ANNUAL REVIEWS

Annual Review of Entomology

How Nutrients Mediate the Impacts of Global Change on Locust Outbreaks

Arianne J. Cease

School of Sustainability, School of Life Sciences, and Global Locust Initiative, Arizona State University, Tempe, Arizona, USA; email: acease@asu.edu

Annu. Rev. Entomol. 2024. 69:527–50

The *Annual Review of Entomology* is online at ento.annualreviews.org

https://doi.org/10.1146/annurev-ento-120220-110415

Keywords

nitrogen, protein, carbohydrate, grasshopper, Orthoptera, plant–insect interactions, nutrient limitation

Abstract

Locusts are grasshoppers that can migrate en masse and devastate food security. Plant nutrient content is a key variable influencing population dynamics, but the relationship is not straightforward. For an herbivore, plant quality depends not only on the balance of nutrients and antinutrients in plant tissues, which is influenced by land use and climate change, but also on the nutritional state and demands of the herbivore, as well as its capacity to extract nutrients from host plants. In contrast to the concept of a positive relationship between nitrogen or protein concentration and herbivore performance, a five-decade review of lab and field studies indicates that equating plant N to plant quality is misleading because grasshoppers respond negatively or neutrally to increasing plant N just as often as they respond positively. For locusts specifically, low-N environments are actually beneficial because they supply high energy rates that support migration. Therefore, intensive land use, such as continuous grazing or cropping, and elevated ambient CO_2 levels that decrease the protein:carbohydrate ratios of plants are predicted to broadly promote locust outbreaks.

1. BACKGROUND

Locust: a type of grasshopper (Acrididae) that exhibits a gregarious phenotype in response to high density and, at some point, migrates en masse

In an era with increasing recognition of anthropogenic impacts on insects, locusts remain mostly categorized as driven by precipitation patterns. However, locusts and grasshoppers also respond quickly to land-use change, not only in numbers but also through altered physiology and behavior, which often corresponds with variation in nutrient availability (80). Furthermore, increased atmospheric CO_2 has been correlated with grasshopper population dynamics via shifts in host plant carbon and nitrogen balance (144). Understanding how anthropogenic factors influence locust and grasshopper outbreaks can open the door to powerful alternative management approaches and decrease the devastating impacts of these outbreaks on livelihoods (153).

Locusts are grasshoppers in the family Acrididae that develop into gregarious and swarming phenotypes when at high density (34, 99). This capacity to become a gregarious locust has evolved independently multiple times (121). Thus, the mechanistic pathways that promote a shift from solitarious to gregarious phenotypes (or vice versa) vary among locust species. The suite of traits that differ between the forms is also species specific and may include aspects of behavior, color, morphology, and physiology. However, behavioral patterns that typify all gregarious locusts include increased activity and attraction to conspecifics—the combination of which sometimes leads to mass migration of marching nymphs or swarms of adults (98). Grasshoppers that readily exhibit extreme versions of these characteristics and require multination locust commissions to manage, such as the desert locust (*Schistocerca gregaria*), are readily classified as locusts. Other species that exhibit less frequent or extreme behavioral shifts, smaller swarms, and shorter migrations fall into a gray area and are sometimes referred to as nonmodel locusts (121). At low densities, grasshoppers and locusts are recognized as important components of ecosystems. They are often the dominant herbivore in grasslands (19) and support many ecosystem functions (11). However, when these insects reach outbreak levels, they wreak havoc on agriculture and livelihoods, even more so if they are migratory (22, 84, 153).

Many factors influence grasshopper and locust population dynamics, including abiotic factors (temperature, precipitation), food availability and quality, habitat availability and structure, symbionts, competitors, predators, pathogens, and interactions among these factors (27, 66). Most locust species live in dryland ecosystems where bottom-up regulation tends to be dominant (77). In addition, field studies suggest that predators have limited impacts on outbreaking locust populations (40); similarly, human consumption of outbreaking locusts can improve food security but is unlikely to suppress regional populations due to the sheer scale of locust plagues (115). Beyond the availability of green vegetation, plant nutrients play a significant role in regulating grasshopper population dynamics (23, 144). Research over the past decade has revealed connections between low-N environments and locust outbreaks (23, 26, 78, 80, 82, 83, 129, 130, 134, 146). Most plant N is found in the form of protein, an excess of which can limit consumption of other key macronutrients, including digestible carbohydrates (31). For locusts who are long-distance migrators with high metabolism, low-N environments can support carbohydrate-loading and heightened survival, egg production, and migration (25, 82, 129, 131). However, the relationships between plant nutrients and locusts can vary through ontogeny and with field conditions (130).

This review focuses on how macronutrients (protein and digestible carbohydrates) mediate the effects of land use and climate change on locust and grasshopper outbreaks. For this review, because all species considered to be locusts are scattered taxonomically throughout the family Acrididae, including studies on grasshoppers more generally provides additional insights for outbreaking species, as well as for conserving grasshopper biodiversity. Grasshoppers provide important ecosystem functions, such as nutrient cycling and being a food source for birds and mammals (27). Because all locusts are grasshoppers, the term grasshopper is sometimes used in this review to refer to both broadly.

2. FORAGING AND NUTRITIONAL ECOLOGY FRAMEWORKS

Several frameworks and theories have been developed to guide understanding of herbivore foraging decisions and outcomes.

Foraging theory has its roots in optimization and evolution, typically focused on a single currency, such as energy or nitrogen (62, 117). For example, Optimal Foraging Theory centers total energy as a constraint (62). Single-currency frameworks can work well in environments where a single dietary constituent is almost always limiting and the relationship between the food component and herbivore growth remains linear across the concentrations measured in nature. As ecological research progressed and revealed widespread limitation of primary production in ecosystems by biologically available nitrogen and/or phosphorus, these elements, especially nitrogen, were posited to widely limit herbivore growth as well as plant growth (145). The use of plant quality as a proxy for nitrogen content (and sometimes content of other nutrients, such as phosphorus) is ubiquitous in ecology today. Unfortunately, the single-currency approach and positive linear relationship between plant N and herbivore performance implied in the term plant quality are fraught with challenges when applied to herbivory. For an herbivore, plant quality depends not only on the balance of nutrients and antinutrients in plant tissues, but also on the nutritional state and demands of the herbivore (see Section 3.1), as well as its capacity to extract nutrients from host plants (108, 110). Moreover, these relationships are typically nonlinear, so designating simple linear relationships between plant quality and plant N is misleading.

The field of nutritional ecology was developed to test the complex interactions of different nutrients and deterrents in food items on animal performance (109, 110). Two complementary frameworks emphasize the balance of dietary components: Ecological Stoichiometry (ES) (125) and the Geometric Framework for Nutrition (GFN) (120). ES highlights elements and, as such, can consider nutrients flowing through multiple trophic levels and between abiotic and biotic components of landscapes and ecosystems, making it a powerful tool for multilevel ecological research. However, ES has limitations for the study of organismal biology. For example, plant C content is not a good predictor of digestible carbohydrates available to herbivores, since much of plant C is often in the form of undigestible cellulose. Plant N is roughly correlated with protein. Thus, plant C:N ratios can give a reasonable estimate of plant protein but not of nonprotein energy (carbohydrates and lipids). Conversely, while the GFN has limitations for studying ecosystem ecology because macronutrients are not conserved in a single form throughout ecosystems (unlike elements), it is an excellent framework for organismal biology because it focuses on nutrient currencies relevant to focal organisms (123).

