IV.3 Grasshoppers and Vegetation Communities

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Important links exist between grasshoppers and the vegetation community. Vegetation communities provide the backdrop against which all grasshopper activities occur and determine the availability and distribution of all resources required by grasshoppers. Many critical questions concerning the relationship between vegetation communities and grasshopper communities remain unanswered, even unasked. Given the potential importance of such relationships to both forecasting of changes in grasshopper populations and grasshopper management activities, we summarize the currently available insights relevant to integrated pest management (IPM) activities on rangeland.

In this chapter, we stress that much unfinished research remains on critical questions concerning these communities. At the same time, we also stress that scientists understand a great deal, at least in terms of framing the appropriate questions. We will review the problem at two levels:

(1) At the macroscale level, how do grasshopper assemblies change as vegetational communities shift along environmental gradients? Do the dynamics underlying grasshopper community structure change; and, if they do, what are the consequences to the development of management tactics?

(2) On a more detailed, microscale level, how do grasshoppers actually use the structural and spatial components of their environments? What constitutes a resource in this sense and how do changing vegetational communities alter the quality or availability of resources for grasshoppers?

An extremely broad array of vegetation community types exists within the roughly 753 million acres of the Western United States classified as range (U.S. Department of Agriculture, Forest Service 1972). These plant community types, which range from inland deserts to alpine meadows, contain a collection of insects that often compete with humans for resources. Annual forage losses to grasshoppers alone often exceed 20 percent of the total annual production of rangelands in the Western United States (Hewitt 1977; Hewitt and Onsager 1982, 1983). Of the nearly 600 grasshopper species nationwide (Hewitt and Onsager 1982), 200 exist on rangelands

(Onsager 1987, p. 60–66), and about 25 regularly reach economically damaging densities (Hewitt and Onsager 1983).

Unfortunately, management plans typically treat rangeland grasshoppers as a more or less homogeneous group from Montana to Arizona. Current rangeland pest management strategies seldom, if ever, consider differences among either vegetation patterns or grasshopper communities of varying species composition (Capinera 1987, Onsager 1987). These differences are ignored, even though important differences in biology exist among coexisting rangeland species (Kemp and Onsager 1986, Joern 1987, Kemp and Sanchez 1987, Onsager 1987).

Macroscale Patterns: Grasshopper and Vegetation Classifications

In recent years, plant ecologists have developed an environmental classification system based on the concept of habitat type (HT). Pioneered by Daubenmire (Daubenmire 1978), the methods for identifying HT's are those developed for identifying plant communities. HT's consist of discrete and repeatable vegetational units that characterize various resources, including forage or timber. Land managers use HT's to help predict responses to natural and human perturbations (such as fire, grazing or harvesting) (Mueggler and Stewart 1980, Pfister et al. 1977). The HT concept is being used increasingly in the management of forests and rangelands by the U.S. Department of Agriculture's Forest Service and Natural Resources Conservation Service (formerly the Soil Conservation Service) and the U.S. Department of the Interior's Bureau of Land Management. The HT concept has appeal in terms of resource management because it recognizes habitat heterogeneity yet reduces the complex vegetation landscape to a set of discrete groupings. Sites within the same HT thus can be managed in similar ways, and agencies can develop management strategies that are more rational from an ecological viewpoint.

If HT's can be used to classify sites satisfactorily into discrete groups based on the potential to produce resources and responses to management activities, it seems logical that HT's also will differ in their ability to sustain specific insect communities. A number of studies of mid- and large-scale communities have been con-

ducted on species richness and diversity of both plants and grasshoppers (Vestal 1913, Otte 1976). Otte (1976), for example, observed that the Sonoran Desert of Arizona exhibited a significantly richer grasshopper fauna than the floristically "similar" Monte Desert of Argentina. Total niche space could not adequately account for these differences. Other regional studies that consider the gross distribution of grasshoppers have concentrated heavily on the presence of either grasshoppers (Isely 1937) or plants (Anderson 1973), with anecdotal inclusion of plants in the former and grasshoppers in the latter. Smaller scale studies (Banfill and Brusven 1973, Scoggan and Brusven 1973) that attempt to relate vegetation type to grasshopper community complexity typically lack the sampling intensity within given plant communities required to make regional inferences.

