

THE ECOLOGICAL SIGNIFICANCE OF TALLGRASS PRAIRIE ARTHROPODS

Matt R. Whiles¹ and Ralph E. Charlton²

¹*Department of Zoology, Southern Illinois University, Carbondale, Illinois 62901-6501; email: mwhiles@zoology.siu.edu*

²*Department of Entomology, Kansas State University, Manhattan, Kansas, 66506; email: charlton@ksu.edu*

Key Words ecosystem function, biodiversity, herbivory, detritivory, nutrient cycling

■ **Abstract** Tallgrass prairie (TGP) arthropods are diverse and abundant, yet they remain poorly documented and there is still much to be learned regarding their ecological roles. Fire and grazing interact in complex ways in TGP, resulting in a shifting mosaic of resource quantity and quality for primary consumers. Accordingly, the impacts of arthropod herbivores and detritivores are expected to vary spatially and temporally. Herbivores generally do not control primary production. Rather, groups such as grasshoppers have subtle effects on plant communities, and their most significant impacts are often on forbs, which represent the bulk of plant diversity in TGP. Belowground herbivores and detritivores influence root dynamics and rhizosphere nutrient cycling, and above- and belowground groups interact through plant responses and detrital pathways. Large-bodied taxa, such as cicadas, can also redistribute significant quantities of materials during adult emergences. Predatory arthropods are the least studied in terms of ecological significance, but there is evidence that top-down processes are important in TGP.

OVERVIEW AND PERSPECTIVES

The tallgrass prairie (TGP) is the most endangered ecosystem in North America. Of this once vast expanse of grassland, only 3% to 5% remains, much of which is highly fragmented (112). In the past two decades, there has been increasing interest in the structural organization of TGP along with factors that influence the dynamics of ecosystem processes such as energy flow and nutrient cycling. Most efforts have focused on how fire and ungulate grazing influence primary producer communities and associated ecosystem processes over the landscape mosaic (12, 67, 68).

Arthropods too can have profound influences on TGP ecosystem structure, processes, and function through both direct and indirect mechanisms (Figure 1). In most systems, the predominant metazoan herbivores and detritivores are arthropods; these can influence the amounts of living and dead organic materials in systems and related nutrient cycles (95, 120, 123). The TGP is no exception. Recently, increasing attention has been focused on this ubiquitous component of the TGP, and a growing body of evidence from a variety of ecological perspectives is accentuating the ecological significance of TGP arthropods.

TGP landscapes are composites of several habitat types. These include streams, forested riparian areas, and shrub islands, along with smaller, but still important, habitat features such as moist spring-fed swales and remnant buffalo wallows (105). Ecological processes in TGP are influenced to varying degrees by interactions between different habitat types, and we discuss examples where appropriate. However, most of our discussion centers on patterns and processes in the grass/forb matrix proper, as this habitat type makes up a great majority of the land cover in TGP. This review emphasizes TGP, but selected references to research in other grasslands and systems are used to provide perspective or highlight potentially relevant studies that are lacking in the context of TGPs.

Given the current focus on TGP conservation and restoration and the recent advances in our understanding of the importance of invertebrates to this system, our purpose here is to summarize current information on arthropods and their ecological roles in TGP. In doing so, we also identify potentially fruitful future research directions in this still nascent but rapidly expanding field.

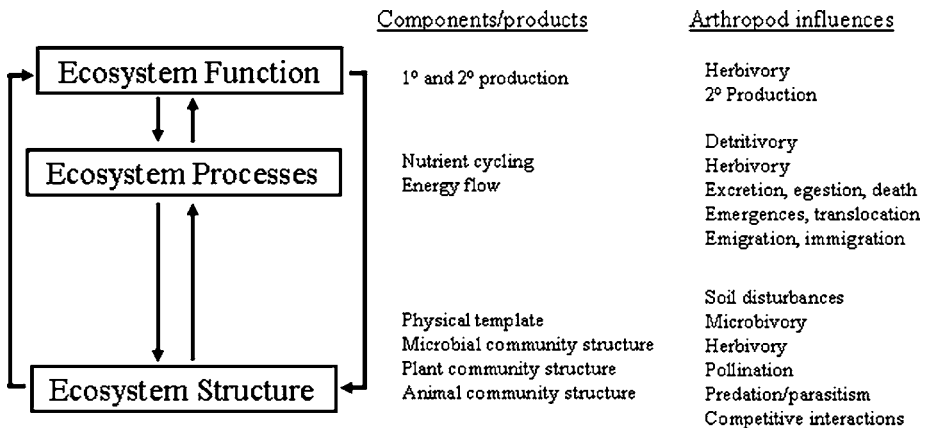


Figure 1 Ways in which grassland arthropods can influence ecosystem structure, processes, and function. Arrows indicate interactions between levels. Note that through various feedback mechanisms, all components and levels are linked; arthropod influences on one affect all others.

THE TALLGRASS PRAIRIE BIOME AND BIOTA

TGP, the most moisture-dependent of the three major grassland types in North America, historically was found in the easternmost third of the Great Plains. Nearly all of the original TGP has been converted to other land cover types; the only extensive remaining tract is the Flint Hills region of eastern Kansas, which contains approximately two thirds of all the remaining unplowed TGP. The TGP represents a subclimax biome dependent on fire or grazing for its perpetuation (69).

An acre of intact TGP hosts between 200 and 400 plant species, nearly 75% of which are forbs (105). Nonetheless, grasses make up the foundation of the prairie. Four warm-season C_4 grasses dominate: switchgrass (*Panicum virgatum*), Indiangrass (*Sorghastrum nutans*), little bluestem (*Andropogon scoparius*) and, most notably, big bluestem (*Andropogon gerardii*). Interspersed among the grasses is a rich variety of wildflowers or forbs. Roots of many grasses descend deep into the soil to access seasonally scarce moisture, with the roots of some species such as big bluestem extending down as much as 3 to 5 m. The extensive and dense root zone not only traps moisture, it also binds the soil and enriches it with organic matter.

Broadly speaking, there are three herb strata apparent in TGP. Nearest to the ground resides a mix of low-growing and recumbent forbs and grasses such as prairie violets (*Viola* spp.) and buffalo grass (*Buchloe dactyloides*). The intermediate layer harbors the highest plant diversity. Plants characteristic of this stratum include little bluestem (*A. scoparius*), coneflowers (e.g., *Echinacea* spp., *Ratibida* spp.), prairie clovers (*Dalea* spp.), beardstongues (*Penstemon* spp.), asters (*Aster* spp.), and milkweeds (*Asclepias* spp.). The uppermost layer is typically occupied by big bluestem, but Indiangrass and switchgrass also are important constituents, as are a few, more mesic forbs such as tall sunflower (*Helianthus giganteus*). This vertical stratification of the vegetation creates myriad microhabitats for arthropods.

Other important microhabitats for arthropods include the detritosphere—the mulch layer of decomposing plant material that accumulates on the ground. Even bare ground, the proportion of which can vary according to many abiotic and biotic factors, is vital to some arthropods such as certain ant, beetle, and hemipteran species, along with antlions. In addition, soil beneath and crevices within or under rocks represent important, moisture-retentive microhabitats that are utilized by an array of geophilous arthropods.

Arthropods are the most diverse group of organisms in TGP. Even so, surprisingly little work has been done to characterize the occurrence and distribution of the arthropod fauna, although this situation is beginning to improve. Some groups, notably butterflies, grasshoppers, and selected Homoptera, have been relatively well surveyed, but almost nothing is known concerning the biodiversity of most other taxa. In fact, it has been estimated that up to half of North American prairie insect species still await description (4). Reed (104) provides a comprehensive treatment of taxa reported from tall- and mixed-grass prairie, their trophic status, habitat affinities, and references thereto. Reed's (104) compendium emphasizes

prairie specialists, but all hexapod orders with prairie representatives are discussed. There are a variety of ways to categorize arthropods for ecosystem-level studies (e.g., guilds, functional groups). For our purposes, we loosely group them into general feeding groups and habitat associations.

ECOLOGICAL ROLES OF TALLGRASS PRAIRIE ARTHROPODS

Aboveground Herbivores

Phytophagous insects comprise a large proportion of the biodiversity of prairie communities. Many prairie plant species support communities of generalist and specialist herbivores, which in turn support generalist and specialist natural enemies (141). Aboveground herbivores can be categorized into several groups: the mandibulate folivores, including Orthoptera and Lepidoptera larvae and some coleopterans, hemipteroid sap-feeders, and insects that feed and remain hidden in plant tissues such as gall-makers.

The ubiquity and relative ease of study of aboveground arthropods in grasslands and other systems has created a bias toward them in the literature. This group can influence ecosystem structure, processes, and function in many ways, both directly and indirectly (Figure 2). The obvious direct impact of aboveground herbivores

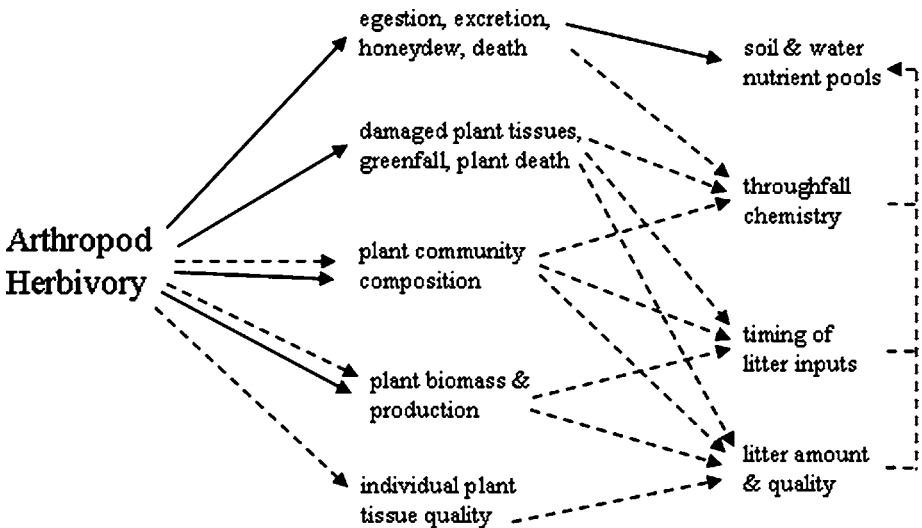


Figure 2 Direct and indirect pathways by which aboveground arthropod herbivores can influence grassland ecosystem components, processes, and function. Solid arrows represent direct impacts and dashed arrows represent indirect effects.

is removing and/or damaging plant tissues. Estimates from a variety of systems indicate that folivores can consume up to 50% to 150% of their body mass per day (16, 116). However, consumption estimates for TGP arthropod communities are few and variable. While some (50, 117) have suggested that insect herbivores in the TGP utilize the bulk of aboveground primary production, estimates from a Missouri TGP indicated that total consumption by the aboveground herbivore and detritivore community was <5% of annual aboveground production (113). The lack of estimates and disparities among the few that exist accentuate the need for more research on this topic. Although evidence to date suggests that arthropod herbivores do not limit primary production in TGP, established relationships between plant population dynamics, community structure, and ecosystem processes and functioning in grasslands (91, 132, 140) suggest that even subtle effects by herbivores may have ecosystem-level consequences.