Since it was first used in an empirical study in 1993 (106), the GFN has developed into a framework that can bridge foraging theory and nutritional ecology by considering foraging strategy in a multidimensional nutritional space and measuring performance and fitness variables (109). The amount of nutrients an animal needs to eat to reach its optimal mixture is referred to as the intake target (IT). If complementary food sources are available, then an herbivore can eat selectively among plants and plant tissues, representing nutritional rails, to balance multiple nutrients and achieve its IT (**Figure 1*a***). If their nutritional landscape only includes plants distant from their IT (**Figure 1*b–c***), then performance will decline (**Figure 1*d***). An animal's IT can vary based on many factors (see Section 3.1).

The relative protein and carbohydrate requirements of locusts, and their capacity to achieve their IT by eating plants in their environment, have profound implications for their growth (23); survival (23, 83); reproduction (64, 65, 82); and, ultimately, population dynamics (23, 146) and development of migratory swarms (25, 81, 129, 131). The GFN is summarized in an earlier *Annual Review of Entomology* article (8) and covered in depth in a book by its developers (120).

Ecological Stoichiometry (ES): considers how the balance of energy and elements influences living systems, in particular, organisms and their interactions in ecosystems

Geometric Framework for Nutrition (GFN): a state-space modeling approach that explores how an animal simultaneously regulates the intake of multiple nutrients

Intake target (IT): the amount of nutrients that an animal needs to ingest to reach its optimal blend

Nutritional rail: a trajectory, starting at the origin in nutrient space, that represents a food's balance of nutrients

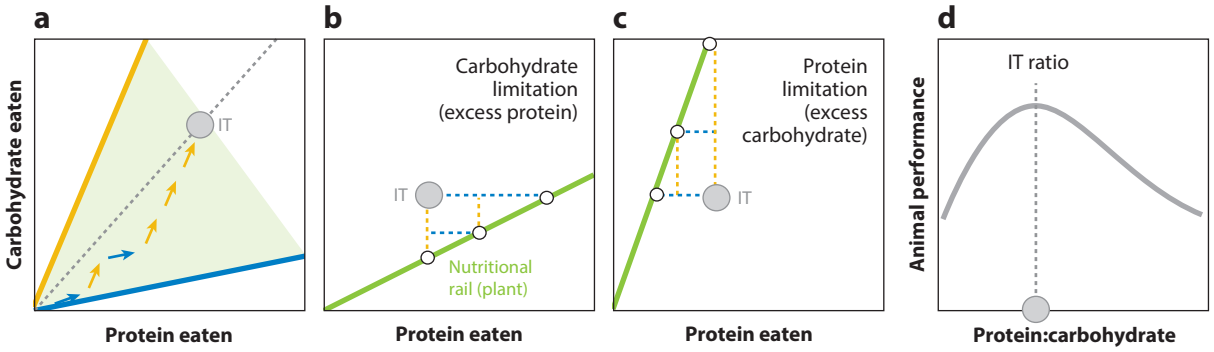

Figure 1

Different scenarios explained using the Geometric Framework for Nutrition (GFN) (106, 120). (*a*) A grasshopper eats between two complementary plants (nutritional rails) to achieve its intake target (IT) (*gray circle*). (*b*,*c*) A grasshopper faced with a nutritionally imbalanced landscape where it cannot reach its IT. In these scenarios, an animal has three choices: overeat the excess nutrient to reach its target for the limited nutrient, undereat the limited nutrient, or a compromise between the two. (*d*) Peak performance (growth, survival, reproduction) typically occurs when animals eat a ratio of protein to carbohydrate that aligns with their IT. Figure adapted with permission from Reference 8.

This review explores how land use and climate change impact locust outbreaks through changes in plant macronutrients using this nutritional framework as the theoretical basis (**Figure 2**).

3. NUTRIENT DEMANDS AND ACQUISITION: WHAT FACTORS INFLUENCE GRASSHOPPER MACRONUTRIENT DEMANDS AND CAPACITY TO EXTRACT NUTRIENTS FROM PLANTS?

3.1. How Abiotic and Biotic Factors Influence Grasshopper Macronutrient Intake Targets

For chewing herbivores eating mainly leaves, foraging is highly attuned to balancing protein with carbohydrates (nonprotein energy) because these macronutrients make up the vast majority of nutrients in their diet, and plant sources rarely match the balance needed (120). For pollinators

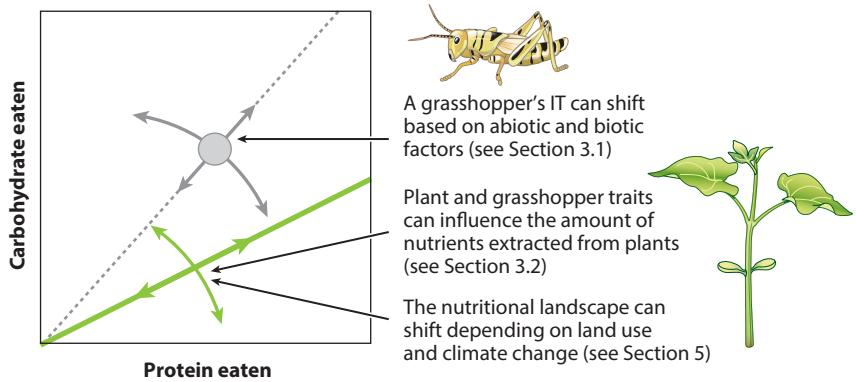

Figure 2

Many biotic and abiotic factors and interactions can shift a grasshopper's intake target (IT) and the nutritional rails available to the insect. Understanding these interactions can aid in predicting grasshopper population dynamics and advancing sustainable management tools.

eating pollen, balancing protein:lipid ratios is critical (137). Herbivores that are restricted to diets that diverge from their required protein-to-nonprotein energy balance can suffer deficits in growth rate, development time, body mass, reproduction, and survival (8, 120). ITs can be determined by giving an individual two complementary diets, for example, one with a low and one with a high protein:carbohydrate (p:c) ratio (**Figure 1*a***). Grasshoppers tend to be tight regulators, and a given population will consistently select the same ratio. Most studies have measured ITs in final-instar juveniles or adult grasshoppers and show interspecific variation spanning from the most protein-biased 1p:0.6c ratio (*Melanoplus femurrubrum*) (9) to the most carbohydrate-biased 1p:2.5c ratio (*Schistocerca cancellata*) (130). There can even be substantial variation within a genus. Final-instar *Melanoplus* nymphs from the same habitat but different species select unique ITs ranging from 1p:0.6c to 1p:1.6c (9). A given population in each environment tends to maintain a consistent IT for a given developmental stage. For example, final (fifth)-instar *Oedaleus senegalensis* in millet–groundnut cropping systems in Senegal consistently select an IT of approximately 1p:1.6c across different years (81, 83). However, while a species' IT reflects its life history strategy and can remain consistent, an IT is not a set feature of a species and varies throughout ontogeny and in response to environmental factors. Known impacts of abiotic and biotic factors on the protein and carbohydrate intake of grasshoppers are summarized in **Table 1**.