In a replicated study of patterns of plants and grasshoppers on Montana rangeland, Kemp et al. (1990a) found that the presence and relative dominance of about 40 individual grasshopper species changed with HT. The environmental gradients (precipitation and elevation) and plant species compositions of the different habitats determined grasshopper presence and dominance (fig. IV.3–1). In comparisons among plant communities associated with grasshopper communities along a natural elevational gradient, the native *Stipa comata–Bouteloua gracilis* HT (lower elevation and drier) and *Festuca idahoensis–Agropyron spicatum* HT (higher elevation and wetter) contained very different species complexes (Kemp et al. 1990a). Species like *Phlibostroma quadrimaculatum* and *Xanthippus corallipes* were found only in the drier habitats, whereas species such as *Melanoplus dawsoni* were found only in wetter sites.
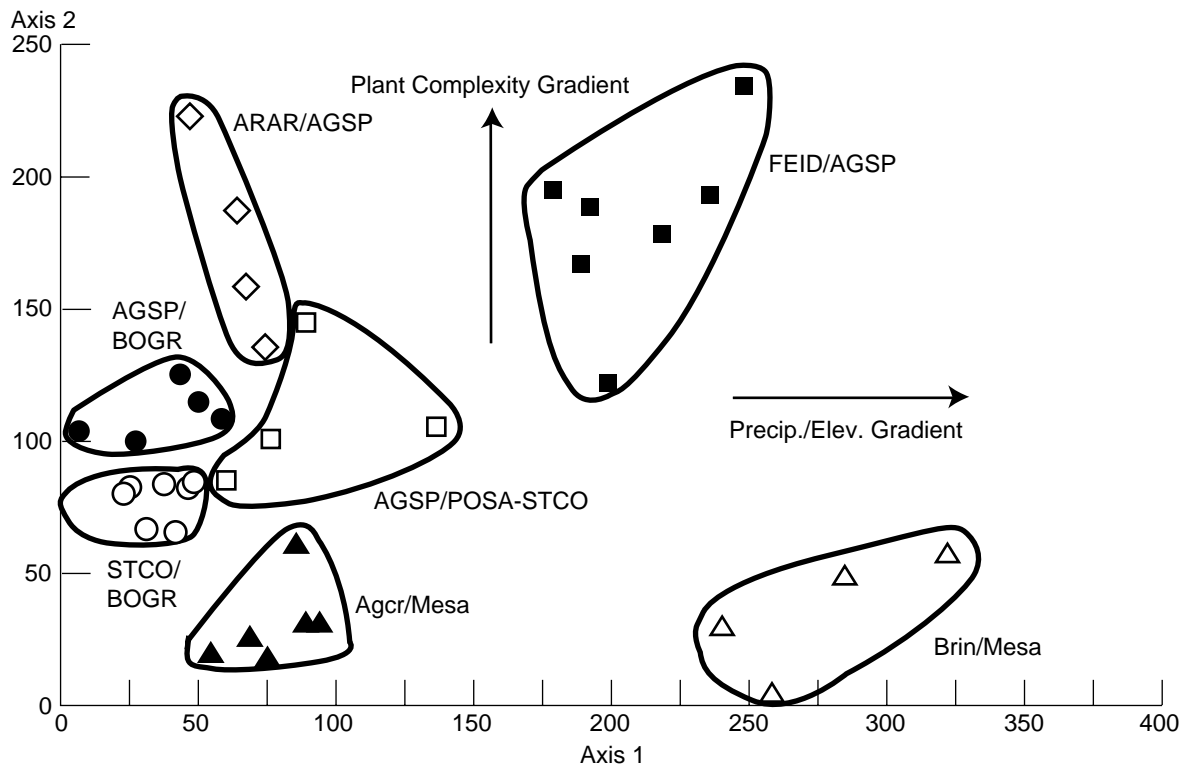