Consumption of plant tissues reduces biomass, and removal of appreciable amounts of biomass reduces production. Nevertheless, there is evidence that light to moderate herbivory by both arthropods and ungulates in grasslands can elicit compensatory responses and stimulate plant production [e.g., herbivore or grazing optimization hypothesis (3, 81, 121)]. The specifics of these relationships need further investigation. Some studies suggest that benefits to plants are overestimated (9, 142), whereas others imply that these interactions reach the level of plant-grazer mutualisms (41, 96), a controversial view among ecologists. Plant responses to arthropod herbivory may be even more complex than previously thought, as recent evidence suggests that mycorrhizal symbionts may increase compensatory growth responses of plants grazed by grasshoppers (72).

Arthropod herbivores can influence ecosystem processes and function by altering plant population and community dynamics (8, 85, 86, 91, 109). The influence of aboveground herbivores can also extend to detrital and soil food webs. Through feeding, egestion, and excretion, insects and other arthropods alter the quality and timing of litter inputs, contribute nutrients via by-products such as frass and honeydew, change throughfall chemistry by damaging plant tissues, and alter energy budgets of damaged plants, which can affect root dynamics (6, 32, 80, 126). Herbivorous insects influence even landscape-level processes such as nutrient retention and export at the watershed scale in some systems (42, 139), although these effects are limited to outbreaks, and impacts of this magnitude have not been documented in TGP.

Few studies have shown substantial direct impacts on plant biomass and production in established TGP. Rather, investigations to date suggest that arthropod herbivores in established TGP remove only moderate amounts of annual net primary production (ANPP) (53, 71, 84). It has also been suggested that this group may have more important influences on early successional systems (53). The general lack of obvious direct impacts of herbivorous arthropods in studies to date in TGP may be related to the combined role of ungulate and arthropod grazers in the evolution of the system and dominance by grazing-tolerant grasses. Warm-season grasses, which form the matrix of the TGP, are generally considered a low-quality food

resource because of their relatively low nutritional value and abundant refractory components such as silica (33, 142). Although armed with structural defenses, grasses generally do not have the array of secondary compounds found in other plants (142). The tolerance of grasses to grazing is further enhanced by the proximity of the meristematic zones to the ground. In contrast, the forbs and woody vegetation of the TGP are generally more nutritious than grasses—but have more chemical defenses. Hence, the nongraminoid components of the TGP are generally more resistant to grazing, whereas the grasses are more resilient. The TGP is also more diverse than other North American grasslands, mostly due to abundant forbs and shrubs, and the impact of herbivory in systems with higher floristic diversity, as in TGP, can be less pronounced (21).

In addition to aspects of the plant community, the influence of large-scale, frequent disturbances such as fire and drought may obscure finer scale processes such as herbivory by arthropods. Hypotheses regarding relationships between disturbance and diversity suggest that the relative importance of biotic interactions is reduced in more disturbed systems because frequent and/or intense disturbances limit development of competitive hierarchies and predator-prey interactions (38, 131) and thus might also limit the relative importance of herbivory. As such, studies examining the importance of arthropod herbivory should account for disturbance frequency and intensity during and prior to studies. Focusing on early successional TGP systems (e.g., restorations) might also be fruitful in this regard. There is evidence from other systems that herbivore-induced changes in ecosystem structure are most pronounced during succession and could affect linked processes and function (22, 24, 129).

GRASSHOPPERS The Orthoptera are primarily folivores and a significant and species-rich group in TGP, as they are in all grasslands. Microhabitat requirements and feeding preferences vary considerably among orthopterans; some are generalists, feeding on a wide range of grasses and forbs, whereas others are monophagous or oligophagous, usually feeding on selected forbs, but grass specialists occur as well. Of the vast array of aboveground herbivorous arthropods in the TGP, acridid grasshoppers have received the most attention. Grasshoppers have significant impacts on plant populations, communities, and production in other grasslands, as well as in agricultural systems (8, 16). However, the significance of grasshoppers in TGP is not clear, and studies that have addressed the issue suggest they may remove only moderate (generally $\leq 5\%$) amounts of ANPP (71, 84). There is still much to be learned about the ecosystem-level role of grasshoppers, because they are patchily distributed and population sizes can vary greatly from year to year (43, 62, 63). Therefore, it may not be prudent to generalize from measurements of their importance at a given time and place.

On the basis of production estimates and ecological efficiencies, Meyer et al. (84) found that grasshoppers removed a relatively small fraction of ANPP in a Kansas TGP, $\sim 1\%$ to 5% of total ANPP, depending on burn history, compared with native ungulate grazers, *Bison bison*, which remove $\sim 20\%$ of total ANPP

(68). Consumption of forbs by forb-feeding acridids was most significant because they consumed higher proportions of available forb ANPP compared with consumption of grasses by grass-feeders. This pattern was most pronounced in more frequently burned areas where forb production was lowest (84). Hence, in terms of percent removal of ANPP, grasshoppers and ungulates, in this case bison, affect different components of the TGP; whereas bison selectively consume dominant C₄ grasses and thus promote forb production (67), the most significant impact of grasshoppers may be on forbs. These patterns suggest that complex interactions involving fire, ungulate grazing, and arthropod herbivory are in need of further study. Studies from other North American grasslands have also demonstrated plant-mediated interactions between grasshoppers and ungulate grazers (57, 101).

Comparing ungulate with grasshopper grazing is difficult because of the spatial patchiness and annual variability of grasshopper populations and the dependence of ungulate values on stocking densities, rotations, and prevailing land management. A recent estimate (84) that grasshoppers in TGP may remove up to 20% of the amount of ANPP that bison remove is notable, considering that grasshoppers are only one component of the larger community of aboveground insect herbivores in the TGP. Future studies of grasshopper consumption should also account for differential feeding patterns and rates associated with forage quality, which, like grasshopper populations, varies in time and space (149, 150).

ABOVEGROUND HERBIVORES AND NUTRIENT CYCLING RATES Like ungulates, herbivorous arthropods can influence ecosystem function and processes through feedbacks between plant communities and associated patterns of production, pools of inorganic nutrients, and mineralization rates. Through these pathways, acceleration or deceleration of nutrient cycling can occur, depending on feeding patterns, plant community responses, and limiting resources (8, 98). Conceptual stoichiometry-based models predict acceleration of cycling when abundant, moderate- to low-quality plants (e.g., moderate to high C:N) are consumed in greatest quantity; in the case of TGP, the C₄ grasses meet these criteria. In response, the plant community is predicted to shift toward increasing proportions of higher quality plants (e.g., many forbs in TGP), which results in higher quality litter inputs to detrital food webs, faster decomposition rates, and enhanced nutrient cycling (99, 109). In contrast, deceleration is predicted when herbivores favor plants with higher tissue quality, which increases the abundance of plants with lower tissue quality (e.g., higher C:N) and in turn decreases the quality of litter inputs (99, 109).

Along with potential influences on plant communities and associated relatively slow nutrient cycling processes, herbivores can influence cycling in the short term by converting plant tissues into frass, which is generally more nutritious and labile than leaf litter (115, 123). Dead bodies of arthropod herbivores also represent a relatively rich and labile nutrient input to soil systems (114, 115, 127). Contributions of frass and dead body tissues are considered components of the "fast cycle" in ecosystems because decomposition occurs relatively rapidly (8).

Most studies conducted in a diversity of ecosystems suggest that arthropod herbivores tend to accelerate nutrient cycling through a variety of mechanisms (8, 32, 77, 123). However, acceleration and deceleration models for arthropods remain relatively untested in the TGP. The influence of arthropod herbivores on N cycling rates in TGP might be expected to vary in time and space because of the dynamic nature of the system. The TGP is primarily N limited, and models suggest that herbivory should decelerate N cycling rates under these conditions. However, disturbance regimes (e.g., fire) and a highly variable climate can result in dynamic patterns of water and light limitation (12, 13, 68), which could alter the overall influence of arthropod herbivores on nutrient cycling (56, 82).

In a test of the nutrient acceleration hypothesis, Belovsky & Slade (8) found that plant abundance increased with grasshopper abundance in the Palouse prairie. This was attributed to enhanced N availability due to grasshoppers feeding primarily on lower quality plants that produced slowly decomposing litter, thus accelerating N cycling. In this case, ecosystem processes (N cycling), function (ANPP), and structure (plant community composition) were influenced by grasshoppers, and ANPP peaked at intermediate grasshopper densities (8). In contrast, long-term exclusion of insect and mammalian herbivores from an oak and tallgrass savannah in Minnesota resulted in increased legume and total plant biomass and increased N in aboveground plant tissues, litter, and roots (109). Exclusion also increased soil N availability, suggesting that herbivores decelerated N cycling by selectively feeding on and decreasing aboveground biomass of higher quality plants.