For all consumers, protein is the main building block for growing tissues, and carbohydrates (and/or lipids) are the primary energy fuel. Vertebrate studies suggest that protein requirements are generally higher in early ontogeny, matching higher specific growth rates (for a review, see 130). A study of South American locusts (*S. cancellata*) measuring ITs for each developmental stage from hatchlings to adults demonstrated that mass-specific protein intake decreases in a predictable way with development and decreased growth rate, representing a fourfold decrease

Table 1 Summary of abiotic and biotic factors that can influence protein and carbohydrate intake in grasshoppers

Factor	Effects on grasshopper macronutrient intake
Growth	Protein consumption decreases up to 70% from hatchling to young adult, while carbohydrate consumption stays similar, shifting IT from 1p:0.8c to 1p:2.5c (130)
Reproduction	Not tested, but adult females likely defend a protein target, especially protein matching the amino acid profile of Vg (52) to support egg development (64, 65)
Difference between lab and field	Up to 50–90% higher carbohydrate consumption rates in locusts collected from field-marching bands relative to sedentary lab-reared nymphs, while protein consumption is similar, shifting IT from 1p:1.2c to 1p:2c (130)
Migration	For 2 h of flight, up to 30% carbohydrate intake increase and 10% protein increase, shifting IT from 1p:1.08c to 1p:1.26c (107)
Predation	For juveniles, up to 25% increase in protein and 45% increase in carbohydrate intake over 5 weeks, shifting IT from 1p:1.3c to 1p:1.5c (53); up to 73% decrease in protein and 132% increase in carbohydrate intake over 3 days, shifting IT from 1p:0.4c to 1p:3.5c (89)
Pathogens and immune response	In *Metarhizium*-infected locusts, up to 7% decrease in protein and 8% increase in carbohydrate, shifting IT from 1p:0.89c to 1p:1.04c (47)
Water	With no water, up to 70% decrease in protein and 55% decrease in carbohydrate consumption over 10 days, shifting IT from 1p:1.4c to 1p:2.3c (R.P. Overson, J.K. Brosemann, R.H. Farington, M. Diaz and A.J. Cease, unpublished data)
Temperature	For juveniles, up to a 30% increase in carbohydrate and 50% increase in protein intake over a 6°C increase (32°C to 38°C) for 6 days (93), and up to a 4% increase in carbohydrate and 30% increase in protein intake over a 10°C increase (25°C to 35°C) over 5 weeks, shifting IT from 1p:1.35c to 1p:1.06c (116); further studies are needed on adults

Abbreviations: IT, intake target; p:c, protein:carbohydrate; Vg, vitellogenin.

in mass-specific protein consumption (130). Comparing the locust data with data on a variety of taxa (fish, rats, chickens, pigs, cats, caribou, and dairy cattle) reveals a common pattern of older, larger animals consuming proportionally less protein. Furthermore, comparison of several distinct locust populations indicates that the range of mass-specific protein consumption remains consistent for a given developmental stage, regardless of substantial environmental variation (26, 129, 130). Therefore, for juvenile grasshoppers, protein intake is likely to correlate closely with growth and decline with age.

Adult female grasshoppers likely increase protein intake to support egg production, similar to fast-growing juveniles, but the extent to which their ITs might shift has not been tested. Because insect eggs are typically half egg yolk protein and half lipid, it is plausible that carbohydrate-rich diets might be favored to synthesize lipid (128), which is more calorically dense than protein or carbohydrate. Studies comparing reproductive responses of three grasshopper species to factorial variations in nitrogen and carbohydrate concentrations showed that nitrogen concentration has the most significant impact on reproductive events, with egg production peaking at approximately 4–5% N for all species and dropping off at lower and higher levels (64, 65). Carbohydrate concentrations weakly affect egg production and exert different patterns for the three different species tested (*Melanoplus sanguinipes*, *Phoetaliotes nebrascensis*, and *Ageneotettix deorum*) (64, 65). Extensive research on reproduction in eastern lubber grasshoppers (*Romalea microptera*) showed that adult females accumulate hexameric storage proteins and the egg yolk protein vitellogenin (Vg) preceding egg production (51). Both of these protein accumulations, and subsequent egg production, are promoted by eating high-quality protein that has a mix of amino acids matching that of Vg (52). Thus, foraging for high-quality protein is likely prioritized for all female grasshoppers to support egg production, but the relative balance with dietary carbohydrates may be species and environment specific. A future area for research will be exploring how environment might shape egg nutrients and subsequent viability. For instance, eggs developing in hot, arid environments might fare better with higher lipid contents, in which case mothers with access to energy-rich diets could produce more viable eggs.

Carbohydrates and lipids are the primary energy fuels for consumers, and higher activity levels increase intake. It is plausible that carbohydrate intake could scale with growth rate similarly to protein intake, but careful measurement of locust ITs across ontogeny indicates that mass-specific carbohydrate intake is relatively invariant in a lab setting (130). In contrast, age-matched field populations had similar protein intake but nearly double the carbohydrate intake relative to the sedentary lab population. These field locusts were collected from active marching bands and had approximately 23% higher mass-specific resting oxygen consumption than lab-reared nymphs, partially explaining their higher carbohydrate intake. Insect flight is very energetically costly (142) and can further increase carbohydrate demands. For the first 15–30 min of flight, locusts use carbohydrates; for longer flights, they rely on lipid stores synthesized from ingested carbohydrates (7). Indeed, flight increases locust carbohydrate consumption at triple the rate of protein consumption (107), and high carbohydrate consumption increases lipid storage and promotes migratory flight (128, 129, 131).

The General Stress Paradigm (GSP) (54) predicts that exposure to predators will increase stress hormones in prey, in turn elevating gluconeogenesis and respiration and increasing carbohydrate use for maintenance rather than production of new tissues. Consequently, nutrients associated with structural tissues, such as nitrogen and phosphorus, will be excreted at higher rates, body tissues will have higher ratios of carbon to nitrogen and phosphorus levels, and the stressed prey will seek carbohydrate-rich foods. Indeed, chronic exposure of *M. femurrubrum* grasshoppers to hunting spiders (*Pisaurina mira*) increases metabolic rate and relative carbohydrate intake under moderate (but not high) temperatures, which alters local ecosystem carbon and nitrogen

transfer rates back to the soil (53, 116). Furthermore, in response to predation risk, feeding *M. femurrubrum* grasshoppers will flee sooner if they are eating protein-rich diets than if they are eating carbohydrate-rich diets (89), suggesting that grasshoppers under threat of predation are more likely to be carbohydrate limited in nature. However, exposure of three Ozark glade grasshopper species to collared lizards revealed that only one of the species responds as predicted by the GSP, with increased body carbon:nitrogen ratios (111), indicating that there are species-specific differences in responses to predation stress. More studies are needed to understand how broadly spread the pattern of stress inducing carbohydrate intake might be across taxa and environments, as well as the duration and magnitude of this impact.

Macronutrient balance additionally affects insect immune function and susceptibility to pathogens, including those used as biopesticides (48, 101, 124). This underscores the importance of understanding the interactions between nutrition and susceptibility to widely used biopesticides, such as *Metarhizium* spp., to improve the efficacy of these pesticides (152). Increased protein intake can support host immune responses, but carbohydrate-biased diets may starve pathogens of protein for growth and reproduction (47). Two studies have explored these hypotheses. Australian plague locusts (*Chortoicetes terminifera*) (47), but not migratory grasshoppers (*M. sanguinipes*) (151), shift to more carbohydrate-biased ITs when infected with fungal *Metarhizium* spp. *Chortoicetes terminifera* locusts that eat higher-protein diets are more susceptible to *Metarhizium*. Interestingly, *M. sanguinipes* grasshoppers confer a benefit when eating either carbohydrate- or protein-biased diets when infected; grasshoppers eating the balanced 1p:1c diet die the earliest, and their cadavers support much greater fungal sporulation (151). Additional research is needed to understand if and how species, age, and/or locust phase (solitarious versus gregarious) influences the interactive effects of diet and immune response on pathogen–host outcomes.