Figure IV.3–1A—Ordination of plant communities using detrended correspondence analysis of a range of habitat patches found in Gallatin Valley, MT, in 1988. A precipitation–elevation gradient is mostly responsible for spreading out the sites along the x axis, while a plant complexity gradient explains the spread along the y axis. Habitat codes relate to dominant plant species: Agcr=*Agropyron cristatum*, AGSP=*Agropyron spicatum*, ARAR=*Artemesia arbuscula,* BOGR=*Bouteloua gracilis*, Brin=*Bromus inermis*, FEID=*Festuca idahoensis,* Mesa=*Medicago sativa,* POSA=*Poa sandbergii,* STCO=*Stipa comata*. (Adapted from Kemp et al. 1990a.)
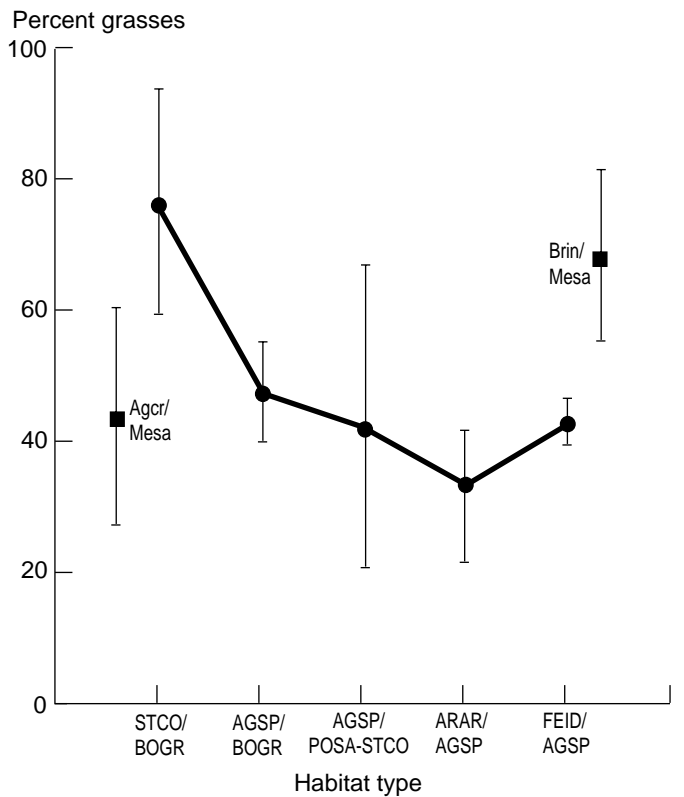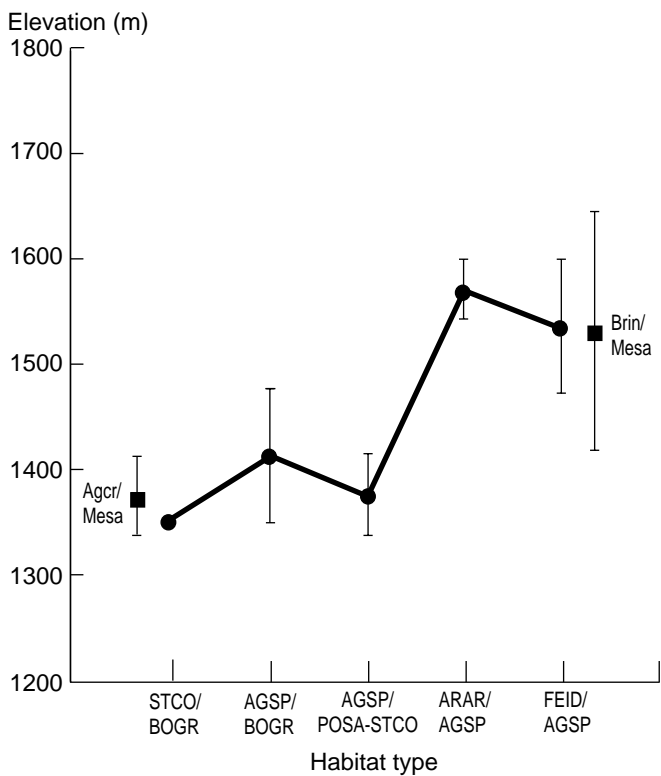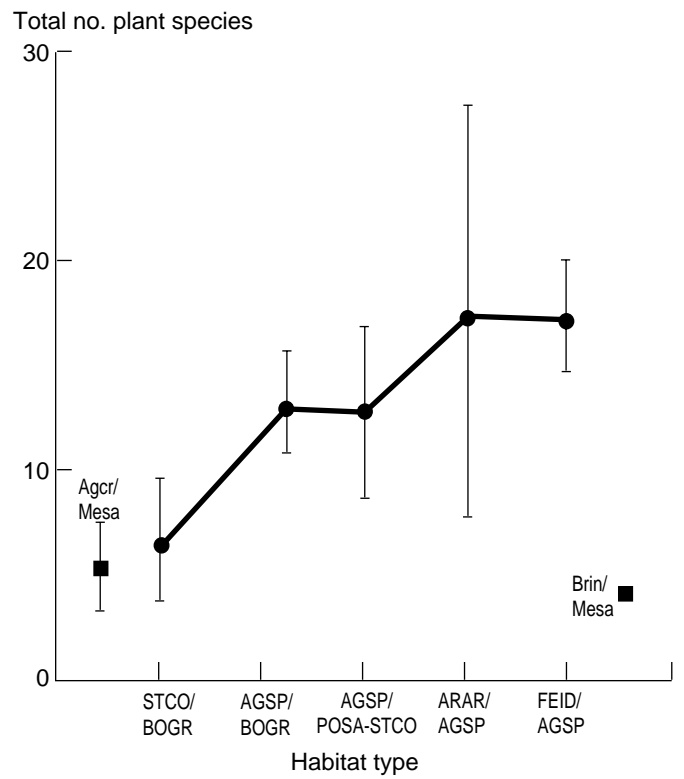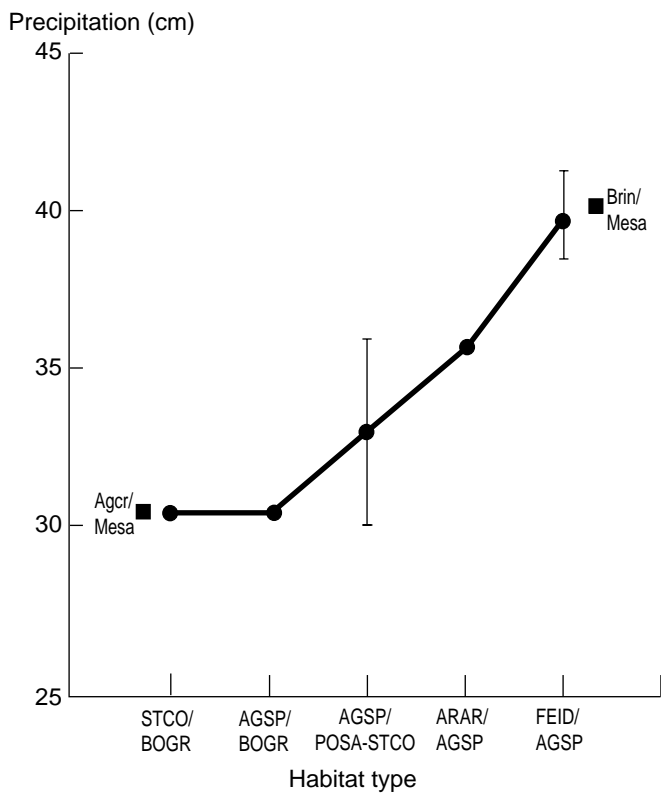
Precipitation (cm)