The differences in results of these two studies may be related to disparate limiting factors in each system, as deceleration of N cycling by herbivores should be increasingly evident in more N-limited systems. Both systems are N limited, but the Palouse prairie can also be water limited, particularly during dry summer months. Differences in the focal herbivores could also influence the outcome of these investigations. The focal grasshoppers in the Palouse prairie selectively feed on relatively low-quality grasses, whereas the diverse mix of herbivores (deer and mostly orthopteran and homopteran insects) excluded from the oak savannah feed on a variety of high- and low-quality plants. Thus, the taxonomic composition and/or selective feeding behavior of the herbivore assemblage may determine the outcome of these types of investigations. Likewise, within a system, groups that feed on different components of plant communities might result in null or neutral effects in terms of processes. For example, grasshopper assemblages in the Flint Hills TGP include forb-feeders that should decelerate cycling, grass-feeders that likely accelerate cycling, and generalists that should have no net effect (28, 84). Furthermore, the relative importance of these groups in a given area varies between years (43, 84).

Herbivory by arthropods may also alter litter quality through changes in individual plant tissue quality associated with responses to herbivory (7, 32, 48). Herbivore damage can induce chemical alterations in plant tissues including changes in nutrient concentrations and/or production of secondary compounds such as phenolics and tannins that increase C:N ratios (1, 66). Higher concentrations of phenolics

and tannins are associated with slower leaf decomposition rates (145), but these relationships are relatively unstudied in TGP. Studies with *Agropyron smithii* and *Andropogon scoparius* in short- and mixed-grass prairie suggest that the silica level in grasses is not an inducible defense (20, 33). Still, much remains to be learned about other potential chemical changes in grasses and the many potentially inducible chemical defenses in forbs.

Herbivores can also influence litter quality and associated detrital cycles through premature leaf fall. This "greenfall" can include tissues that are removed during feeding but not ingested, leaves that are prematurely abscised in response to damage, and leaves that are clipped off by herbivores. Greenfall represents relatively high-quality detrital inputs compared with senesced litter and, along with associated leaching of nutrients and other materials from damaged leaves, can enhance nutrient and energy fluxes from the canopy to litter layer (107, 115). Although these fluxes are relatively unstudied in TGP, Meyer et al. (84) provided one estimate showing that adult *Phoetaliotes nebrascensis* grasshoppers from a Kansas TGP severed and dropped 17% to 40% of the amount of grass they ingested, although this value was much lower (~3%) for nymphs.

BELOWGROUND RESPONSES TO ABOVEGROUND HERBIVORY Along with influencing the quantity, quality, and timing of litter inputs, aboveground herbivores can influence belowground communities through changes in plant tissue chemistry and root and rhizosphere dynamics. Although studies in a variety of systems suggest that insect foliage-feeders negatively affect root-feeders (15, 79, 80), many of these studies were performed in agricultural or otherwise simplified systems. There is some evidence that populations of belowground arthropod herbivores in established grasslands may be enhanced by aboveground herbivory, although studies to date have focused on simulated ungulate grazing (e.g., clipping and mowing) rather than on arthropods. Root biomass generally decreases with aboveground grazing in grasslands (121, 126), but root quality (e.g., C:N) and N availability in the rhizosphere can be enhanced, resulting in higher densities of root-feeding arthropods such as scarab larvae and cicada nymphs (124, 126).

More recent investigations in long-term experimental plots in a Kansas TGP showed variable but mostly negative responses by root-feeders such as beetles (mostly scarab, curculionid, and elaterid larvae) and cicadas (mostly *Tibicen aurifera* and *Cicadetta calliope*) to mowing (26). Responses of belowground herbivores to aboveground herbivory likely vary with taxonomic group, type of herbivory (e.g., leaf chewing, leaf mining, sap feeding), timing and duration of herbivory, disturbance regime (e.g., burning history), and other limiting factors (14, 26). Based on the few studies to date, the emerging pattern is negative responses of belowground arthropods to aboveground herbivory in agricultural or otherwise simplified systems and variable responses in established prairies. These relationships in the TGP may be complex and involve multiple trophic levels, as there is evidence that arthropod grazing can enhance mycorrhizal colonization of plant roots (72), which in turn alters plant nutrient status and growth patterns.

SAP-FEEDERS AND GALL-FORMERS Sap-sucking herbivores can affect plants by feeding on phloem or xylem. Xylem-feeders remove mostly water and amino acids and can cause water stress, reduced photosynthetic rates, and reduced production (64, 85, 86). Phloem-feeders remove appreciable amounts of sugars in addition to water and nitrogen and can act as additional carbohydrate sinks on plants (59). Moreover, xylem- and phloem-feeders can cause structural damage to plants during feeding and transmit diseases (85). Although difficult to quantify, estimates indicate that, on average, sap-feeders consume approximately 2.5 mg dry sap per milligram of dry insect mass per day (116).

Few studies have specifically examined the ecological significance of sap-feeding insects in TGP. However, Johnson & Knapp (64) found that high densities of *Ischnodemus falicus* (Hemiptera: Lygeidae) significantly reduced photosynthetic rates and production of prairie cordgrass in mesic TGP. This finding suggests that sap-feeders may exert some control over primary production, but *I. falicus*, like most other insect herbivores, is patchily distributed and population sizes show great annual variability (64). Hence, as with other arthropod herbivores, understanding the long-term and large-scale consequences of the feeding activities of sap-feeders is elusive. Further, there is a lack of basic information on this group of insects, as it is not known whether many sap-feeders, including *I. falicus*, are tapping phloem or xylem. Given the different effects associated with each type of feeding, this type of basic natural history information could enhance our knowledge of the potential impacts of this guild in the TGP.

Gall-forming insects are common on many TGP forbs, and their effects have been examined to some degree. In general, galls can act as carbohydrate and nutrient sinks and can also restrict transport of materials in stems (59, 83). In a Kansas TGP, *Antistrophus silphii* wasp galls reduced shoot growth, reduced leaf and flower production, and delayed flowering of *Silphium integrifolium* (46). Galls also completely stopped apical growth and flower formation in 65% of galled shoots. As a result, plants with more galls had lower total biomass and allocated less energy to flowering (46). Furthermore, galls influenced the timing of flowering, potentially disrupting synchrony with pollinators. In a subsequent study of the same system, galls reduced plant height, leaf area, and inflorescence production of rosinweed in the field, although impacts were modulated by water and nutrient availability (47). Results of both studies suggested that galls represent architectural constraints on meristem activity and that levels of competition among plants regulate responses. As with many other impacts of herbivory, effects should be most pronounced when limited resources such as N, water, and light are least available.

SEED AND FLOWER HERBIVORY Numerous insects feed directly on flowers, seeds, and other reproductive parts with potential consequences to individual plant fitness. Insects feeding on plant reproductive parts can greatly affect plant reproductive output, influencing the abundance and distribution of plants (45, 75). As with other forms of herbivory, there is controversy regarding the impacts of this group because

some studies provide evidence that plants produce an excess of reproductive parts to account for losses (136) and may exhibit compensatory responses (55). Plant responses and effects likely depend on the level of damage inflicted, life-history characteristics of the herbivores and plants, and timing of damage to seeds relative to dispersal.

Various seed- and flower-feeding insects affect the reproductive output of forbs in tallgrass and mixed-grass prairies. *Apion rostrum* weevils feeding on *Baptisia leucantha* seeds in mesic TGP can increase selective seed pod abortion by lowering the number of seeds in pods (100). Tephritids and pyralids feeding on inflorescences of Platte thistle (*Cirsium canescens*) in the Nebraska sandhills greatly limited seed production, seedling recruitment, plant density, and maternal fitness of this native forb (76). The measured impacts on Platte thistle in this system were high compared with other similar studies, possibly because it is a short-lived perennial with a transient seed bank (76). Plants that have intermediate life histories (e.g., biennials and short-lived perennials), that are patchily distributed, or that rely heavily on current seed production for regeneration may be most susceptible to this type of herbivory (76). Many forbs fall into this category. Hence, flower- and seed-feeding herbivores may influence ecosystem structure and function more so in the TGP than in other systems.

Timing of flowering may also influence the impacts of flower- and seed-feeders. The early flowers of *Baptisia australis*, a conspicuous legume in the TGP, are susceptible to damage from olethreutid moth (*Grapholitha tristegana*) and weevil (*Tychius sordidus*) larvae, which together can affect 80% to 100% of developing seed pods (45). Although late flowers are less susceptible to the moths and weevils, they are increasingly vulnerable to blister beetle (*Epicauta fabricii*) adults, which can destroy more than 80% of flowers, buds, and young fruits (44, 45). This dynamic, coupled with the timing issues associated with insect pollinators, suggests that temporal patterns of plant and insect interactions may be complex and should be accounted for in future investigations.

Pollinators

TGP pollinator communities include pollination specialists, which visit only selected families, genera, or even species, and, at the other end of the spectrum, a great variety of pollination generalists (103). Although not often a focus of ecosystem-level studies, arthropod pollinators can influence ecosystem structure and thus processes and function, because at least some members of plant communities depend on them for successful reproduction (29). Given the often intimate coupling between plants and their pollinators, changes in pollinator abundance, diversity, or temporal dynamics could result in changes in ecosystem structure.

While the dominant prairie grasses are wind pollinated, the forbs and shrubs that represent the bulk of plant diversity in the TGP are mostly insect pollinated. For example, four of five species of *Penstemon*, which are important components of forb diversity in TGP, failed to set seed when insect pollinators were experimentally

excluded (34). On the basis of flower and pollinator morphology, Hymenoptera were the most important pollinators of *Penstemon* spp. (34). A comparison of the ecological attributes of rare and common plant species in southern Ontario revealed that rare species were associated more with open habitats such as TGP and were more likely to be insect pollinated (25).