Most locust species live in dryland ecosystems where water can be limiting. Australian plague locusts (*C. terminifera*) regulate water as a third nutrient rail, along with protein and carbohydrate, to a ratio of 1p:1.13c:13.2 H_2O (30). When locusts have no access to water, *C. terminifera* survival increases from 18 to 30 days when they are fed carbohydrate-biased diets (R.P. Overson, J.K. Brosemann, R.H. Farington, M. Diaz and A.J. Cease, unpublished data), potentially because dehydrated locusts build up more nitrogenous waste from higher-protein diets, which can be deleterious. When able to self-select their IT, locusts without water decrease protein consumption to a larger extent than carbohydrate consumption, shifting to an even more carbohydrate-biased IT. How water shapes nutrient balance and performance in different environments is an important area for future research.

How insects respond physiologically to heat remains poorly understood (46). Because metabolic rates increase exponentially with temperature (44), carbohydrate intake may be expected to increase to fuel higher energetic demands. However, higher temperatures also increase growth rates for developing insects, at least in part due to improved digestion rates (49, 147), and faster growth rates increase protein consumption (130). Grasshopper studies have shown mixed results. For migratory locusts (*Locusta migratoria*) measured over a single stadium (approximately 6 days), temperatures increasing from 26°C to 38°C nearly triples growth rate linearly, but protein and carbohydrate intake remain constant from 26°C to 32°C, after which intake of both macronutrients increase approximately 30% for carbohydrate and 50% for protein between 32°C and 38°C (93). For the red-legged grasshopper (*M. femurrubrum*) measured over 5 weeks of development, the IT remains similar, but total consumption increases, from 15°C to 25°C (116). However, from 25°C to 35°C, carbohydrate consumption remains similar, but protein consumption increases 30%, corresponding with a dramatic increase in growth and development rate over the 5-week period. These studies suggest that increasing temperatures over shorter durations or lower ranges are unlikely to shift ITs, but temperature increases over higher ranges, moving toward a

species' thermal optimum, and over longer durations may increase protein consumption faster than carbohydrate intake to accommodate faster somatic growth. How temperature–nutrient interactions affect field populations more broadly or adults specifically is an open question.

3.2. How Plant and Grasshopper Traits Influence Nutrient Extraction from Plants and Are Affected by Temperature

Many factors can influence macronutrient extraction from plants, including physical and chemical properties. Grasshoppers likely evolved from polyphagous ancestors with adaptations to tolerate many plant secondary compounds (12). The Sahelian tree locust (*Anacridium melanorhodon*) binds certain phenols in its cuticle and has higher growth and survival when these phenols are in its diet (13, 14). Gregarious desert locusts (*S. gregaria*) gain an antipredator benefit from eating toxic host plants (*Hyoscyamus muticus*); solitarious locusts avoid eating *Hyoscyamus* (127). However, plant secondary compounds can still be deleterious, and grass feeders who have lost some of the protective characteristics may be more vulnerable (12). Tannic acid (TA) is an effective feeding deterrent for the graminivorous migratory locust (*L. migratoria*), particularly when added to protein-poor foods, potentially because more TA is unbound and interacting with mouthpart taste receptors in these foods (10). TA binds to protein and reduces nitrogen utilization efficiency, especially for locusts eating protein-biased diets, although its impacts on performance are minimal if locusts can balance macronutrient intake (119). Future studies should expand this research to examine other allelochemicals common in plants across locust habitats, such as alkaloids, terpenoids, and saponins.

The physical properties of leaves can reduce the capacity of locusts to access and assimilate nutrients, and this relationship can vary based on locust developmental stage and plant species. Older Australian plague locust (*C. terminifera*) nymphs eating two grasses with the same protein and carbohydrate content (*Dactyloctenium radulans* and *Astrebla lappacea*) have decreased carbohydrate assimilation, growth, and survival when eating *A. lappacea* (31). These differences are not found when plants were lyophilized and ground, indicating that plant cell walls are likely a physical barrier to carbohydrate extraction in some plants. Younger locusts perform equally well on both grasses, potentially because they can chew leaves into smaller particles. Overall, tougher leaves slow consumption and gut passage rates, decreasing growth rate and survival, although fractal properties of dried grass may make carbohydrates more accessible when chewed by locusts (32). For softer leaves, such as young cereal crop seedlings, intact leaves do not decrease locust growth; instead, locusts perform better when eating intact turgid wheat (*Triticum aestivum*) than when eating dried, ground wheat leaves (20).

Grasshoppers can postingestively regulate assimilation and nutrient use to a certain extent. Migratory locust (*L. migratoria*) nymphs use ingested protein and carbohydrate differently when feeding on different amounts. On protein-rich diets, more nitrogen is excreted as uric acid (150). Eating excess carbohydrate increases CO_2 production (149, 150), likely due to converting carbohydrate to lipid—a process that elevates the ratio of CO_2 produced to O_2 consumed above 1 (128). Populations of migratory grasshoppers (*M. sanguinipes*) at higher latitudes (Alaska) achieve faster growth rates than temperate populations (Idaho) through increased assimilation and retention of dietary nitrogen (41), which is presumably an adaptation to allow them to grow quickly during short summers. Migratory locusts (*L. migratoria*) increase gastrointestinal tract size in response to diets with a surplus of protein or those diluted with cellulose (28, 105). These larger guts increase total macronutrient absorption up to 30% but do not affect relative absorption of protein or carbohydrate (28). Research on the locust gut microbiome is limited (75), but microbial community shifts in response to host plants likely influence digestion (139) and will be an important area for future nutritional ecology research.

Temperature has many interactive effects on digestion and nutrient assimilation (33). Higher temperatures (40°C) improve digestion rates and are predicted to trigger range expansion in outbreaking South American locusts (*S. cancellata*) (147). Fittingly, migratory locusts (*L. migratoria*) select higher temperatures (38°C) to maximize growth rates, even at the expense of efficient nutrient use (93). In addition to increasing digestion rates, locusts can choose microclimates to achieve nutritional homeostasis based on locust and plant species–specific interactions. For migratory locusts (*L. migratoria*) eating wheat (*T. aestivum*), higher temperatures support faster digestion rates but do not change relative absorption of macronutrients (29). In contrast, when eating kangaroo grass (*Themeda triandra*), migratory locusts absorb carbohydrate with a higher efficiency at 32°C and protein at 38°C—locusts can learn this relationship and use it to redress a nutritional imbalance (29)! There are likely myriad plant–locust species-specific nutritional interactions altered by temperature that have yet to be uncovered.

In summary, the lab analyses used to measure plant nutrient content do not necessarily reveal what a given herbivore is able to extract. Nevertheless, measuring nutrient contents in plants to construct a nutritional landscape remains an important foundation for estimating the range of nutritional rails available to grasshoppers and is often well correlated with grasshopper preference and abundance (83).