Elevation (m)

Figure IV.3–1B—Mean values (± 2 SE) for precipitation and elevation for a range of HT's surveyed for grasshoppers and vegetation in Gallatin Valley, MT, 1988. (Adapted from Kemp et al. 1990a.)

Total no. plant species

Percent grasses

Figure IV.3–1C—Mean values (± 2 SE) for the total number of plant species and percent grasses for a range of HT's surveyed for grasshoppers and vegetation in Gallatin Valley, MT, 1988. (Adapted from Kemp et al. 1990a.)

Further, over a range of HT's, more than 10 common grasshopper species exhibited significant affinities for either end of the precipitation–elevation gradient.

Recent investigations in southern Idaho using mapping by ecological condition (another form of HT mapping) revealed a historic association between increased grasshopper densities and ecological disturbance, especially shrub loss from wildfires and other causes (Fielding and Brusven 1993a). Grasshopper assemblages from areas dominated by annual vegetation exhibited higher densities, lower species diversity, and broad diet breadths (Fielding and Brusven 1993b). Grasshopper assemblages from areas of perennial grasses largely contained grass-feeding species and exhibited high species diversity. Sagebrush–grass-dominated areas exhibited high grasshopper species diversity and lower densities. Therefore, land managers should not expect grasshopper communities to exhibit the same species composition from place to place when vegetational or environmental gradients exist.

Additional support for the use of HT to make inferences concerning invertebrate herbivore communities comes from avian research. In a study of HT's (as defined herein), Harvey and Weaver (1976) found very distinct use patterns among approximately 50 bird species in the northern U.S. Rocky Mountains. The presence or absence of bird species differed seasonally and in space among replicated stands of six HT's.

On a small scale, HT and differences found among grasshopper communities over a range of HT's will influence the need for and expected success of some research and management activities on rangelands. Rangeland grasshopper species typically vary in their susceptibility to biological control agents such as *Nosema locustae* (Henry 1971, Ewen and Mukerji 1979). Grasshoppers also differ in their willingness to feed on bran bait, which is often used for applying such biologicals (Onsager et al. 1980). For example, both *M. sanguinipes* and *Ageneotettix deorum* are known to accept bait (Onsager et al. 1980). However, Quinn et al. (1989) found that densities of *Trachyrhachys kiowa*, a species known to reject bait (Onsager et al. 1980), were unaffected by the bait treatment. Therefore, communities composed of significant proportions of grasshopper species that either will not accept bran bait, are not susceptible to

