IV.4 Host Plant Quality and Grasshopper Populations

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Understanding how grasshopper populations respond to food availability and quality may contribute critical components to models predicting outbreaks. In this chapter, I examine the relationships between demographic features of grasshopper population biology (growth rate, developmental rate, survival, and reproductive output) in the context of host plant quality. Because these relationships can be readily modeled and easily monitored under field conditions, models developed to forecast grasshopper outbreaks could incorporate this information for better accuracy (see chapters IV.1 and VI.2).

Like all range herbivores, grasshoppers require a diet that provides adequate protein, energy, and water plus trace nutrients and minerals. Sometimes, requirements include unique needs, such as a specific amino acid or sterol to complete development or fuel a specific biochemical pathway. After paying the cost to acquire and process food input, grasshoppers then allocate remaining nutrients to fuel physiological and biochemical processes. This allocation process determines developmental rate, growth, survival, and reproductive output. Host plant quality varies seasonally, among years and among habitats. Toxic substances in plants may hinder nutrient acquisition by either slowing feeding rate, reducing digestibility, requiring detoxification, or otherwise making the diet suboptimal. Each of these effects reduces the availability of nutrients for other grasshopper needs. Investigators need to understand how variable plant nutritional quality affects central features of grasshopper biology and population dynamics. Managers must assess range quality for grasshoppers in addition to standard measures applied to the effects of livestock, wildlife, or other range activities. Information on plant quality for grasshoppers can then be used to forecast population changes.

A grasshopper does not typically encounter optimal food items in a normal day's foraging. To obtain needed nutrients, an individual grasshopper may sample a variety of leaves from a few to many plant species that vary in levels of each critical nutrient category (see IV.7). After grasshoppers locate and consume the best possible diet, how does that diet drive population dynamics of a particular species? Do different grasshopper species respond to nutrient availability in the same fashion? In this chapter, I also describe basic grasshopper responses to diets of different quality in order to provide a framework for assessing grasslands from the grasshopper's perspective. So, from a manager's perspective, a good sense of available food quality and quantity will provide some useful "rules of thumb" for assessing potential problems. What features can be factored into these decisions? Such insights will contribute to forecasting capabilities (see VI.2 and VII.14).

A General Framework to the Problem

Range grasshopper populations, as with many insect herbivores, often fluctuate in response to variable plant quality. As suggested in several comprehensive reviews (White 1978, 1984, 1993; Mattson and Haack 1987; Joern and Gaines 1990; Jones and Coleman 1991), nutrients often limit grasshopper populations, and any environmental condition that increases plant quality will increase population growth in insect herbivores. Environmental stress routinely causes plant quality to shift as plants respond to drought, temperature, nutrient availability, or tissue loss to feeding (herbivory) (Mattson and Haack 1987, Jones and Coleman 1991). Natural environments seemingly fluctuate as a matter of course and multiple stresses capable of altering plant quality abound (see IV.5).

Following initial arguments of White (1978, 1984), the link between plant quality and climatic variation may explain many of the statistical links between climatic variation and variability in grasshopper densities. Moderately stressed host plants exhibit increased plant quality in two ways: food quality goes up, and there is also an increase in the quantity of high-quality leaf material relative to grasshopper population densities. These two improvements in host material contribute to increased grasshopper densities. By explicitly including density dependence, I am extending White's framework.

Variation in plant quality results from many sources. Available soil nutrients and environmental stress (drought, for example) can significantly change plant quality (Levitt 1972, Mooney et al. 1991). Stress (broadly defined) can result in increased total-N (protein) (Mattson and Haack 1987), increased total soluble protein and free amino acids (Wisiol 1979, White 1984), or altered levels of energy-containing compounds, such as

total nonstructural carbohydrates (TNC) or free sugars like sucrose (Levitt 1972). Herbivore feeding can alter subsequent plant quality by forcing reallocation of mineral and energy resources within the plant (Coley et al. 1985, Bazzaz et al. 1987, Chapin et al. 1987, Mooney et al. 1991). Variable plant quality resulting from these combined effects significantly influences insect herbivore populations: As plant quality increases, insect populations increase (Mattson and Haack 1987, Berryman 1987, Joern and Gaines 1990, Jones and Coleman 1990). Growth, developmental rates, survival, and reproduction rates, or some combination of these demographic forces, vary according to these shifts in plant quality.

How Variable Is Plant Quality in Nature?

Range plants routinely undergo significant stresses from many sources, especially drought and herbivory (grazing animals). These stresses ultimately alter the nutritional plant quality available to grasshoppers. Thus, grasshoppers experience a wide range of "nutritional environments" within and among years. Many readily measured attributes contribute to food quality variation—plant species-specific differences, plant growth stage, or environmental conditions (especially water and nutrient availability, which affect physiological function). Similarly, different grasshopper species or developmental stages for a particular species often exhibit variable nutritional needs. Care is required when directly specifying quality based on simple plant chemical measures. However, direct measures of key plant chemical classes provide an unambiguous baseline for comparison.