4. LAB AND FIELD PATTERNS: ARE LOCUSTS LIMITED OR PROMOTED BY LOW PLANT NITROGEN?

The sections above highlight that macronutrient demands and acquisition can be highly variable for grasshoppers eating different plants. How does this translate to patterns found in lab and field studies? To address this question, I queried Scopus for publications using the following keywords: locust, grasshopper, nitrogen, protein, and carbohydrate (see **Supplemental Table 1** for more details). Thus, one limitation of this literature search is that it did not capture articles written in languages other than English. Of these publications, approximately 60 measured grasshopper responses to plant nitrogen, protein, and/or digestible carbohydrate content. I summarize descriptions of the studies and grasshopper responses by grasshopper species in **Supplemental Table 1**. For each study, I then categorized each grasshopper species response (survival, growth, reproduction, food selection, field distribution) as being positive, neutral, or negative in relation to increasing plant nitrogen, protein, and/or p:c content (**Figure 3**). There were 42 responses reported for lab studies and 106 reported for field studies. Species are listed in **Table 2**.

Supplemental Material >

In aggregate, the studies show a variety of responses (**Figure 3**). Some species, such as the grasshopper *A. deorum*, respond negatively, neutrally, or positively based on the plant consumed, as well as other environmental contexts. Similarly, results from field abundance surveys find that grasshopper populations are negatively, positively, or not at all correlated with plant N content, with multiple grasshopper species spanning two or three correlation types across studies.

Most results from lab-based studies (defined as grasshoppers lab reared for at least one generation, including eggs incubated and hatched in a laboratory) report a positive or neutral relationship between plant N and grasshopper response—52% and 29% of responses reported for lab studies, respectively. Growth and development are the most measured variables for lab-reared grasshoppers; the vast majority of these studies show positive or neutral effects of high plant N ($P = 0.02$). Younger juveniles require more protein relative to older individuals (130), and lab populations require less carbohydrate relative to field populations (80, 130); therefore, studies using lab-reared, early instar grasshoppers are more likely to find that higher-N plants increase grasshopper growth. Despite the positive effects of increasing plant N on grasshopper growth in lab experiments, some authors conclude that low plant N imposes no relevant constraint on field populations based on comparing experimental plants with those found in the grasshoppers' environments (15). Results

	Lab studies				Field studies			
	Positive	**No effect**	**Negative**	ChiSq	**Positive**	**No effect**	**Negative**	ChiSq
Survival	3 Barakat et al. (2015), 3 van Huis et al. (2008), 13 Bownes et al. (2013a), 29 Das et al. (2012) **4 reports**	12 Berner et al. (2005) **1 report**	13 Bownes et al. (2013b), 24 Brosemann et al. (2023), 24 Clissold et al. (2006), 29 Das et al. (2012) **4 reports**	 P = 0.37 N = 8	4 Joern & Mole (2005), 30 Trisnawati et al. (2015) **2 reports**	4 Branson (2006), 10 Zhu et al. (2019), 18 Zhang & Fielding (2011), 20 Ritchie & Tilman (1993), 22 Asshoff & Hättenschwiler (2005), 23 Ritchie & Tilman (1993), 23 Joern & Mole (2005), 28 Ritchie & Tilman (1993), 24 Lawton et al. (2023), 27 Le Gall et al. (2020a) **10 reports**	4 Joern & Mole (2005), 10 Zhu et al. (2019), 26 Qin et al. (2019), 26 Cease et al. (2012), 27 Le Gall et al. (2020a) **5 reports**	 P = 0.06 N = 17
Growth and/or development	3 Barakat et al. (2015), 3 van Huis et al. (2008), 5 Franzke & Reinhold (2011), 6 Rode et al. (2017), 12 Berner et al. (2005), 13 Bownes et al. (2013a), 14 Mariottini et al. (2019), 19 Johnson & Lincoln 1991, 19 Johnson & Lincoln (1990), 21 Hinks & Erlandson 1995, 21 Hinks et al. (1991), 25 Webb et al. 1998), 29 Das et al. (2012) **13 reports**	1 Nabity et al. 2012, 13 Bownes et al. (2013a), 14 Mariottini et al. (2019), 21 Johnson & Lincoln (1990), 21 Barbehenn et al. (2004) **5 reports**	24 Brosemann et al. (2023), 24 Clissold et al. (2006), 29 Das et al. (2012) **3 reports**	 **P = 0.02 N = 21**	20 Strengbom et al. (2008), 22 Asshoff & Hättenschwiler (2005), 30 Trisnawati et al. (2015), 31 Kaspari et al. (2022), 31 Ritchie (2000) **5 reports**	4 Joern & Mole (2005), 6 Rode et al. (2017), 18 Zhang & Fielding (2011), 22 Asshoff & Hättenschwiler (2005), 23 Joern & Mole (2005), 24 Lawton et al. (2023), 27 Le Gall et al. (2022), 30 Trisnawati et al. (2015), 31 Ritchie (2000) **9 reports**	2 Talal et al. (2020), 10 Zhu et al. (2019), 26 Qin et al. (2019), 26 Cease et al. (2017), 26 Cease et al. (2012), 31 Kaspari et al. (2022) **7 reports**	 P = 0.56 N = 21
Reproduction	3 van Huis et al. (2008), 5 Franzke & Reinhold (2011), 13 Bownes et al. (2013a) **3 reports**	– **0 reports**	– **0 reports**	**P = 0.05 N = 3**	4 Branson (2006), 22 Asshoff & Hättenschwiler (2005) **2 reports**	18 Zhang & Fielding (2011), 27 Le Gall et al. (2022) **2 reports**	27 Le Gall et al. (2020a) **1 report**	 P = 0.82 N = 5
Host plant selection	12 Berner et al. (2005), 21 Hinks et al. (1991) **2 reports**	14 Mariottini et al. (2019), 19 (Johnson & Lincoln (1990), 21 Johnson & Lincoln (1990), 21 Barbehenn et al. (2004) **4 reports**	24 Brosemann et al. (2023) **1 report**	 P = 0.37 N = 7	4 Heidorn & Joern (1987), 9 Zhu et al. (2020), 14 Amadio et al. (2020), 31 Ibanez et al. (2017), 31 Sparks & Cebrian (2015) **5 reports**	16 Jonas & Joern (2008), 27 Le Gall et al. (2022) **2 reports**	2 Talal et al. (2020), 10 Zhu et al. (2020), 26 Qin et al. (2019), 26 Cease et al. (2012), 27 Le Gall et al. (2022), 31 Ibanez et al. (2017) **6 reports**	 P = 0.37 N = 13
Nutrient extraction from plants, or nutrient selection post–plant feeding	– **0 reports**	6 Fielding et al. (2013), 18 Fielding et al. (2013) **2 reports**	– **0 reports**	 P = 0.14 N = 2	– **0 reports**	6 Fielding et al. (2013), 7 Abbas et al. (2014), 18 (Fielding et al. (2013), 21 Zembrzuski et al. (2021), 24 Lawton et al. (2021) **5 reports**	2 Cease et al. (2023), 2 Talal et al. (2020), 7 Abbas et al. (2014), 24 Lawton et al. (2023) **4 reports**	 P = 0.10 N = 9
Abundance (field surveys)	– Not applicable	– Not applicable	– Not applicable	–	3 Trisnawati et al. (2015), 4 Ozment et al. (2021), 8 Torrence (1975), 9 Zhu et al. (2020), 11 Heidorn & Joern (1987), 15 Torrence (1975), 20 Ozment et al. (2021), 23 Heidorn & Joern (1987), 30 Trisnawati et al. (2015), 31 Ozment et al. (2021), 31 Heidorn & Joern (1987), 31 Welti et al. (2020b), 31 Welti et al. (2020a), 31 Sparks & Cebrian (2015), 31 Hess & Beck (2014), 31 Joern et al. (2012), 31 Loaiza et al. (2011), 31 Ritchie (2000) **18 reports**	4 Heidorn & Joern (1987), 16 Jonas & Joern (2008), 17 Jonas & Joern (2008), 23 Ozment et al. (2021), 31 Heidorn & Joern (1987), 27 Le Gall et al. (2021), 31 Lenhart et al. (2015) **7 reports**	10 Zhu et al. (2020), 10 Zhu et al. (2019), 16 Ozment et al. (2021), 17 Ozment et al. (2021), 20 Torrence (1975), 23 Jonas & Joern (2008), 24 Lawton et al. (2020), 26 Cease et al. (2012), 27 Le Gall et al. (2022), 27 Le Gall et al. (2021), 27 Le Gall et al. (2020b), 27 Word et al. (2019), 31 Hassan et al. (2021), 31 Hendriks et al. (2013), 31 Ritchie (2000) **16 reports**	 P = 0.08 N = 41
Total reports	**22 reports**	**12 reports**	**6 reports**	 **P = 0.2 N = 42**	**32 reports**	**35 reports**	**39 reports**	 P = 0.71 N = 106