N. locustae, or both will not be vulnerable to this type of control plan.

Additionally, exploiting the relationship between HT and grasshopper species composition offers entomologists and ecologists a way of simplifying experimental design problems. For example, two problems could occur if a series of test and control plots designed to assess efficacy of a particular treatment were selected without regard to HT. First, the target grasshopper communities could be completely different among sites and therefore respond differently to the treatment. If this happens, decision makers may draw conclusions based upon misleading evidence. Second, the assessment of block, treatment, and interaction effects in standard Analysis of Variance type experimental designs could be confounded by other indirect influences of HT on grasshopper community complexity and sampling. Such confounding would severely limit interpretations of cause and effect in this hypothetical case, a serious problem because the investigator would be unaware of the confound.

The perception of what processes might lead to different insect community structure among HT's will also influence research directions on natural processes that affect insect populations. The effectiveness of natural enemies in stabilizing pest populations may vary among HT's and disturbance levels. Joern (1988) has shown that electivities (food choices) of the grasshopper sparrow *(Ammodramus savannarum)* for particular grasshopper species are dependent upon their relative abundance. Perhaps rangeland habitats of lower plant diversity also harbor less diverse communities of predators and parasitoids, as seems to be the case for cultivated systems (Russell 1989). Further, when food is a limiting factor (Belovsky 1986), we expect that grasshopper community composition will vary among HT's, the difference depending on the varying intensities of interspecific competition.

Within the rangelands of the Western United States, the relationships between grasshopper community composition, HT, and long-term population trends become important. Certain HT's may serve as indicators of impending general population increases or declines. Such HT's warrant continuous monitoring, even during years where general densities are low. These sites could comprise a

regional early warning system for grasshopper population eruptions. Alternately, other HT's may rarely support high grasshopper densities.

The HT concept deserves additional emphasis in both pest management and insect ecology (Kemp et al. 1990b). The recognition of vegetational communities confers to the problem of pest management a discreetness that helps managers design appropriate remedies. The HT concept also helps identify links between a site and its biotic (species interactions) and abiotic (weather) attributes.

In terms of insect pest management, the use of the HT concept could allow managers to describe units in several different but related layers to facilitate the use of Geographic Information Systems. At any given moment, all of the aspects described in the preceding paragraphs will influence what insect species can occupy sites within a given HT. Further, all of these factors will contribute to the susceptibility to pest outbreaks (short-term increases in densities) or infestations (long-term, sustained high-level densities). If pest managers can employ "type" communities as indicators of current or future pest conditions, preventative rather than reactive management activities can be used. While it is obvious that reactive efforts will always be necessary in certain areas, the HT concept could also help managers anticipate the location of insect outbreaks in space and time.

Microscale: Vegetation Structure and Resources

Vegetation communities described earlier rely strictly on taxonomic (species) relationships. However, grasshoppers typically react solely to the resources supplied by the composite plant assemblage and seldom employ the same cues used by biologists or range managers to recognize plant communities. From a grasshopper's perspective, plant community means more than just a list of coexisting plant species. How the plant species present in a community are spaced relative to one another define the entire physical environment encountered by a grasshopper. For example, microclimatic features such as air temperature, wind speed, and incoming solar radiation levels are intricately entwined with the structural profile of the environment.

What are the consequences of these differences in perspective? If macroscale analyses correctly predict grasshopper assemblages, what are such analyses actually measuring from the grasshopper's viewpoint? Will such insights at this level contribute to developing successful control strategies? In this chapter, we identify critical resources that are needed by grasshoppers and that vary as plant communities change. These resources likely explain the large-scale patterns.

In choosing microhabitats or a range of microhabitats, grasshoppers must choose sites in which they can make a living. Actual microhabitat selection by grasshoppers represents a compromise among multiple factors that determine habitat suitability as shown in figure IV.3–2 (Joern 1979, 1985). Important attributes that define microhabitat suitability and correlate well with grasshopper microhabitat selection include (reviewed in Joern 1982) microclimatic variables (temperature, light intensity, humidity), food availability, structural qualities, oviposition sites, substrate characteristics that render an individual cryptic (hidden), or biotic features (presence of competitors or predators). Dynamics (availability and use) of each of these resource attributes underlie macroscale patterns and become important in developing grasshopper integrated pest management (IPM) tactics. Understanding each may provide the appropriate clues to devise sound practices that work in concert with naturally occurring processes. We provide several representative examples to indicate the impact of specific resources on habitat use or the reciprocal (effect of habitat structure on resource availability and use). In this sense, we emphasize elements of habitat structure determined by the plant community. Remember, a lot of research remains before scientists fully understand these issues.