Phytophagous arthropods that are not pollinators can also indirectly influence pollination success of prairie forbs, because feeding damage and resultant changes in the energy budget of an angiosperm can influence aspects of flowering. Fay and colleagues (46, 47) found that cynipid wasp galls resulted in reduced flower production and altered flower timing of *S. integrifolium*. Along with the obvious implications of reduced flower production, a change in the timing of flowering could influence pollination success because many insect-plant pollination systems are temporally synchronized.

There is rising concern among ecologists over declines in pollinator abundance and diversity and the potential consequences for biodiversity and ecosystem health (2). Because TGP forbs are mostly insect pollinated, the importance of insect pollinators to the maintenance of TGP ecosystem structure is obvious. Furthermore, there is increasing evidence of important relationships between plant species diversity and ecosystem function in grasslands and other systems (31, 94, 140). Smith & Knapp (132) found that as diversity of subordinate species in TGP plots, most of which were insect-pollinated forbs, was experimentally reduced, overall productivity of these species declined. This finding implies that the loss of TGP plant diversity could have consequences for the resistance and resilience of the system to invasive species, climate change, and other threats.

Belowground Herbivores

Among herbivorous soil arthropods, notable macrofaunal elements include the xylem-feeding cicada nymphs and root-feeding scarab larvae. Both groups can attain high abundance and moderate richness on prairie sites. Total macroarthropod density and biomass in TGP soils have been estimated at 100 individuals per m² and 1.5 g per m², respectively (102, 128). There is also a great diversity and abundance of microarthropods, whose small size belies their ecological importance. Brand & Dunn (18) recorded 27 different taxa of springtails alone from leaf litter in native and restored prairie sites. The Acari, which include detritivores, fungivores, and predators, are the most abundant and one of the most diverse groups, with densities exceeding 120,000 individuals per m² and corresponding biomass of up to 36 mg/m² reported for shortgrass prairie soils (73). In an Oklahoma TGP, 15 orders and 46 families of soil arthropods were identified, and the biomass of belowground arthropods greatly exceeded that of their aboveground counterparts (108).

Although not as conspicuous as their aboveground counterparts, belowground herbivores are considered equally or more important in grasslands. Most primary production occurs below the soil surface in North American grasslands and, accordingly, the majority of herbivory occurs there as well (15, 134). There is also

growing evidence that root-feeders have more influence on plant populations and communities than do aboveground insects in established systems (15, 90). As with aboveground herbivory, low to moderate levels of root herbivory are often tolerated and in some cases may even stimulate production, but higher levels have negative impacts (15). In some cases, impacts of root-feeders on grasslands are dramatic, resulting in obvious aboveground effects and collapses of host plant populations (138, 143, 146). As with aboveground herbivores, there is also evidence that root-feeders can alter patterns of succession in systems such as old-fields, including increasing diversity and rates of succession (52). Community-level impacts of this magnitude are not the norm in established grasslands, but TGP restorations provide an opportune venue for the study of these effects.

Along with removal of root biomass or fluids and associated impacts on individual plants, root-feeding arthropods can also influence belowground nutrient and energy exchanges among plants by causing leakage and through excretion (92, 93). The ultimate importance of root-feeding arthropods to belowground nutrient and energy exchanges needs further investigation, but evidence from studies of nonarthropod root-feeders suggests they may be important. Experimental studies have shown that root-feeding nematodes in grasslands can facilitate nutrient transfers in soils, stimulate root growth of host and neighboring plants, and stimulate rhizosphere microbial communities (5, 40). Belowground nutrient and energy exchanges among plants due to root herbivory may also influence competitive interactions among plants (92, 93) and thus, ultimately, community structure.

Various studies provide evidence that belowground herbivory can influence plant production (15, 90). However, these relationships are still poorly understood in TGP, and relationships between belowground herbivores and plant productivity may be complex in this system. Multiple years of organophosphate insecticide treatment to experimental TGP plots in eastern Kansas resulted in no clear effects on above- or belowground plant production (53, 124, 128). These negative results have been interpreted as reflecting antagonistic effects on different components of the plant community that result in little net change in total production and may also be related to differential effects of the insecticide used on various invertebrate groups. These results are also in sharp contrast to results of similar manipulations in shortgrass prairie (61, 135), suggesting there may be important differences in belowground herbivore-plant relationships in different grassland types. The influence of arthropods on these relationships in grasslands is also difficult to discern from these manipulations because the bulk of observed effects is attributed to herbivorous nematodes.

Scarab beetle larvae can attain high densities, heavily graze roots, and have visible impacts on patterns of aboveground growth in grasslands (143, 146). Even so, there is relatively little quantitative information regarding their influences on ecosystem structure and function in the TGP. Studies from other North American grasslands suggest that scarab larvae can have significant influences on grass production (35, 143) and, although they are often patchily distributed and their populations vary greatly between years, they can have lasting effects (35).

The influence of root-feeding scarabs may also depend on complex interactions with other herbivores and disturbances. For example, grass mortality from scarab larvae increased where ungulate grazing occurred in a shortgrass prairie, presumably because of changes in root resource quality and/or the more even spatial distribution of roots caused by ungulate grazing (35).

The various roles of arthropods in ecosystems are generally considered regulatory and arthropods themselves are not considered significant resource pools at the ecosystem level. However, cicadas, a conspicuous component of belowground arthropod communities in TGP soils, may be an exception to this generalization. Periodical cicadas are well known because of their spectacular, synchronized emergences every 13 or 17 years. Although generally associated with forests in the eastern United States, periodical cicadas can attain exceptionally high densities in forest edges (110) and can be abundant in the linear, fragmented riparian forests in TGP. During an emergence of *Magicicada cassini* in Kansas, an estimated 4.5 metric tons of cicada biomass emerged from a 59-ha riparian forest, representing ~0.5 metric tons of N (147). Although originating in gallery forest soils, adult cicadas were abundant in all adjacent habitats following emergence. The N flux associated with this emergence represented ~40% of annual inputs of "new" N in this area via average bulk precipitation and ~20% of N associated with average litterfall in gallery forest habitats (147). Periodical cicada emergences may become more widespread in the TGP as forest habitats expand in response to fire suppression (70).

Annual grassland cicadas have not received the attention in the literature that periodical species have, but recent evidence suggests that grassland cicadas are more significant to material and energy cycling than are periodical cicadas because of their consistently high belowground densities and large-scale annual emergence. Some prairie cicadas, including *Tibicen aurifera* and *Cicadetta calliope*, live in open, treeless habitats, feed on roots of native warm-season grasses, and oviposit in grass stems (27). Annual emergence production of these two species from Kansas TGP averaged 3 to 4 g per m² per year, representing an annual N flux of ~4 kg per ha per year, which greatly exceeded values for annual species in adjacent gallery forest habitats (27). Even though the annual redistribution of energy and nutrients associated with annual and periodical cicada emergences in the TGP is impressive, information on long-term, spatiotemporal emergence patterns and the ultimate fate of adult cicada biomass is still lacking.

ABOVEGROUND RESPONSES TO BELOWGROUND HERBIVORY In addition to their varied effects on the belowground environment, belowground herbivores can also influence aboveground productivity, communities, and processes (6, 23). Many studies indicate that root-feeders positively influence aboveground herbivores by eliciting plant stress responses that result in changes in tissue chemistry and increases in food quality, and aboveground herbivores can negatively affect root-feeders by reducing root production (15, 80, 142). However, most support for this general pattern is from studies of early successional or otherwise simplified systems (15). The handful of studies from mature grassland systems appear to contradict

this generalization (35, 90). Furthermore, there is evidence that these relationships may be complex in established grasslands because of interactions with ungulate grazing and climate (35). The influence of root-feeders on aboveground herbivores is virtually unknown for TGP, but evidence from other grasslands suggests that this is a fruitful area of research and that studies need to account for potential interactions with disturbances such as fire and drought to fully assess relationships. Moreover, there is growing evidence that mycorrhizal symbionts may mediate relationships between plants and arthropod herbivores in TGP (72) and may thus influence interactions between above- and belowground herbivores.

Detritivores and Scavengers

Despite the persistent bias toward the more obvious "green world" of most ecosystems, detrital pathways dominate energy flow and nutrient cycling in most systems, and a diversity of detritivorous invertebrates play key roles in the decomposition process. The fundamental roles of arthropods and other invertebrates in detrital pathways entail reducing particle size through comminution, which in turn influences leaching, microbial dynamics, and mineralization, and feeding directly on microbes (87, 120, 123). These relationships can be complex, as the ultimate influence of arthropods can range from net mineralization to net immobilization of nutrients, depending on the substrate nutrient concentrations and interactions with microbes (123). Dead arthropods themselves, particularly their exoskeletons, can also contribute to detrital resources and represent significant pools of elements such as calcium (127).

Numerous studies from a variety of systems link arthropods and other invertebrates to the decomposition of plant detritus (123, 134, 144), but these processes and relationships are insufficiently studied in TGP. One of the only investigations of the role of invertebrates in TGP litter decomposition (124) found no differences in decomposition rates of insecticide-treated versus untreated litterbags. Seastedt et al. (124) speculated that usage of grass detritus in the TGP was limited compared with other systems because it was of low quality (e.g., low N and high silica concentrations) and that moisture in soil surface habitats was often limiting to biological activity. The use of insecticides in these types of studies has been questioned, as it may alter microbial dynamics and differentially affect invertebrate groups (60, 120). Studies that control or account for pesticide effects and nutrient and water limitations are needed to assess the role of arthropods and other invertebrates in TGP detrital pathways. Similar investigations in shortgrass prairie imply that their significance to this vital ecosystem process is high (144).

Understanding the role of arthropods and other invertebrates in litter dynamics in the TGP requires accounting for the array of factors that influence litter quality, accumulation, and persistence and the complex interactions among them. Two major forces that shape the TGP, fire and ungulate grazing, have opposing influences on litter quality. Fire tends to reduce plant tissue quality (12, 13) and shifts community structure toward lower quality (e.g., higher C:N) C_4 grasses (36, 54),

both of which translate into lower quality detritus. In contrast, ungulate grazing increases individual plant tissue quality and favors the more nutritious forbs (67) and thus should result in higher quality litter. Moreover, fire and grazing interact at the landscape scale through a series of positive and negative feedbacks resulting in a shifting mosaic of vegetation (19, 37, 51). As such, aboveground plant litter in the TGP is a dynamic and less predictable resource compared with many other systems. The scant available evidence suggests that detritivorous arthropods may be less important in TGP than in some other systems, but their role has yet to be adequately assessed and should be examined in the context of the complex spatiotemporal patterns of litter in this system.