(Caption appears on following page)

Figure 3 (*Figure appears on preceding page*)

How does increasing plant N affect grasshoppers? This figure summarizes a survey of studies looking at the effects of increasing plant nitrogen, protein, and/or protein:carbohydrate content on grasshopper responses. For additional details on these studies, see **Supplemental Table 1**. Data are listed as a species number (see **Table 3**), followed by the reference. Each paper may be represented more than once if the study tested multiple species or multiple responses for a single species. Studies using grasshoppers that had been reared in the lab for at least one generation were classified as lab (*left columns*), whereas studies using grasshoppers collected directly from field populations were classified as field (*right columns*). Locust and nonmodel locust species, as identified by References 34, 80, and 121, are bolded and in red. The ChiSq columns include pie charts and chi-square tests summarizing each row for lab and field studies separately. Chi-square tests compare the distribution of reports within a row across positive, no effect, or negative responses relative to the null prediction that the reports should be evenly distributed across response types. Significant *P* values indicate that the reports are higher in one or more response categories, relative to the others for that row and study setting (lab or field), than expected by chance. Blue indicates a positive grasshopper response to increasing plant protein content (i.e., protein limitation), gray indicates no relationship between plant protein and grasshopper response, and gold represents a negative grasshopper response to increasing plant protein content or protein:carbohydrate ratio.

from field studies tend to be consistent with this conclusion. For field populations, grasshopper responses were more evenly distributed across positive, null, or negative effects of increasing plant N (all chi-square tests were not significant, as shown on the right side of **Figure 3**). In aggregate, these studies suggest that more sedentary grasshoppers in controlled environmental settings may be N limited, but that environmental variation among factors in field settings (e.g., microclimates, activity, predators, plant types) in turn drives variation in grasshopper response, resulting in no consistent pattern of N limitation for field populations.

Supplemental Material >

One consideration is that studies that find null results are less likely to be published (94). This tendency means that the "no effects" responses that made up 32% of all responses (**Figure 3**) were likely an underrepresentation of studies that found null results, since many probably were left unpublished. Despite the likely biases against publishing null results and results that go against the dominant predicted relationship (in this case, the dominant prediction is a positive relationship between plant N and grasshopper response), only approximately one-third of responses (36% of lab and field combined) report a positive relationship between plant N and grasshoppers. In summary, these data collected across five decades and over 30 species indicate that grasshoppers are not consistently limited by low plant N in nature and are just as likely to respond positively, neutrally, or negatively to increasing or decreasing plant N.

For those grasshoppers generally considered to be locusts, there are consistent patterns of negative or neutral effects of high plant N on field populations (**Figure 4**). In nature, locusts tend to select low-N plants ($P = 0.07$); abundance is most often negatively correlated with plant N ($P = 0.02$); and, collectively, locust responses to high plant N are most often negative ($P < 0.001$). The only field-based evidence to the contrary is one survey that reported a positive relationship between plant N and locust abundance; comparing two localized outbreak areas in Sudan shows that the habitat type with more locusts (*S. gregaria*) has plants with higher N content (136). However, host plant preference was not tested for field locusts, and other environmental factors may be responsible for differences in population density. All remaining field studies on locusts indicate a neutral or negative effect of high plant N (**Figure 4**). Field populations of locusts consistently have poor growth on high-N plants, select low-N plants and plants with low p:c ratios, and/or are found at higher density in low-nitrogen areas. These patterns have been shown on several continents, including South America (*S. cancellata*) (26, 129), Australia (*C. terminifera*) (78), China (*Oedaleus decorus asiaticus*) (23, 25, 104), and West Africa (*O. senegalensis*) (79, 81–83, 146).

While most research on plant–locust interactions has been done on field populations, there were five lab studies that tested locust responses to plant nutrients. Two found a negative effect of high plant protein on the Australian plague locust (*C. terminifera*) (20, 31). The other three studies measured locust (*L. migratoria* and *S. gregaria*) growth from hatchling to adult on single-plant

Table 2 Acrididae species referenced in Figure 3

Reference number	Subfamily	Species
1	Cyrtacanthacridinae	*Schistocerca americana* (Drury)
2	**Cyrtacanthacridinae**	***Schistocerca cancellata* (Serville)**
3	**Cyrtacanthacridinae**	***Schistocerca gregaria* (Forskål)**
4	Gomphocerinae	*Ageneotettix deorum* (Scudder)
5	Gomphocerinae	*Chorthippus biguttulus* (Linnaeus)
6	Gomphocerinae	*Chorthippus curtipennis* (Harris)
7	Gomphocerinae	*Chorthippus parallelus* (Zetterstedt)
8	Gomphocerinae	*Eritettix simplex* (Scudder)
9	Gomphocerinae	*Euchorthippus cheui* (Xia)
10	Gomphocerinae	*Euchorthippus unicolor* (Ikonnikov)
11	Gomphocerinae	*Mermiria bivittata* (Serville)
12	Gomphocerinae	*Omocestus viridulus* (Linnaeus)
13	Leptysminae	*Cornops aquaticum* (Bruner)
14	Melanoplinae	*Dichroplus maculipennis* (Blanchard)
15	Melanoplinae	*Hesperotettix speciosus* (Scudder)
16	Melanoplinae	*Hesperotettix viridis* (Thomas)
17	Melanoplinae	*Melanoplus bivittatus* (Say)
18	Melanoplinae	*Melanoplus borealis* (Fieber)
19	Melanoplinae	*Melanoplus differentialis* (Thomas)
20	Melanoplinae	*Melanoplus femurrubrum* (De Geer)
21	Melanoplinae	*Melanoplus sanguinipes* (Fabricius)
22	Melanoplinae	*Miramella alpina* (Kollar)
23	Melanoplinae	*Phoetaliotes nebrascensis* (Thomas)
24	**Oedipodinae**	***Chortoicetes terminifera* (Walker)**
25	**Oedipodinae**	***Locusta migratoria* (Linnaeus)**
26	**Oedipodinae**	***Oedaleus decorus asiaticus* (Bey-Bienko)**
27	**Oedipodinae**	***Oedaleus senegalensis* (Krauss)**
28	Oedipodinae	*Spharagemon collare* (Scudder)
29	Oxyinae	*Oxya hyla* (Serville)
30	Oxyinae	*Oxya japonica* (Thunberg)
31	NA	Multiple species