Food Resources.—Plant community structure and taxonomic composition combine to define food availability. For some grasshopper species, especially for grasshoppers that exhibit restricted food preferences, the habitat becomes good or bad depending on the presence or absence of preferred food plants: nothing else may matter (Joern 1983). For grasshopper species that eat a variety of food plants, the relative abundance of grasshopper species varies according to the array of suitable food plants (including quality and productivity). Because the broad-scale habitat patterns described above include shifts in
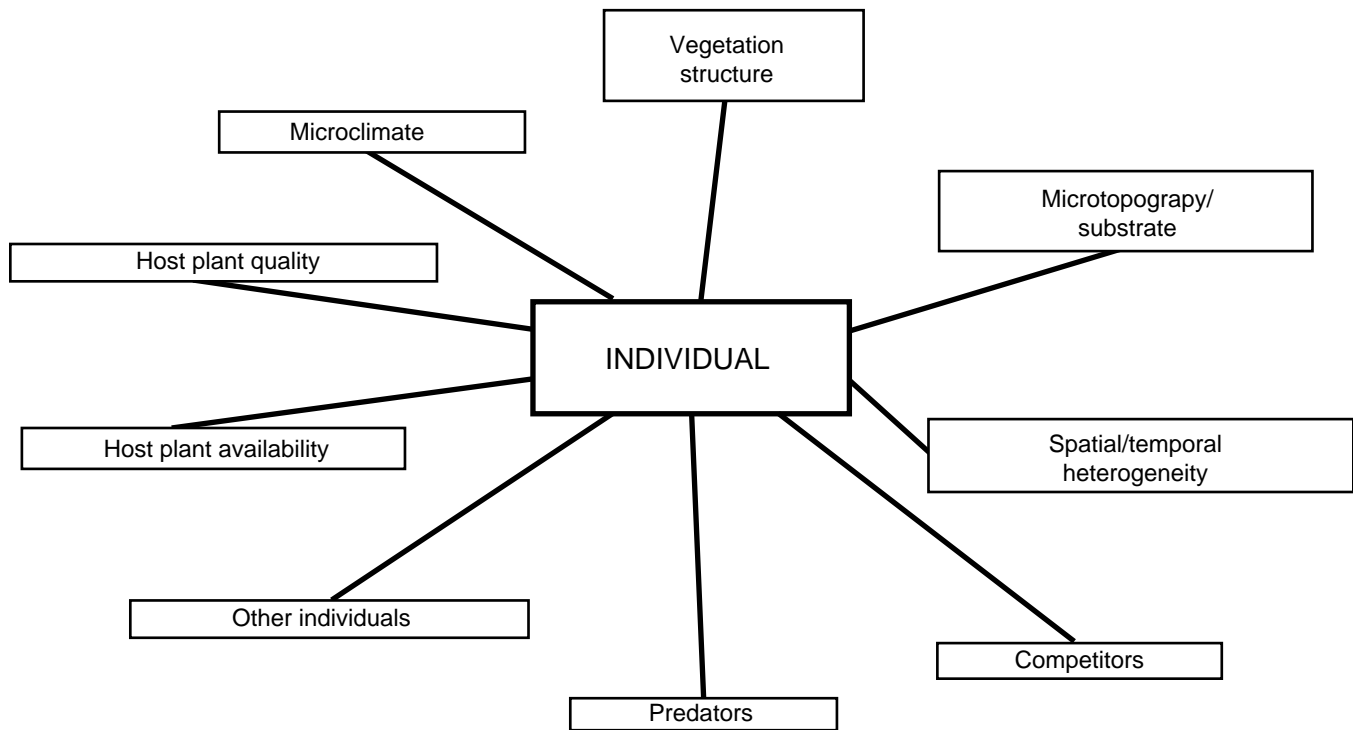
Figure IV.3–2—Environmental pressures that direct behavioral responses in patterns of resource use. (Adapted from Joern 1987.)

both the absolute and relative abundances of both plant and grasshopper species, responses at the grasshopper community level may relate to local food-use patterns. However, feeding responses by grasshopper assemblies to plant communities are not entirely species indepen-dent. Average diet breadth for entire grasshopper assem-blies (an estimate of the range of plant species eaten) increases as average precipitation increases (fig. IV.3–3). Sites with low average precipitation (deserts and desert grasslands) contain fewer plant species, and grasshoppers tend to eat mainly more predictable plant species (Otte and Joern 1977), even though the diversity of plant spe-cies on a daily basis can be very high when present. At sites with higher average precipitation, average diet breadths increase, probably because more plant species exist at more predictable levels.

