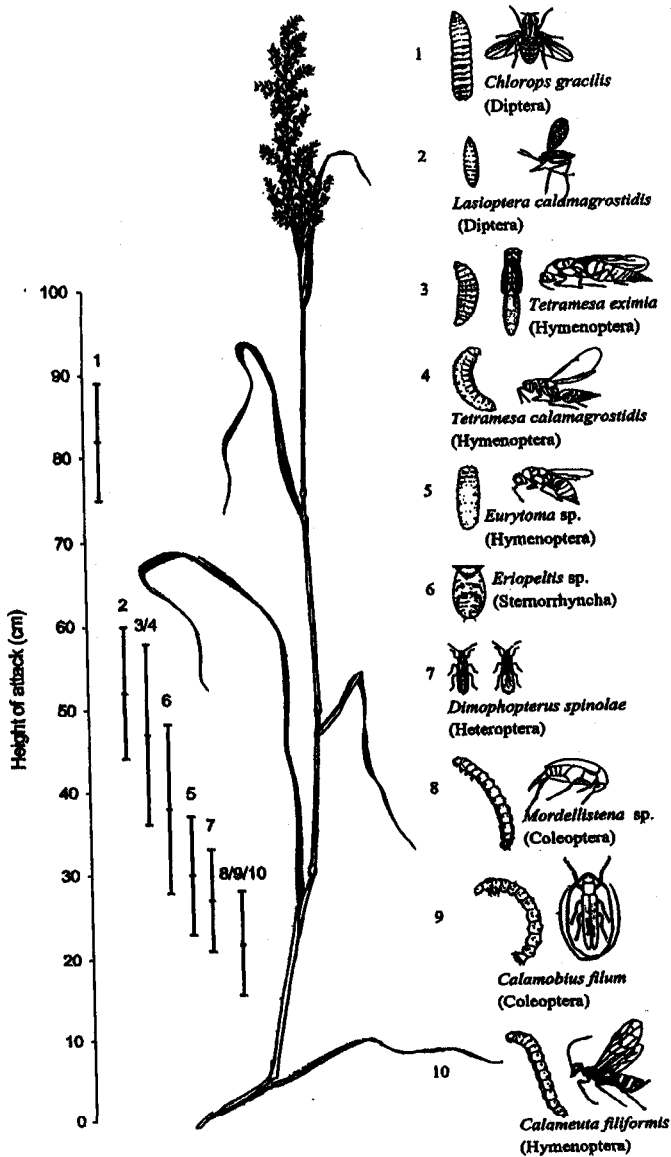


FIGURE 2 The stem-boring insects feeding on pure stands of the grass *Calamagrostis epigeios*. Height of attack (arithmetic means and 95% confidence limits) is given for each of the 10 species. (Reproduced, with permission, from M. Dubbert, T. Tscharrntke, and S. Vidal, 1998, *Ecol. Entomol.* 23, 271–280.)

and true bugs) becomes extremely poor. Moderate cutting or grazing may promote grasshopper populations, possibly through tillering rejuvenation or through changes in the proportions of nutritious grasses. Because the quality of grass shoots as a food resource declines with age, the induction of tillers and side shoots by cutting make nutritious food available later in the season (for example, for the populations of many grasshoppers and enhanced infestations of stem-boring Diptera). In conclusion, the effects of cutting or grazing on insect communities can be divided into short-term effects (simplification of plant architecture, regrowth of young and nutrient-rich plants) and long-term effects caused by changes in the structure of plant communities.

Grazing adds to the effects of cutting in that grazers feed selectively on the more palatable plants, compress or loosen the ground by trampling, and fertilize grassland patches by

urination and the deposition of dung. Accordingly, the changes in the plant community following grazing affect insect community structure in a complex way and make the habitat more heterogeneous than a homogeneous cutting regime. Further, grazing is a gradual form of vegetation removal, except at high stocking densities, and thereby differs from the large-scale disturbance of cutting (or burning). Cattle feed on taller vegetation than sheep and may open up tall vegetation. The cattle's trampling effects are usually high compared to those of sheep and enhance vegetation heterogeneity with disturbed and bare areas that improve habitat quality of many invertebrates. High cattle densities, however, lead to short and uniform swards and create problems due to vegetation damage, especially on wetter soils and on slopes. Most of the nutrients removed by grazing are returned through the deposition of urine and dung. Cow dung harbors a unique and speciose insect community. The breakdown of ungulate dung in temperate environments is enhanced by fly maggots, such as *Scatophaga* sp. and dung-burying beetles such as the scarabeid *Geotrupes* sp. Deposition of bovine dung poses no problems where bovines have an evolutionarily associated fauna that exploits the fecal resources. However, in Australia, native detritivores could not process cow dung because cows were brought over by the first English colonists only at the end of the 18th century. The loss of pasture under dung has imposed a huge economic problem to agriculture in Australia, and only the decision in 1963 to establish African dung beetles there led to a solution.

Burning grassland is less common in Europe than in America or Australia, where burning is a widespread natural phenomenon. Burning, like cutting and grazing, tends to produce a greater floristic uniformity, and it is considered to be very detrimental to grassland invertebrates. Controlled burning has been suggested as an alternative to chemical or biological control of pest arthropods. Direct effects are diverse, depend on the intensity of the burn, and include the escape of many flying insects as well as few changes in many soil insects. Indirect effects are the xeric conditions after burning and the mineral-rich regrowth after burning, which for many animals is a superior resource quality.

**See Also the Following Articles**

*Biodiversity • Plant–Insect Interactions • Soil Habitats*

**Further Reading**

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