Knowledge of nutritional requirements for dominant species at a site simplifies monitoring changes in plant quality to predict possible grasshopper responses. My examples will illustrate the main responses that can be expected for dominant nutritional classes. From a land manager's perspective, an estimate of shifts in plant quality may help when assessing range condition and how that condition is changing from the standpoint of feeding by both grasshoppers and cattle. Low-cost chemical assays exist to help managers assess plant quality on rangeland.

Total Nitrogen.—The amount of total nitrogen (g N per g dry green plant material) indicates protein availability: percent protein $\sim 6 \times$ (percent of total N). Total N varies significantly among plant species, seasonally and among years at a given site, while important differences are often observed among sites in the same year and season. Forbs typically exhibit higher total N levels than grasses, all else being equal. However, forbs also include many secondary compounds that may act as feeding deterrents or toxins. As a rule of thumb, 1 percent total N becomes a lower limit to support grasshopper growth and development satisfactorily, although notable exceptions exist (such as *Phoetaliotes nebrascensis)*. After starting at high levels ($\geq$ 4–5 percent total N) when growth just begins in spring, total N concentrations often drop to about 1 percent (or lower) in late July or early August for northern grasslands. A moderate rebound typically occurs in early September. However, in some years, when conditions are particularly favorable, total N may never drop to 1 percent. Also, certain plants may exhibit high N levels, and others, low concentrations. A grasshopper faces such variation as it searches for good food.

Total Nonstructural Carbohydrates (TNC).—These compounds represent the immediate products of recent photosynthesis and show a more irregular seasonal pattern than that observed for nitrogen. TNC represent an immediate energy source for grasshoppers. While carbohydrates affect grasshopper growth, the availability of proteins tends to be more significant in limiting it.

Total Free Sugars and Total Free Amino Acids.—These nutritional components change in ways similar to total N and TNC, respectively, and may be important as feeding cues as well as nutrients. Both can vary with environmental stress (see IV.5 and IV.7). The amino acid proline provides a good example. Proline can either provide a good source of amino acids or can be metabolized as an energy source. It often increases in plants under drought stress, presumably to aid plant osmoregulation (maintain water balance) (Wisiol 1979, Behmer and Joern 1994). Along with the common free sugar sucrose, proline significantly stimulates feeding in some grass-feeding grasshoppers during phases of their life cycle when nutritional resources are limited.

How Does Altered Host Plant Quality Affect Feeding?

Feeding includes searching for acceptable food, selecting foods from among several choices, and then digesting the food. The grasshopper actively controls each of these phases in the feeding cycle (for more details see IV.7).

Food intake provides resources for all subsequent physiological processes. In general, higher quality food leads to larger individual meals but lowered overall time spent feeding, increased time in the gut, and increased digestibility. Each individual grasshopper requires less total food when feeding on higher quality tissue, and high-quality plants lose less total tissue per grasshopper. However, individual plants vary in quality. Overall grasshopper feeding becomes context dependent. For example, a poor-quality host plant by itself may lose much leaf mass to support a grasshopper (it takes more tissue to provide adequate nutrients) but will not be fed upon as much when it grows alongside high-quality plants. Thus, potential loss to an individual plant shifts depending on the alternate plants available to the grasshopper.

Accumulating evidence suggests that most grasshoppers mix food to balance diets. Some species select from a great number of host plants. Grasshoppers that feed on multiple host plants often exhibit higher survival and fecundity (reproductive ability) than those fed single food plants. *Melanoplus sanguinipes*, for example, does not do nearly as well when fed either grass or forbs alone as when fed both grasses and forbs. In experiments with other grass-feeding grasshopper species, *M. sanguinipes* often surpasses other species in food gathering when grasses and forbs are present but loses if forbs are absent (Chase and Belovsky 1994). In a similar vein, some grasshoppers often mix turgid with wilted tissue of the same food plant, typically resulting in increased fecundity (Lewis 1984).

It appears that few host plants provide a completely balanced diet for most grasshopper species and that grasshoppers can adjust behaviorally to optimize diets (Simpson and Simpson 1990). Very few species exist that are truly specialists and feed on a single host plant species. If we can learn what is required for balanced

diets by economically important grasshopper species and remove that balance, then we may be able to manipulate plant communities to decrease grasshopper populations. In the case of *M. sanguinipes*, controlling densities of preferred forbs may prove important, both to alter individual growth and reproduction as well as to shift the competitive balance with other species.

How Does Plant Quality Affect Key Demographic Attributes?

Key demographic parameters, such as survival, fecundity, developmental rate, and growth, significantly respond to changes in plant quality. Poor-quality food results in poor demographic performance and vice versa (Bernays et al. 1974). Total food availability directly affects these factors (Mulkern 1967, Mattson and Haack 1987, Joern and Gaines 1990). From a grasshopper's viewpoint, plant quality surely includes both nutritional and defensive properties of the host plant.