Structural Relationships.—Grasshoppers often position themselves in space based on structural aspects of the environment and exhibit clear species-specific differ-

ences (Joern 1979, 1981, 1982). For example, squat-looking species, such as *Ageneotettix deorum*, typically exist in open patches with little or no vegetation canopy compared with morphologically elongated species that live *on* vegetation *(Mermiria bivittata* or *Paropomala wyomingensis).* For entire grasshopper assemblages, spe-cies partition available microhabitats in such a way that coexisting species tend to use microhabitats very differ-ently (Joern 1979, 1982, 1986).

Grasshoppers exhibit the behavioral ability and visual sharpness to use structural and spatial cues to select mi-crohabitats. Vegetation-inhabiting grasshoppers move toward vertical rather than horizontal cues (Williams 1954, Mulkern 1969). Presumably, ground-dwelling spe-cies are less responsive to these cues, but definitive stud-ies have not yet been done. In addition to responding to vertical structure, many grasshoppers select microhabitats so that they blend with the background (Gillis 1982). Active microhabitat selection based on clearcut physical
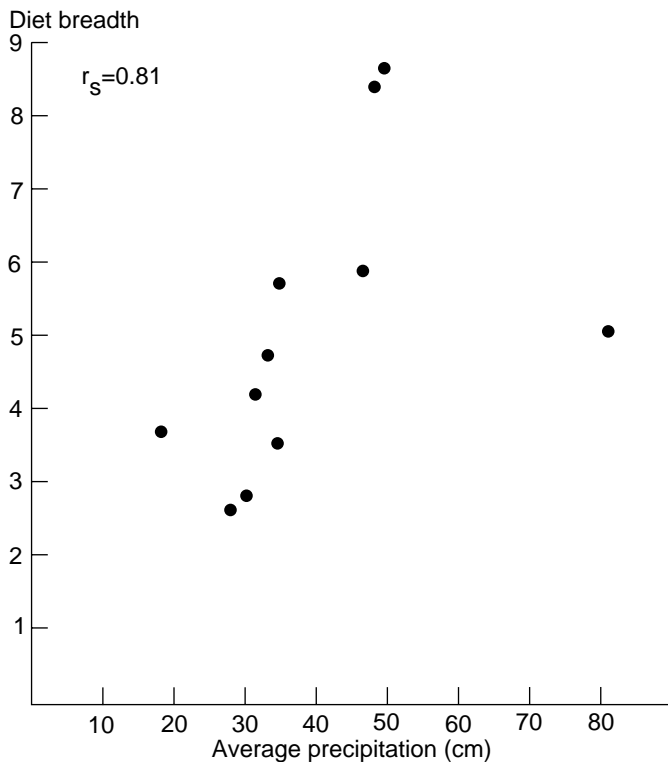
Diet breadth

$r_s = 0.81$

Figure IV.3–3—Average diet breadth of grasshoppers from sites across the United States that differ in total average precipitation. (Adapted from Yang and Joern 1994a and b.)

features of the environment supports our contention that structural resources provide important clues to understanding grasshopper distributions on a larger scale. These structural components derive directly from the vegetation community.

Thermal Attributes.—Body temperature underlies most physiological and biochemical processes associated with patterns of resources use. For example, developmental rates, food-processing capabilities, reproductive activity, life-cycle characteristics, and metabolic activity all are temperature-driven processes (Chappell and Whitman 1990). Perhaps more importantly for grasshopper IPM, many population processes are temperature dependent (Hilbert and Logan 1983, Begon 1983, Kemp and Onsager 1986, Kemp and Dennis 1989). Any factor that alters accumulated temperature by grasshoppers (either too little or too much) can profoundly influence population responses (Kingsolver 1989, Dunham et al. 1989).

As small animals with little control of body temperature (coldblooded animals), grasshoppers must rely on external heat sources and sinks to control body temperature. As with most insects, incoming solar radiation, windspeed, and air temperature coupled to anatomical features set the limits on grasshopper body temperatures (fig. IV.3–4A). Physical structure in the habitat directly affects each of these attributes. If grasshoppers were unable to thermoregulate, their body temperatures would track the temperature of the surrounding environment. However, using behavioral means, grasshoppers readily manipulate their body temperatures within a limited range, resulting in characteristic daily thermoregulation patterns (fig. IV.3–4B) (Joern 1981b, Kemp 1986).