Given that most primary production occurs belowground in TGP, decomposition of belowground plant detritus is likely an important process. Further, grass root detritus is of higher quality than detritus derived from foliage, and decomposition and mineralization rates of roots are more rapid (122, 124, 125). Seastedt et al. (124) examined root decomposition dynamics in a Kansas TGP and found that decomposition was ~25% faster in coarse mesh bags, which allowed macroinvertebrate access, compared with fine mesh bags, which permitted entry of only microarthropods and nematodes. This resulted in ~50% more N mineralized from the coarse mesh bags compared with the fine mesh bags (124). Although macroarthropods are an important component of this system, quantifying their contribution is difficult because nonarthropods such as earthworms were also abundant in these studies. Nonetheless, results of these investigations demonstrate that invertebrate detritivores in TGP soils can enhance decomposition, nutrient mineralization, and nutrient availability to plants, and these processes may compensate for any negative impacts of belowground herbivores (106, 124).

Translocation of nutrients by scavengers and detritivores is another potential ecological role of grassland arthropods. Ants have not received the attention in the North American prairie that they have in tropical grasslands, but evidence from some grasslands in North America suggests that they may influence the distribution of nutrients. By moving food materials, scavenging ants at arid grassland sites in the western United States redistribute nutrients laterally and thus influence the patchiness of resources (11). A similar study in shortgrass prairie (111) revealed that soil C, N, and P concentrations increased near ant nests.

Predators

Predatory arthropods are a conspicuous component of the TGP, but their role in the system is poorly studied. Predatory arthropods can exert various controls on primary consumer populations through lethal effects and influence individual behavior and fitness through nonlethal effects. Through their impacts on primary consumers, arthropod predators can also influence basal resources via trophic cascades (74, 78). For example, Moran and colleagues (88, 89) demonstrated that mantids (*Tenodera sinensis*) in an old-field system in Delaware could enhance plant biomass through reductions in herbivory. In addition to effects of individual

predators on specific prey populations and food web linkages, predator diversity may also be important. Increasing arthropod predator diversity facilitates intraguild interactions among predators, reduces impacts on herbivores, and dampens top-down trophic cascades (49).

Predators may influence diversity of other arthropod groups in the TGP. Relationships between plant diversity and herbivorous insects in grasslands, as with other ecosystems, suggest that there are strong interactions between the two and that plant diversity generally enhances herbivorous insect diversity (39, 65, 130). However, herbivorous arthropod diversity was correlated more strongly with arthropod predator and parasite diversity than with plant diversity in experimental tall-grass plots in Minnesota (130), suggesting that top-down forces can be as important as plant communities in maintaining arthropod diversity in grasslands. These results, in light of increasingly evident linkages between arthropod biodiversity and ecosystem stability and function (30, 91), underscore the importance of documenting the role of predators in promoting and maintaining biological diversity in the TGP. Arthropod predators are vulnerable in the TGP parcels that remain because they are sensitive to landscape-level features such as perimeter-to-area ratios (137), which increase with continued fragmentation.

The potential importance of predatory arthropods is not limited to aboveground habitats. In desert and shortgrass prairie soils, predatory arthropods indirectly influence decomposition and nutrient cycling by feeding on nematodes that control microbial populations (58, 97). Belowground processes are particularly important in grasslands because the bulk of production occurs below the soil surface. Thus, belowground predators, which are abundant and diverse in TGP soils (26, 118, 119), may be the most important, but least studied in terms of their ecological roles, arthropod predators in the system.

CONCLUSIONS AND FUTURE DIRECTIONS

The paucity of information on prairie arthropod biodiversity points to the need for detailed faunal surveys encompassing all groups, particularly for some of the important but heretofore neglected ones such as spiders, ants and selected other Hymenoptera, moths, many Diptera, and the belowground and litter-dwelling fauna. Continued taxon-specific biotic surveys of individual prairie plots, both large and small, will help alleviate this knowledge shortfall. However, what really is needed is a coordinated and comprehensive initiative that culminates in the creation of an extensive, accessible database of prairie arthropod fauna and ecological correlates. Good templates for such an endeavor are the All Taxa Biodiversity Inventory (ATBI) currently conducted in the Great Smoky Mountains National Park (a project of Discover Life in America) or the Arthropods of Canadian Grasslands project (an initiative of the Biological Survey of Canada).

More effort also needs to be directed toward elucidating the basic biology of many taxa. Life cycles, feeding habits, diet breadth, and habitat affinities are but

a few examples of basic information that is lacking for nearly all of the prairie arthropod biota. For example, stable isotope analyses could be used in conjunction with behavioral observations or gut content analysis to discern cryptic trophic status of individual species (27, 141), investigate the contribution of plant- or animal-based resources to the diet of omnivores, or elucidate prairie food webs as has successfully been done in other systems (17).

Although few would argue *prima facie* that arthropods are not an important component of the TGP, there is still an obvious lack of specific, quantitative information on the roles of arthropods in the TGP. Much of the information that we provide is gleaned from individual investigations or extrapolated from studies in other grasslands or systems. As a result, there exist tremendous opportunities for quantifying the ecological roles of TGP arthropods, particularly in terms of ecosystem-level processes and functions such as decomposition, nutrient cycling, and primary production. While numerous studies indicate that arthropods influence various components of the system (e.g., individual plant fitness or population dynamics), very few linked these findings with ecosystem processes and function.

Secondary production is one of the most relevant metrics for quantifying the role of consumers in ecosystem processes and function; yet production estimates for terrestrial arthropods in the TGP as well as for many other systems remain scarce. Production estimates for consumers can be tedious and logistically difficult to produce, but benefits can offset costs because these estimates allow for linking consumers directly to ecosystem processes. Benke (10) reviewed production methods for freshwater insects, and these same techniques are applicable to many terrestrial groups if accurate estimates of densities, mass, and life cycles are available (84). Production estimates coupled with estimates of ecological efficiencies can be used to estimate consumption and egestion, as has been done with wetland caddisflies (148), stream insects (133), and grasshoppers (84) in TGP.

There is evidence from other regions that herbivores may be most influential in early successional systems. Given the current focus on restoration throughout the historic range of the TGP, there is great opportunity to examine the potential influence of arthropods in this context. There is also need for further studies on the influence of arthropods on nutrient cycling rates (e.g., acceleration versus deceleration models) because studies from other grasslands show variable results and because this information is completely lacking for the TGP. Finally, there is a clear need for a better understanding of interactions between above- and belowground herbivores. Studies of herbivorous groups will be most informative if potential interactions with fire and ungulate grazing are taken into account.

Ecological roles of TGP arthropod groups may, in some cases, prove elusive and variable because of the dynamic nature of the TGP. Studies to date suggest that arthropods, including herbivores and pollinators, have more influence on the forb component of the TGP. Studies that account for spatiotemporal variability in resource quantity and quality (e.g., patterns of plant community structure,

primary production, and detritus dynamics associated with fire and ungulate grazing) will be most useful for assessing the varied roles of primary consumers in TGP processes and function. In effect, arthropods operate on the backdrop of fire, ungulate grazing, and climate, which interact to form the dynamic TGP ecosystem template.

ACKNOWLEDGMENTS

We would like to thank Drs. M.A. Callahan, L. Hanks, A.J. Joern, C.C. Reed, J. Tooker, and S.G. Baer for constructive comments that greatly improved this manuscript. We are also grateful to D.A. Walther and S. Peterson for logistical support.

The *Annual Review of Entomology* is online at <http://ento.annualreviews.org>

LITERATURE CITED

1. Agrawal AA, Tuzun S, Bent E. 1999. *Induced Plant Defense Against Pathogens and Herbivores: Biochemistry, Ecology and Agriculture*. Saint Paul, MN: Am. Phytopathol. Soc.
2. Allen-Wardell G, Bernhardt P, Bitner R, Burquez A, Buchmann S, et al. 1998. The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conserv. Biol.* 12:8–17
3. Alward RD, Joern A. 1993. Plasticity and overcompensation in grass responses to herbivory. *Oecologia* 95:358–64
4. Arenz CL, Joern A. 1996. Prairie legacies—invertebrates. See Ref. 112, pp. 91–110
5. Bardgett RD, Cook R, Yeates GW, Denton CS. 1999. The influence of nematodes on below-ground processes in grassland ecosystems. *Plant Soil* 212:23–33
6. Bardgett RD, Wardle DA. 2003. Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* 84:2258–68
7. Bardgett RD, Wardle DA, Yeates GW. 1998. Linking above-ground and below-ground interactions: how plant responses to foliar herbivory influence soil organisms. *Soil Biol. Biochem.* 30:1867–78
8. Belovsky GE, Slade JB. 2000. Insect herbivory accelerates nutrient cycling and increases plant production. *Proc. Natl. Acad. Sci. USA* 97:14412–17
9. Belsky AJ, Carson WP, Jensen CL, Fox GA. 1993. Overcompensation by plants: herbivore optimization or red herring? *Evol. Ecol.* 7:109–21
10. Benke AC. 1993. Concepts and patterns of invertebrate production in running waters. *Verh. Int. Ver. Limnol.* 25:15–38
11. Bestelmeyer BT, Wiens JA. 2003. Scavenging ant foraging behavior and variation in the scale of nutrient redistribution among semi-arid grasslands. *J. Arid Environ.* 53:373–86
12. Blair JM. 1997. Fire, availability, and plant response in grasslands: a test of the transient maxima hypothesis. *Ecology* 78:2359–68
13. Blair JM, Seastedt TR, Rice CW, Ramundo RA. 1998. Terrestrial nutrient cycling in tallgrass prairie. See Ref. 69, pp. 222–43
14. Blair JM, Todd TC, Callahan MA. 2000. Response of grassland soil invertebrates to natural and anthropogenic disturbances. In *Invertebrates as Webmasters in Ecosystems*, ed. DC Coleman, PF Hendrix, pp. 43–71. New York: CAB Int.