Species names and authority are from GBIF. Locust and nonmodel locust species as identified by References 34, 80, and 121 are in bold. Abbreviations: GBIF, Global Biodiversity Information Facility; NA, not applicable.

diets and showed that plants with higher protein and N concentrations support the best growth, survival, and reproduction rates (5, 136, 141). These results are similar to those of other studies using artificial diets, which showed that South American locusts (*S. cancellata*) require much higher protein as juveniles than as adults (130) and that, if locusts are only fed a single diet over their lifetime, then diets that best matched early juvenile needs supported the best growth through development (S. Talal, J.F. Harrison, R. Farington, H.E. Medina, R.P. Overson and A.J. Cease, unpublished data). In field populations, protein requirements are similar to those of lab populations, but carbohydrate requirements can be 90% higher (130), shifting locust p:c ITs to be quite carbohydrate biased (i.e., shifting locust IT as seen in **Figure 2**). This lab-to-field comparison suggests that plants with lower N and higher carbohydrate would better support locust development in

Locust data only	Lab studies	Field studies
	ChiSq	ChiSq
Survival	P = 0.37 N = 4	 P = 0.25 N = 5
Growth and/or development	P = 0.25 N = 5	 P = 0.14 N = 6
Reproduction	P = 0.37 N = 1	 P = 0.61 N = 2
Host plant selection	P = 0.37 N = 1	 P = 0.07 N = 5
Nutrient extraction from plants, or nutrient selection post–plant feeding	–	 P = 0.17 N = 4
Abundance (field surveys)	–	 **P = 0.02 N = 9**
Total reports	P = 0.06 N = 11	 **P < 0.001 N = 31**

Figure 4

Summary pie charts and chi-square tests including only the locust data from **Figure 3**. Blue indicates a positive grasshopper response to increasing plant protein content (i.e., protein limitation), gray indicates no relationship between plant protein and grasshopper response, and gold represents a negative grasshopper response to increasing protein content or protein:carbohydrate ratio (i.e., carbohydrate limitation).

field populations. Indeed, the two studies that have measured locust (*O. d. asiaticus*) performance when reared on different plant diets starting at either the first or third instar found that high plant N is deleterious for growth and survival (23, 104).

Outbreaking locusts exist at high density, and repeated interactions with conspecifics through touch, smell, and/or sight causes individuals to shift from solitarious to gregarious phenotypes (34, 99). Locust species exhibit distinct suites of traits as gregarious locusts (behavior, morphology, physiology, color), but the core consistent traits and the first to shift during phase change are behavioral, specifically, increased activity and attraction to conspecifics (34, 121). These two behaviors can lead to mass migrations—over ground as juveniles in marching bands and in the air as adults in swarms. Flight increases carbohydrate, but not protein, consumption, and carbohydrate-rich diets increase lipid stores and support longer flight durations (107, 131) (**Table 1**). While

the energetic costs of marching have not been measured in locusts, in other insects, terrestrial locomotion increases metabolic rates 2–12 times above resting (58). Gregarious locusts rely on carbohydrate and lipid stores for flight and, likely, also to fuel marching (45, 72, 128, 129). Indeed, marching bands of South American locusts (*S. cancellata*) are overwhelmingly carbohydrate, not protein, hungry (26, 129). Even when not actively marching or flying, gregarious locusts have a higher resting metabolic rate relative to solitarious locusts (3, 21, 24, 56, 135), potentially due to elevated maintenance costs of larger flight muscles (96). Taken together, these studies suggest that gregarious, migrating locusts would rarely be N limited in nature and that carbohydrate limitation is likely to be common for outbreaking locust populations.

5. GLOBAL CHANGE: HOW HAVE LAND USE AND CLIMATE CHANGE AFFECTED LOCUST POPULATIONS VIA NUTRIENT-MEDIATED PATHWAYS?

As described in Section 4, gregarious, outbreaking locusts have elevated carbohydrate, relative to protein, demands, and low-N plants (low protein and high carbohydrate) tend to support higher growth, survival, reproduction, and abundance for field populations (**Figure 4**). Thus, any practices that alter plants to have higher carbohydrate and lower protein contents (i.e., low-N environments) are predicted to facilitate locust outbreaks by supporting gregarious locusts. In addition, it is possible that optimal diets lower the threshold for gregarization. High population density is the primary trigger for solitarious locusts to shift to gregarious forms, acting through mechanical, olfactory, and visual sensing pathways that are species specific (34, 99). Australian plague locusts (*C. terminifera*) confined to diets differing in p:c ratio only fully transition to behavior typifying gregarious phenotypes in response to high density or direct mechanical stimulation via a paintbrush (e.g., 118) when eating their preferred IT (A.J. Cease, S.M. Rogers, T. Dodgson and S.J. Simpson, unpublished data). Environments with patches of nutrients representing complementary diet rails can also promote gregarization if locusts bump into each other more frequently as they seek to balance their nutrient intake (37).

While its effects have not been tested for locust species, atmospheric CO_2 enrichment is likely to promote locust outbreaks by making plants more carbohydrate biased. Elevated atmospheric CO_2 spurs plant growth, typically elevating soluble carbohydrate and/or reducing nitrogen and protein contents, an effect termed nutrient dilution (4, 6, 70, 126, 144). For nonlocust grasshopper species, CO_2 enrichment can have positive (144), negative (4, 69, 70, 144), mixed (126), or no (6, 69) effects on growth and survival. Long-term ecological data sets reveal declines in North American grasshopper populations correlated with nutrient dilution (144), which may be explained by slow maturation rates when eating low-N plants (73). The nutrient shift in response to CO_2 enrichment can be greater in C_3 versus C_4 grasses (6). In addition, whether a crop is grown in mono- or polyculture can mediate the impacts of CO_2 enrichment on grasshopper growth (126). Grasshopper digestion and growth may also be hindered by secondary metabolites under elevated CO_2 conditions (69, 70). For example, allelochemical concentrations may be unaffected by CO_2 enrichment (69), meaning that compensatory feeding would increase the amount of dietary allelochemicals ingested for each unit of protein consumed. How elevated atmospheric CO_2 affects locust populations through shifts in plant nutrients and/or antinutrients is an area that needs more research.