Evidence indicates that different species of host plants influence fecundity (Pfadt 1949; Pickford 1958, 1962, 1966). For example, *Camnula pellucida* performed poorly (developmental rate, nymphal and adult survival, and fecundity) when fed native vegetation in Canada compared to spring and summer wheat (Pickford 1962). Egg production makes significant demands on the grasshopper's nutritional economy and depends significantly on protein and energy obtained from the diet. Nutrient stores cannot supply the reproductive process for long. *M. sanguinipes* laid few eggs when fed wheat seedlings low in nitrogen (Krishna and Thorsteinson 1972). Similarly, when *Locusta migratoria* females fed on low-protein diets, egg production dropped and terminal eggs were resorbed (McCaffery 1975). Similar results have been observed for other species. In addition, extreme drought often results in a decrease in the food's quality and quantity, decreasing reproduction in a number of grasshopper species. Such results become important for understanding grasshopper population dynamics, as reproductive changes can drive population change.

Fecundity in common range grasshoppers varies in response to both protein and carbohydrates. While lifespan has some effect on fecundity and is also dependent on food quality, total N significantly affects repro-

ductive output. Dramatic species differences exist. While these different patterns are yet unexplained, they should alert managers to the potential problem of generalizing results from a small set of species to all grasshopper species.

Grasshopper survivorship is sensitive to food plant quality. As with fecundity, species-specific survivorship varies according to host plant eaten (Pickford 1962, Mulkern 1967, Bailey and Mukerji 1976, Joern and Gaines 1990). For example, *A. deorum* lives longest in experiments with highest N-levels in the leaves of its primary food plant. To emphasize the importance of species-specific differences, *P. nebrascensis* exhibits the opposite response to plant quality as seen in *A. deorum.* Furthermore, in a third species, *M. sanguinipes*, total N only minimally affects survival. But *M. sanguinipes* requires a mixture of grasses and forbs, indicating that a varied diet is important for this species.

How Does Plant Quality Affect Spatial Distribution of Grasshoppers?

While grasshopper integrated pest management (IPM) is primarily concerned with overall densities, the distribution of grasshoppers in time and space offers important insights into grasshopper demographic responses. Often, individual patches of range reach very high grasshopper densities while most of the remaining range experiences low densities. It is not generally clear why these distributional patterns arise. Grasshoppers forage in a variable environment, with plant quality often changing over short distances. If some plant patches reach higher quality levels than others, local grasshopper densities may increase as individuals move into the patch and remain (Heidorn and Joern 1987). In typical rangeland situations, grasshoppers often move onto adjacent areas after haying, possibly in response to a significant removal of quality food material. However, because haying changes so many environmental features, reasons other than loss of available high-quality food may explain this movement.

Trap Strips as a Management Tool

It seems clear that any range management technique that increases plant quality in a patchy fashion may increase local grasshopper densities. By adding fertilizer to areas to enhance plant growth, land managers can expect increased grasshopper densities. While untested, a promising idea is to develop treatable trap strips by fertilizing sufficiently large patches to reduce overall densities elsewhere. If trap strips remained ungrazed, they would also provide superb nesting habitat for grassland birds and thereby further support control. Optimal spacing and size for these strips is not known, nor is the year-to-year dynamics of grasshopper populations on or near these proposed strips. For example, will grasshoppers lay more eggs leading to greater buildups? Will hot spots develop from such treatments? Will increased grasshopper density greatly reduce food on these trap strips, leading to movement away from the trap? Or will density-dependent mortality kick in and greatly reduce the infestation? Will bird predators seek out these high-density patches and greatly reduce numbers? While each of these issues hold promise or concern for grasshopper IPM, insufficient data currently exist to predict responses accurately. I feel, however, that clever managers will find ways to incorporate these approaches using trial-and-error techniques coupled with accurate records and thoughtful interpretations. While such manipulations have been poorly studied, I believe that they hold great practical promise for developing innovative grasshopper IPM programs.

Final Comments

My major take-home message in this section concerns how alteration of plant quality can affect grasshopper population processes. In quick summary, most host plants that are routinely consumed by grasshoppers vary significantly in nutritional quality, over any time or space scale that may interest land managers. Often, host plant quality responds directly to stresses induced by climatic variation. Moderate amounts of environmentally induced stress typically increase the quality of grasshopper food, especially with regard to protein.

In response to changing host plant quality, grasshoppers alter feeding patterns as well as allocation of assimilated food. All key demographic variables respond to altered plant quality, although managers must remember that all grasshopper species do not respond in the same fashion. Grasshopper IPM programs must be pegged to the amount of forage eaten by individual grasshoppers, the significance of these losses, and the number of grasshoppers that are eating relative to available forage. Grasshopper population processes become important only in the context of long-term issues: those programs that keep grasshopper populations at low levels will incur less forage loss over the long term. But the interaction is two sided and dynamic: variability in both host plant quality and grasshopper demographic responses interact to drive forage loss.

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