15. Blossley B, Hunt-Joshi TR. 2003. Below-ground herbivory by insects: influence on plants and aboveground herbivores. *Annu. Rev. Entomol.* 48:521–47
16. Blumer P, Diemer M. 1996. The occurrence and consequences of grasshopper herbivory in an alpine grassland, Swiss central Alps. *Arctic. Alp. Res.* 28:435–40
17. Blüthgen N, Gebauer G, Fiedler K. 2003. Disentangling a rainforest food web using stable isotopes: dietary diversity in a species-rich ant community. *Oecologia* 137:426–35
18. Brand RH, Dunn CP. 1998. Diversity and abundance of springtails (Insecta: Collembola) in native and restored tallgrass prairie. *Prairie Nat.* 33:65–91
19. Briggs JM, Nellis MD, Turner CL, Henebry GM, Su H. 1998. A landscape perspective of patterns and processes in tallgrass prairie. See Ref. 69, pp. 48–66
20. Brizuela MA, Detling JK, Cid MS. 1986. Silicon concentrations of grasses growing in sites with different grazing histories. *Ecology* 67:1098–101
21. Brown BJ, Ewel JJ. 1987. Herbivory in complex and simple tropical successional ecosystems. *Ecology* 68:108–16
22. Brown VK. 1985. Insect herbivores and plant succession. *Oikos* 44:17–22
23. Brown VK, Gange AC. 1990. Insect herbivory below ground. *Adv. Ecol. Res.* 20:1–58
24. Brown VK, Gange AC. 1992. Secondary plant succession: How is it modified by insect herbivory? *Vegetatio* 101:3–13
25. Cadotte MW, Lovett-Doust J. 2002. Ecological and taxonomic differences between rare and common plants of southwestern Ontario. *Ecoscience* 9:397–406
26. Callaham MA, Blair JM, Todd TC, Kitchen DJ, Whiles MR. 2003. Macroinvertebrates in North American tallgrass prairie soils: effects of fire, mowing, and fertilization on density and biomass. *Soil Biol. Biochem.* 35:1079–93
27. Callaham MA, Whiles MR, Meyer CK, Brock BL, Charlton RE. 2000. Feeding ecology and emergence production of annual cicadas (Homoptera: Cicadidae) in tallgrass prairie. *Oecologia* 123:535–42
28. Campbell JB, Arnett WH, Lambley JD, Jantz OK, Knutson H. 1974. Grasshoppers (Acrididae) of the Flint Hills Native Tallgrass Prairie in Kansas. *Rep. Res. Pap. No. 19*, Agric. Exp. Stn., Kans. State Univ., Manhattan
29. Cane JH, Tepedino VJ. 2001. Causes and extent of declines among native North American invertebrate pollinators: detection, evidence, and consequences. *Conserv. Ecol.* 5(1):1. <http://www.consecol.org/vol5/iss1/art1>
30. Cardinale BJ, Palmer MA, Collins SL. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature* 415:426–29
31. Chapin FS, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, et al. 2000. Consequences of changing biodiversity. *Nature* 405:234–42
32. Chapman SK, Hart SC, Cobb NS, Whitham TG, Koch GW. 2003. Insect herbivory increases litter quality and decomposition: an extension of the acceleration hypothesis. *Ecology* 84:2867–76
33. Cid MS, Detling JK, Brizuela MA, Whicker AD. 1989. Patterns in grass siliification: response to grazing history and defoliation. *Oecologia* 80:268–71
34. Clinebell RR, Bernhardt P. 1998. The pollination ecology of five species of pentstemon (Scrophulariaceae) in the tallgrass prairie. *Ann. Mo. Bot. Gard.* 85:126–36
35. Coffin DP, Laycock WA, Lauenroth WK. 1998. Disturbance intensity and above- and belowground herbivory effects on long-term (14 y) recovery of a semiarid grassland. *Plant Ecol.* 139:221–33
36. Collins SL, Glenn SM, Gibson DJ. 1995. Experimental-analysis of intermediate disturbance and initial floristic composition: decoupling cause and effect. *Ecology* 76:486–92
37. Collins SL, Steinauer EM. 1998. Disturbance, diversity, and species interactions

- in tallgrass prairie. See Ref. 69, pp. 140–58
38. Connell JH. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–10
 39. Dennis P, Young MR, Gordon IJ. 1998. Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. *Ecol. Entomol.* 23:253–64
 40. Denton CS, Bardgett RD, Cook R, Hobbs PJ. 1999. Low amounts of root herbivory positively influence the rhizosphere microbial community in a temperate grassland soil. *Soil Biol. Biochem.* 31:155–65
 41. Dyer MI, Bokhari UG. 1976. Plant-animal interactions: studies of the effects of grasshopper grazing on blue grama grass. *Ecology* 57:762–72
 42. Eshlemen KN, Morgan RPI, Webb JR, Deviney FA, Galloway JN. 1998. Temporal patterns of nitrogen leakage from mid-Appalachian forested watersheds: role of insect defoliation. *Water Resour. Res.* 34: 2005–116
 43. Evans EW. 1988. Grasshopper (Insecta: Orthoptera: Acrididae) assemblages of tallgrass prairie: influences of fire frequency, topography, and vegetation. *Can. J. Zool.* 66:1495–501
 44. Evans EW. 1990. Dynamics of an aggregation of blister beetles (Coleoptera, Meloidae) attacking a prairie legume. *J. Kans. Entomol. Soc.* 63:616–25
 45. Evans EW, Smith CC, Gendron RP. 1989. Timing of reproduction in a prairie legume: seasonal impacts of insects consuming flowers and seeds. *Oecologia* 78: 220–30
 46. Fay PA, Hartnett DC. 1991. Constraints on growth and allocation patterns of *Silphium integrifolium* (Asteraceae) caused by a cynipid gall wasp. *Oecologia* 88: 243–50
 47. Fay PA, Hartnett DC, Knapp AK. 1996. Plant tolerance of gall-insect attack and gall-insect performance. *Ecology* 77: 521–34
 48. Findlay S, Carreiro M, Kruschik V, Jones CG. 1996. Effects of damage to living plants on leaf litter quality. *Ecol. Appl.* 6:269–75
 49. Finke DL, Denno RF. 2004. Predator diversity dampens trophic cascades. *Nature* 429:407–10
 - 49a. French NR, ed. 1979. *Perspectives in Grassland Ecology: Results and Applications of the US/IBP Grassland Biome Study*. New York: Springer-Verlag
 50. French NR, Steinhorst RK, Swift DM. 1979. Grassland biomass trophic pyramids. See Ref. 49a, pp. 59–87
 51. Fuhlendorf SD, Engle DM. 2004. Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. *J. Appl. Ecol.* 41:604–14
 52. Gange AC, Brown VK. 2002. Soil food web components affect plant community structure during early succession. *Ecol. Res.* 17:217–27
 53. Gibson DJ, Freeman CC, Hulbert LC. 1990. Effects of small mammal and invertebrate herbivory on plant-species richness and abundance in tallgrass prairie. *Oecologia* 84:169–75
 54. Gibson DJ, Hulbert LC. 1987. Effects of fire, topography, and year-to-year climatic variation on species composition in tallgrass prairie. *Vegetatio* 72:175–85
 55. Hendrix SD. 1979. Compensatory reproduction in a biennial herb following defoliation. *Oecologia* 42:107–18
 56. Holland EA, Detling JK. 1990. Plant response to herbivory and belowground nitrogen cycling. *Ecology* 71:1040–49
 57. Holmes ND, Smith DS, Johnson A. 1979. Effect of grazing by cattle on the abundance of grasshoppers. *J. Range Manag.* 23:310–11
 58. Hunt HW, Coleman DC, Ingham ER, Ingham RE, Elliot ET, et al. 1987. The detrital foodweb in a shortgrass prairie. *Biol. Fertil. Soils* 3:57–68
 59. Inbar M, Eshel A, Wool D. 1995. Interspecific competition among phloem-feeding