Vegetation structure and topography interact with regional weather to determine the "microclimatic resources" that grasshoppers encounter for thermoregulation. Air temperature and incoming solar radiation levels ultimately determine a grasshopper's energy budget (Dunham et al. 1989, Kingsolver 1989, Grant and Porter 1992). The number of hours of sunlight per day, the likelihood of cloud cover, or the effect of the vegetation canopy ultimately restrict access to solar radiation and can significantly alter the number of hours per day that a grasshopper can achieve optimal body temperatures. These restrictions limit the ability of the grasshopper to find, eat, and assimilate food and then allocate nutrients. As such, demographic responses will be shifted, not because of food quality, but because the grasshopper cannot take in and use the maximal levels.

Final Comments

Given the importance of the plant community as a provider of resources, it should not be surprising if grasshopper species and resulting communities correspond with vegetation changes in some predictable manner. Preliminary studies described in this section strongly suggest this possibility. IPM programs should refine and then exploit these relationships. For managers responsible for particular land parcels, detailed maps will provide insight about where to concentrate IPM efforts. For individuals responsible for larger areas, perhaps on a regional basis, vegetation-based analyses will provide a framework for efficient monitoring because survey efforts can be parceled more precisely.
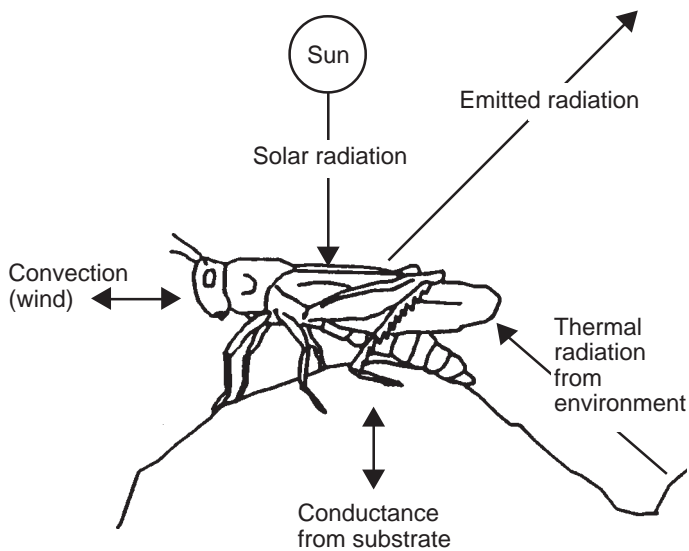
Figure IV.3–4A—Generalized heat-exchange pathways for a grass-hopper on the ground. (Reproduced from Chappell and Whitman 1990; used by permission of John Wiley and Sons.)
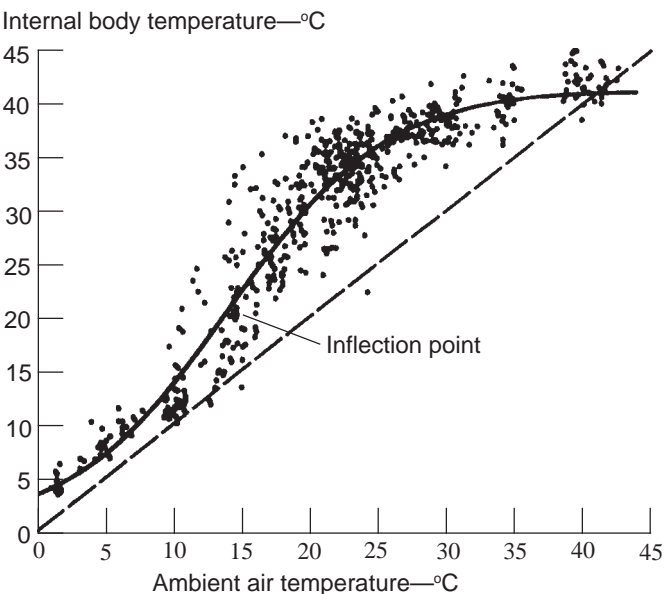

Figure IV.3–4B—The relationship between internal body temperature and ambient air temperature for *Aulocara elliotti* females over a broad range of ambient temperatures. (Adapted from Kemp 1986.) The solid line represents temperatures predicted from a logistic equation of the body temperature relationship based on ambient air temperature and incoming solar radiation. The dashed line indicates the situation where body and ambient air temperatures are equal.

However, important additional information that could help design effective IPM strategies derives from specific details associated with how grasshoppers actually use resources. We presented some representative but not exhaustive examples to clarify exactly what we mean here. Both forecasting efforts as well as cultural control (including grazing rotations to manipulate vegetation structure) can benefit from such insights. Finally, the behavioral responses that affect resource use and the resulting ecological patterns are truly complex. Scientists and land managers are just beginning to understand these interactions.

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