Several studies have looked at the potential of land-use change to affect locust populations explicitly via plant protein and carbohydrate contents. These studies have generally found that land-use practices that degrade soils promote locust outbreaks by lowering plant nitrogen; conversely, practices that improve soil fertility generally dampen outbreaks (22, 23, 83, 90, 146). In Senegal agroecosystems, *O. senegalensis* locusts are most abundant in field-cropping systems that have low soil organic matter and plants with low nitrogen and protein and high carbohydrate

contents (83, 146). Fertilizing millet decreases the palatability of millet leaves to locusts, as well as locust survival and egg mass (82). Similarly, in China, pastures degraded by heavy livestock grazing promote outbreaks of *O. d. asiaticus* locusts by lowering nitrogen and creating an optimal nutritional niche for the species (23). Field-marching South American locusts (*S. cancellata*) prefer high-carbohydrate invasive grasses over native plants (129). These marching locusts only grow when eating low-protein, high-carbohydrate plants, suggesting that land-use changes including roadways that harbor invasive grasses or conversion of forests to pastures promote outbreaks and migration. Other research links deforestation to migratory locust (*L. migratoria*) outbreaks in Australia (39) and Indonesia (85) and outbreaks of the Central American locust (*Schistocerca piceifrons*) in Mexico (102). In Australia, ecological change brought about by introduction of European livestock and agriculture is linked to the start of Australian plague locust (*C. terminifera*) swarms (38). In contemporary times, localized populations of Australian plague locusts (*C. terminifera*) are negatively correlated with plant protein content (78). This pattern can be corroborated at a continental scale using approximately 190,000 locust survey records from 2000–2017 from the Australian Plague Locust Commission and CSIRO soil nutrient data. After accounting for climatic variables and sampling bias, large outbreaks (>80 m^2) are negatively correlated with soil nitrogen with an R^2 of approximately 0.8 (D. Lawton, J. Learned, C. Waters, I. Toole, N. Thompson, C. Hales, C. Adriaansen, T. Deveson, S.J. Simpson and A.J. Cease, unpublished data). In sum, these studies show, from the level of individuals, to that of populations, to continental scales, that land use and climate change factors that expand low-N environments promote locust outbreaks.

Rising temperatures are generally predicted to expand locust ranges to higher elevations and latitudes [e.g., *S. gregaria* (147), *Calliptamus italicus* (103), and *Dociostaurus maroccanus* (74)]. Grasshoppers, including locusts, are excellent behavioral thermoregulators. Warmer climates will likely allow grasshoppers to achieve body temperatures closer to optimal over a greater part of the day, allowing them to eat, digest, and grow faster (147). At lower altitudes and latitudes, however, grasshoppers may be unable to avoid damaging temperatures, which begin at roughly 45–49°C, resulting in a predicted range contraction in some areas (91, 147). For juveniles, higher temperatures may increase protein intake up to 20% more than carbohydrate intake by hastening growth rate (93, 116). However, estimates for increases in carbohydrate consumption would likely offset any relative increase in protein (**Table 1**) for wild locusts (up to 90% carbohydrate increase relative to lab locusts; 130) and locusts that are under threat of predation (up to 130% carbohydrate increase; 89) and migrating (20% carbohydrate increase; 107). Thus, access to both higher temperatures and carbohydrate-rich diets will likely promote locust outbreaks. Climate change more broadly, including greater amplitude and unpredictability of extreme weather, has many complex and interacting direct and indirect impacts on locust populations, making long-term predictions challenging (92). Some species are predicted to increase their outbreak potential [*L. migratoria* (148) and *D. maroccanus* (74)], while others could see a decrease in potential [*C. terminifera* (138)] or fail to expand to new regions due to lack of winds supporting migration [e.g., *S. gregaria* is unlikely to invade China (140)]. The solitarious range of the well-known northern desert locust subspecies (*S. g. gregaria*) may contract in some areas; in contrast, the range of the less-studied southern subspecies (*S. g. flaviventris*) is predicted to expand (91). Understanding how the interaction of these anthropogenic and environmental factors will affect locust populations will be important for predicting and managing plagues.

6. GLOBAL CONTEXT AND CONCLUSIONS

Global environmental change is among the most pressing challenges we face today, and many aspects are predicted to increase locust outbreaks, further exacerbating challenges for farmers and

sustainable food system efforts (153). Locust outbreaks can cause complete crop loss within hours (100) and decreased educational outcomes for impacted communities (36). The unpredictable and overwhelming nature of locust outbreaks has contributed to the idea that communities are passive recipients of swarms. Understanding how land use and climate change influence outbreaks through the dial of plant nutrients can provide powerful alternative management approaches, such as area-wide pest management using soil amendments (22, 146), and predictive tools, such as incorporating soil quality maps into models and forecasts, to decrease their devastating impacts on livelihoods.

SUMMARY POINTS

1. The need to balance macronutrients (protein and nonprotein energy) can have powerful effects on individuals and drive landscape-level outbreak and migration patterns.
2. The relative macronutrient demands of species are not fixed. Protein demand may be driven largely by somatic and reproductive growth, but carbohydrate demand can differ more substantially with environmental variation.
3. Variability in specific insect–plant interactions can make it challenging to predict the relative quantities of macronutrients that grasshoppers are extracting from plants.
4. There is a great deal of variation in grasshopper responses to increasing plant nitrogen, but field studies on outbreaking locust populations consistently find negative relationships between plant nitrogen and locust outbreaks.
5. Land degradation and increased atmospheric CO_2 can both decrease plant protein:carbohydrate ratios, which can deleteriously impact some grasshopper species but are generally predicted to support locust outbreaks due to the elevated activity levels that increase the energy demands of locusts.
6. Locust outbreaks can have devastating impacts on livelihoods by causing crop losses of 80–100% in impacted agricultural areas, which causes short-term food insecurity and long-term decreases in educational access for children in plague-affected communities. However, understanding how nutrients mediate the impacts of anthropogenic change on locust outbreaks can provide powerful predictive and sustainable management tools.

FUTURE ISSUES

1. How do grasshopper microbiomes differ among species and environments, and what are their roles in nutritional ecology, physiology, and behavior?
2. What are the mechanistic links between elevated atmospheric CO_2, changes in plant chemistry and structure and grasshopper responses, and how do these differ across lab and field settings and throughout ontogeny?
3. What are the nutritional demands of reproduction, immune function, and migration, and how does environmental variation affect the trade-offs among these?
4. How do interactions among temperature, nutrients, and water availability affect grasshopper growth, survival, and geographic distribution?

5. What is the variation in host plant nutrient extraction based on specific insect–host interactions, and how is this variation predicted to affect grasshoppers in nature?
6. How does relative nutrient availability affect the probability of gregarization?
7. How can we better apply our understanding of human–plant–locust interactions to improve sustainable management practices in a transdisciplinary context?

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

Thank you to Rick Overson and Jon Harrison for reviewing several versions of this manuscript and providing feedback on the scope and approach and to Rick for assistance with finalizing and formatting **Supplemental Table 1**. Thank you to James Elser and Stephen Simpson for teaching me that nutrient ratios are quite important in biology and ecology during my graduate and postdoctoral years. Thanks to Christina Grozinger for encouraging me to write this review and to the Global Locust Initiative and National Science Foundation (NSF) Behavioral Plasticity Research Institute teams for their support and insights on locust research. Much appreciation to the hundreds of researchers who carefully tested the effects of plant nutrients on grasshoppers, whose findings made this review possible. Thank you to the wonderful communities in locust-prone areas around the world that have supported and collaborated on locust research. I acknowledge that Arizona State University resides on the traditional homelands of the Akimel O'odham (Pima) and Pee Posh (Maricopa) communities, whose land stewardship we benefit from daily. This research was supported by NSF grants DBI-2021795 and IOS-1942054.

Supplemental Material >

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