- insects mediated by induced host plant sinks. *Ecology* 76:1506–15
60. Ingham RE. 1985. Review of the effects of 12 selected biocides on target and non-target soil organisms. *Crop Prot.* 4:3–32
 61. Ingham RE, Detling JK. 1990. Effects of root-feeding nematodes on aboveground net primary production in a North American grassland. *Plant Soil* 121:279–81
 62. Joern A, Gaines SB. 1990. Population dynamics and regulation in grasshoppers. In *Biology of Grasshoppers*, ed. RF Chapman, A Joern, pp. 415–82. New York: Wiley
 63. Joern A, Pruess KP. 1986. Temporal constancy in grasshopper assemblages (Orthoptera: Acrididae). *Ecol. Entomol.* 11:379–85
 64. Johnson SR, Knapp AK. 1996. Impact of *Ischnodemus falicus* (Hemiptera: Lygaeidae) on photosynthesis and production of *Spartina pectinata* wetlands. *Environ. Entomol.* 25:1122–27
 65. Jonas JL, Whiles MR, Charlton RE. 2002. Aboveground invertebrate responses to land management differences in a central Kansas grassland. *Environ. Entomol.* 31:1142–52
 66. Karban R, Baldwin IT. 1997. *Induced Responses to Herbivory*. Chicago: Univ. Chicago Press
 67. Knapp AK, Blair JM, Briggs JM, Collins SL, Hartnett DC, et al. 1999. The keystone role of bison in North American tallgrass prairie—bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. *BioScience* 49:39–50
 68. Knapp AK, Briggs JM, Blair JM, Turner CL. 1998. Patterns and controls of aboveground net primary production in tallgrass prairie. See Ref. 69, pp. 193–221
 69. Knapp AK, Briggs JM, Hartnett DC, Collins SL, eds. 1998. *Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie*. New York: Oxford Univ. Press
 70. Knight CL, Briggs JM, Nellis MD. 1994. Expansion of gallery forest on konza prairie research natural area, Kansas, USA. *Landsc. Ecol.* 9:117–25
 71. Knutson H, Campbell JB. 1976. *Relationships of grasshoppers (Acrididae) to burning, grazing, and range sites of native tallgrass prairie in Kansas*. Presented Proc. 6th Tall Timbers Conf. Ecol. Anim. Control Habitat Manag., Tallahassee, FL
 72. Kula AAR, Hartnett DC, Wilson GWT. 2005. Effects of mycorrhizal symbiosis on tallgrass prairie plant-herbivore interactions. *Ecol. Lett.* 8:61–69
 73. Leatham JW, Milchunas DG. 1985. The composition and distribution of soil microarthropods in the shortgrass steppe in relation to soil water, root biomass, and grazing by cattle. *Pedobiologia* 28:311–25
 74. Letourneau DK, Dyer LA. 1998. Experimental test in lowland tropical forest shows top-down effects through four trophic levels. *Ecology* 79:1678–87
 75. Louda SM. 1982. Distribution ecology: variation in plant recruitment over a gradient in relation to insect seed predation. *Ecol. Monogr.* 52:25–41
 76. Louda SM, Potvin MA. 1995. Effect of inflorescence-feeding insects on the demography and lifetime fitness of a native plant. *Ecology* 76:229–45
 77. Lovett GM, Ruesink AE. 1995. Carbon and nitrogen mineralization from decomposing gypsy-moth frass. *Oecologia* 104:133–38
 78. Malmqvist B. 1993. Interactions in stream leaf packs: effects of a stonefly predator on detritivores and organic matter processing. *Oikos* 66:454–62
 79. Masters GJ, Brown VK. 1992. Plant-mediated interactions between two spatially separated insects. *Funct. Ecol.* 6:175–79
 80. Masters GJ, Brown VK, Gange AC. 1993. Plant-mediated interactions between aboveground and belowground insect herbivores. *Oikos* 66:148–51

81. McNaughton SJ. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *Am. Nat.* 113:691–703
82. McNaughton SJ. 1985. Ecology of a grazing ecosystem: the Serengeti. *Ecol. Monogr.* 53:291–320
83. McRea KD, Abrahamson WG, Weis AE. 1985. Goldenrod ball gall effects on *Solidago altissima* ¹⁴C translocation and growth. *Ecology* 66:1902–7
84. Meyer CK, Whiles MR, Charlton RE. 2002. Life history, secondary production, and ecosystem significance of acridid grasshoppers in annually burned and unburned tallgrass prairie. *Am. Entomol.* 48:52–61
85. Meyer GA. 1993. A comparison of the impacts of leaf-feeding and sap-feeding insects on growth and allocation of goldenrod. *Ecology* 74:1101–16
86. Meyer GA, Whitlow TH. 1992. Effects of leaf and sap feeding insects on photosynthetic rates of goldenrod. *Oecologia* 92:480–89
87. Moore JC, Walter DE, Hunt HW. 1988. Arthropod regulation of micro- and mesobiota in below-ground detrital food webs. *Annu. Rev. Entomol.* 33:419–39
88. Moran MD, Hurd LE. 1998. A trophic cascade in a diverse arthropod community caused by a generalist arthropod predator. *Oecologia* 113:126–32
89. Moran MD, Rooney TP, Hurd LE. 1996. Top-down cascade from a bitrophic predator in an old-field community. *Ecology* 77:2219–27
90. Moron Rios A, Dirzo R, Jaramillo VJ. 1997. Defoliation and below-ground herbivory in the grass *Muhlenbergia quadridentata*: effects on plant performance and on the root-feeder *Phyllophaga* sp. (Coleoptera, Melolonthidae). *Oecologia* 110:237–42
91. Mulder CPH, Koricheva J, Huss-Danell K, Hogberg P, Joshi J. 1999. Insects affect relationships between plant species richness and ecosystem processes. *Ecol. Lett.* 2:237–46
92. Murray PJ, Clements RO. 1998. Transfer of nitrogen between clover and wheat: effect of root herbivory. *Eur. J. Soil Biol.* 34:25–30
93. Murray PJ, Hatch DJ. 1994. Sitona weevils (Coleoptera, Curculionidae) as agents for rapid transfer of nitrogen from white clover (*Trifolium repens* L.) to perennial ryegrass (*Lolium perenne* L.). *Ann. Appl. Biol.* 125:29–33
94. Naeem S, Knops JMH, Tilman D, Howe KM, Kennedy T, et al. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* 91:97–108
95. Naiman RJ. 1988. Animal influences on ecosystem dynamics. *BioScience* 38:750–52
96. Owen DF, Wiegert RG. 1981. Mutualism between grasses and grazers: an evolutionary hypothesis. *Oikos* 36:376–78
97. Parker LW, Santos PF, Phillips J, Whitford WG. 1984. Carbon and nitrogen dynamics during decomposition of litter and roots of a Chihuahuan desert annual, *Lepidium lasiocarpum*. *Ecol. Monogr.* 54:339–60
98. Pastor J, Cohen Y. 1997. Herbivores, the functional diversity of plants species, and the cycling of nutrients in ecosystems. *Theor. Popul. Biol.* 51:165–79
99. Pastor J, Naiman RJ. 1992. Selective foraging and ecosystem processes in boreal forests. *Am. Nat.* 139:690–705
100. Peterson CE, Sleboda JA. 1994. Selective pod abortion by *Baptisia leucantha* (Fabaceae) as affected by a curculionid seed predator, *Apion rostrum* (Coleoptera). *Great Lakes Entomol.* 27:143–47
101. Quinn MA, Walgenbach DD. 1990. Influence of grazing history on the community structure of grasshoppers of a mixed-grass prairie. *Environ. Entomol.* 19:1756–66
102. Ransom MD, Rice CW, Todd TC, Wehmüller WA. 1998. Soils and soil biota. See Ref. 69, pp. 48–66

103. Reed CC. 1993. Reconstruction of pollinator communities on restored prairies in eastern Minnesota. *Minn. Dep. Nat. Resour. Nongame Wildl. Program*
104. Reed CC. 1996. List of insects which may be tallgrass prairie specialists. *Minn. Dep. Nat. Resour., Div. Ecol. Serv.*
105. Reichman OJ. 1987. *Konza Prairie: A Tallgrass Natural History*. Lawrence: Univ. Kans. Press. 228 pp.
106. Rice CW, Todd TC, Blair JM, Seastedt TR, Ramundo RA, et al. 1998. Belowground biology and processes. See Ref. 69, pp.
107. Risley LS, Crossley DAJ. 1988. Herbivore-caused greenfall in the southern Appalachians. *Ecology* 69:1118–27
108. Risser PG, Birney CE, Blocker HD, May SW, Parton WJ, et al. 1981. *The True Prairie Ecosystem*. Rep. US/IBP Synth. Ser. 16. Stroudsburg, PA: Hutchinson Ross Publ.
109. Ritchie ME, Tilman D, Knops JMH. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology* 79:165–77
110. Rodenhouse NL, Bohlen PJ, Barrett GW. 1997. Effects of woodland shape on the spatial distribution and density of 17-year periodical cicadas (Homoptera: Cicadidae). *Am. Midl. Nat.* 137:124–35
111. Rogers LE. 1972. The ecological effects of the Western harvest ant (*Pogonomyx occidentalis*) in the shortgrass plains ecosystems. *Rep. Tech. Rep. 206*, Nat. Resour. Ecol. Lab., Colorado State Univ., Fort Collins
112. Samson FB, Knopf FL, eds. 1996. *Prairie Conservation: Preserving North America's Most Endangered Ecosystem*. Washington, DC: Island
113. Schmidt ND, Kucera CL. 1975. Arthropod food chain energetics in a Missouri tall grass prairie. In *Prairie: A Multiple View*, ed. MK Wall, pp. 143–54. Grand Forks: Univ. North Dakota Press
114. Schowalter TD, Crossley DAJ. 1983. Forest canopy arthropods as sodium, potassium, magnesium, and calcium pools in forests. *Forest Ecol. Manag.* 7:143–48
115. Schowalter TD, Hargrove WW, Crossley DAJ. 1986. Herbivory in forested ecosystems. *Annu. Rev. Entomol.* 31:177–96
116. Schowalter TD, Webb JW, Crossley DA. 1981. Community structure and nutrient content of canopy arthropods in clearcut and uncut forest ecosystems. *Ecology* 62:1010–19
117. Scott JA, French NR, Leetham JW. 1979. Patterns of consumption in grasslands. See Ref. 49a, pp. 89–105
118. Seastedt TR. 1984. Belowground macroarthropods of annually burned and unburned tallgrass prairie. *Am. Midl. Nat.* 111:405–8
119. Seastedt TR. 1984. Microarthropods of burned and unburned tallgrass prairie. *J. Kans. Entomol. Soc.* 57:468–76
120. Seastedt TR. 1984. The role of microarthropods in decomposition and mineralization processes. *Annu. Rev. Entomol.* 29:25–46
121. Seastedt TR. 1985. Maximization of primary and secondary productivity by grazers. *Am. Nat.* 126:559–64
122. Seastedt TR. 1988. Mass, nitrogen, and phosphorus dynamics in foliage and root detritus of tallgrass prairie. *Ecology* 69:59–65
123. Seastedt TR, Crossley DAJ. 1984. The influence of arthropods on ecosystems. *Bio-science* 34:157–61
124. Seastedt TR, James SW, Todd TC. 1988. Interactions among soil invertebrates, microbes, and plant growth in the tallgrass prairie. *Agric. Ecosyst. Environ.* 24:219–28
125. Seastedt TR, Parton WJ, Ojima DS. 1992. Mass loss and nitrogen dynamics of decaying litter of grasslands: the apparent low nitrogen immobilization potential of root detritus. *Can. J. Bot.* 70:384–91
126. Seastedt TR, Ramundo RA, Hayes DC. 1988. Maximization of densities of soil animals by foliage herbivory: empirical

- evidence, graphical and conceptual models. *Oikos* 51:243–48
127. Seastedt TR, Tate CM. 1981. Decomposition rates and nutrient contents of arthropod remains in forest litter. *Ecology* 62:13–19
 128. Seastedt TR, Todd TC, James SW. 1987. Experimental manipulations of arthropod, nematode, and earthworm communities in a North American tallgrass prairie. *Pedobiologia* 30:9–17
 129. Shure DJ. 1971. Insecticide effects on early succession in an old-field ecosystem. *Ecology* 52:271–79
 130. Siemann E, Tilman D, Haarstad J, Ritchie M. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. *Am. Nat.* 152:738–50
 131. Sih A, Crowley P, McPeck M, Petranka J, Strohmeier K. 1985. Predation, competition, and prey communities: a review of field experiments. *Annu. Rev. Ecol. Syst.* 16:269–311
 132. Smith MD, Knapp AK. 2003. Dominant species maintain ecosystem function with non-random species loss. *Ecol. Lett.* 6:509–17
 133. Stagliano DM, Whiles MR. 2002. Macroinvertebrate production and trophic structure in a tallgrass prairie headwater stream. *J. North Am. Benthol. Soc.* 21:97–113
 134. Stanton NL. 1988. The underground in grasslands. *Annu. Rev. Ecol. Syst.* 19:573–89
 135. Stanton NL, Allen M, Campion M. 1981. The effect of the pesticide carbofuran on soil organisms and root and shoot production in shortgrass prairie. *J. Appl. Ecol.* 18:417–31
 136. Stephenson AG. 1981. Flower and fruit abortion: proximate causes and ultimate functions. *Annu. Rev. Ecol. Syst.* 12:253–79
 137. Stoner KJL, Joern A. 2004. Landscape vs. local habitat scale influences to insect communities from tallgrass prairie remnants. *Ecol. Appl.* 14:1306–20
 138. Strong DR, Maron JL, Connors PG, Whipple A, Harrison S, et al. 1995. High mortality, fluctuation in numbers, and heavy subterranean insect herbivory in bush lupine, *Lupinus arboreus*. *Oecologia* 104:85–92
 139. Swank WT, Waide JB, Crossley DAJ, Todd RL. 1981. Insect defoliation enhances nitrate export from forest ecosystems. *Oecologia* 51:297–99
 140. Tilman D, Reich PB, Knops J, Wedin D, Mielke T, et al. 2001. Diversity and productivity in a long-term grassland experiment. *Science* 294:843–45
 141. Tooker JF, Hanks LM. 2004. Endophytic insect communities of two prairie perennials (Asteraceae: *Silphium* spp.). *Biodivers. Conserv.* 13:2551–66
 142. Tschardtke T, Greiler HJ. 1995. Insect communities, grasses, and grasslands. *Annu. Rev. Entomol.* 40:535–58
 143. Ueckert DN. 1979. Impact of a white grub (*Phyllophaga crinita*) on a shortgrass community and evaluation of selected rehabilitation processes. *J. Range Manag.* 32:445–48
 144. Vossbrink CR, Coleman DC, Woolley TA. 1979. Abiotic and biotic factors in litter decomposition in a semiarid grassland. *Ecology* 60:265–71
 145. Wardle DA, Bonner KI, Barker GM. 2002. Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. *Funct. Ecol.* 16:585–95
 146. Weiner LF, Capinera JL. 1980. Preliminary study of the white grub *Phyllophaga fimbripes* (Leconte) (Coleoptera: Scarabaeidae). *J. Kans. Entomol. Soc.* 53:701–10
 147. Whiles MR, Callahan MA, Meyer CK, Brock BL, Charlton RE. 2001. Emergence of periodical cicadas (*Magicicada cassini*) from a Kansas riparian forest: densities, biomass and nitrogen flux. *Am. Midl. Nat.* 145:176–87
 148. Whiles MR, Goldowitz BS, Charlton

- RE. 1999. Life history and production of a semi-terrestrial limnephilid caddisfly in an intermittent Platte River wetland. *J. North Am. Benthol. Soc.* 18:533–44
149. Yang YL, Joern A. 1994. Compensatory feeding in response to variable food quality by *Melanoplus differentialis*. *Physiol. Entomol.* 19:75–82
150. Yang YL, Joern A. 1994. Influence of diet quality, developmental stage, and temperature on food residence time in the grasshopper *Melanoplus differentialis*. *Physiol. Zool.* 67:598–616

CONTENTS

SIGNALING AND FUNCTION OF INSULIN-LIKE PEPTIDES IN INSECTS, <i>Qi Wu and Mark R. Brown</i>	1
PROSTAGLANDINS AND OTHER EICOSANOIDS IN INSECTS: BIOLOGICAL SIGNIFICANCE, <i>David Stanley</i>	25
BOTANICAL INSECTICIDES, DETERRENTS, AND REPELLENTS IN MODERN AGRICULTURE AND AN INCREASINGLY REGULATED WORLD, <i>Murray B. Isman</i>	45
INVASION BIOLOGY OF THRIPS, <i>Joseph G. Morse and Mark S. Hoddle</i>	67
INSECT VECTORS OF PHYTOPLASMAS, <i>Phyllis G. Weintraub and LeAnn Beanland</i>	91
INSECT ODOR AND TASTE RECEPTORS, <i>Elissa A. Hallem, Anupama Dahanukar, and John R. Carlson</i>	113
INSECT BIODIVERSITY OF BOREAL PEAT BOGS, <i>Karel Spitzer and Hugh V. Danks</i>	137
PLANT CHEMISTRY AND NATURAL ENEMY FITNESS: EFFECTS ON HERBIVORE AND NATURAL ENEMY INTERACTIONS, <i>Paul J. Ode</i>	163
APPARENT COMPETITION, QUANTITATIVE FOOD WEBS, AND THE STRUCTURE OF PHYTOPHAGOUS INSECT COMMUNITIES, <i>F.J. Frank van Veen, Rebecca J. Morris, and H. Charles J. Godfray</i>	187
STRUCTURE OF THE MUSHROOM BODIES OF THE INSECT BRAIN, <i>Susan E. Fahrbach</i>	209
EVOLUTION OF DEVELOPMENTAL STRATEGIES IN PARASITIC HYMENOPTERA, <i>Francesco Pennacchio and Michael R. Strand</i>	233
DOPA DECARBOXYLASE: A MODEL GENE-ENZYME SYSTEM FOR STUDYING DEVELOPMENT, BEHAVIOR, AND SYSTEMATICS, <i>Ross B. Hodgetts and Sandra L. O'Keefe</i>	259
CONCEPTS AND APPLICATIONS OF TRAP CROPPING IN PEST MANAGEMENT, <i>A.M. Shelton and F.R. Badenes-Perez</i>	285
HOST PLANT SELECTION BY APHIDS: BEHAVIORAL, EVOLUTIONARY, AND APPLIED PERSPECTIVES, <i>Glen Powell, Colin R. Tosh, and Jim Hardie</i>	309

BIZARRE INTERACTIONS AND ENDGAMES: ENTOMOPATHOGENIC FUNGI AND THEIR ARTHROPOD HOSTS, <i>H.E. Roy, D.C. Steinkraus, J. Eilenberg, A.E. Hajek, and J.K. Pell</i>	331
CURRENT TRENDS IN QUARANTINE ENTOMOLOGY, <i>Peter A. Follett and Lisa G. Neven</i>	359
THE ECOLOGICAL SIGNIFICANCE OF TALLGRASS PRAIRIE ARTHROPODS, <i>Matt R. Whiles and Ralph E. Charlton</i>	387
MATING SYSTEMS OF BLOOD-FEEDING FLIES, <i>Boaz Yuval</i>	413
CANNIBALISM, FOOD LIMITATION, INTRASPECIFIC COMPETITION, AND THE REGULATION OF SPIDER POPULATIONS, <i>David H. Wise</i>	441
BIOGEOGRAPHIC AREAS AND TRANSITION ZONES OF LATIN AMERICA AND THE CARIBBEAN ISLANDS BASED ON PANBIOGEOGRAPHIC AND CLADISTIC ANALYSES OF THE ENTOMOFAUNA, <i>Juan J. Morrone</i>	467
DEVELOPMENTS IN AQUATIC INSECT BIOMONITORING: A COMPARATIVE ANALYSIS OF RECENT APPROACHES, <i>Núria Bonada, Narcís Prat, Vincent H. Resh, and Bernhard Statzner</i>	495
TACHINIDAE: EVOLUTION, BEHAVIOR, AND ECOLOGY, <i>John O. Stireman, III, James E. O'Hara, and D. Monty Wood</i>	525
TICK PHEROMONES AND THEIR USE IN TICK CONTROL, <i>Daniel E. Sonenshine</i>	557
CONFLICT RESOLUTION IN INSECT SOCIETIES, <i>Francis L.W. Ratnieks, Kevin R. Foster, and Tom Wenseleers</i>	581
ASSESSING RISKS OF RELEASING EXOTIC BIOLOGICAL CONTROL AGENTS OF ARTHROPOD PESTS, <i>J.C. van Lenteren, J. Bale, F. Bigler, H.M.T. Hokkanen, and A.J.M. Loomans</i>	609
DEFECATION BEHAVIOR AND ECOLOGY OF INSECTS, <i>Martha R. Weiss</i>	635
PLANT-MEDIATED INTERACTIONS BETWEEN PATHOGENIC MICROORGANISMS AND HERBIVOROUS ARTHROPODS, <i>Michael J. Stout, Jennifer S. Thaler, and Bart P.H.J. Thomma</i>	663
INDEXES	
Subject Index	691
Cumulative Index of Contributing Authors, Volumes 42–51	717
Cumulative Index of Chapter Titles, Volumes 42–51	722

ERRATA

An online log of corrections to *Annual Review of Entomology* chapters may be found at <http://ento.annualreviews.org/errata.shtml>