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Grasshoppers affect grassland ecosystem functioning: Spatial and temporal variation

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Abstract

Using experiments and monitoring, we find that grasshoppers in a grassland ecosystem impact ecosystem functioning (nutrient cycling and primary production) in different ways among sites in the ecosystem. Experiments conducted over many years at two sites (21 and 15 years, respectively) with the same grasshopper and plant species demonstrated that grasshoppers increased nitrogen availability (N) and consequently annual plant production (ANPP) at one site, and decreased N and consequently ANPP at the other site. Comparing the two sites, N increased on average by 8% and up to 21.6%, and resulting ANPP increased on average by 18.6% and up to 33.3%. Grasshoppers increase N and ANPP by preferentially feeding on slower decomposing plants, and the opposite occurs by preferentially feeding on faster decomposing plants. Monitoring 20 random sites in the ecosystem, grasshoppers consistently increased N and ANPP over 3 years at 40% of sites, consistently decreased N and ANPP at 35% of sites, and sometimes increased and decreased N and ANPP at 25% of sites. Therefore, grassland grasshoppers, and insects in many ecosystems, may strongly affect ecosystem functioning.

Keywords: Grasshoppers; Grasslands; Nutrient cycling; Primary production; Ecosystem functioning

Introduction

Traditionally, drivers of ecosystem primary production were considered to be abiotic factors operating over large spatial scales (e.g., precipitation, temperature, soils, nutrients, etc.) (Golley 1996). However, herbivores may strongly influence nutrient availability through their consumption, which can slow or accelerate nutrient cycling (Hutchinson & Deevey 1949; McNaughton, Ruess, & Seagle 1988; Pastor, Naiman, Dewey, & McInnes 1988; DeAngelis 1992; Holland, Parton, Detling, & Coppock 1992; Pastor & Naiman 1992; Frank & McNaughton 1993; Pastor, Dewey, Naiman, McInnes, & Cohen 1993; Belovsky & Slade, 2000, 2002; Wardle 2002; Bardgett & Wardle, 2003, 2010). This biotic influence can create positive feedbacks, when consumption enhances nutrient cycling and food for herbivores, or diminishes nutrient cycling and food. It is possible that herbivory's positive feedbacks can impact nutrient cycling and primary production more than abiotic processes.

The effect most often considered occurs when herbivores convert nutrients in recalcitrant decomposing vegetation to more labile forms in excrement and sequester nutrients in their bodies (Schultz 1964). Herbivores with short lifespans, which are less efficient at digesting plants, cycle nutrients faster than herbivores with long lifespans, which are more efficient digesters. However, herbivores may have greater impacts by changing plant species composition: decreasing

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nutrient cycling and availability if they increase abundance of slower decomposing plant species (Pastor et al. 1988) or increasing nutrient cycling and availability if they increase abundance of faster decomposing plant species (McNaughton et al. 1988). The former case occurs when herbivores selectively forage on faster decomposing plants so that faster decomposing plants decrease in abundance (Fig. 1A), while the latter case occurs when herbivores selectively forage on slower decomposing plants so that slower decomposing plants decrease in abundance (Fig. 1B). Positive feedbacks emerge if changes in plant and herbivore abundance enhance or maintain changes in nutrient cycling.

In terrestrial ecosystems, nitrogen (N) is often the limiting nutrient for plant growth, and protein (N) is sought by herbivores (White 1984, 1993). Pastor et al. (1988) demonstrated that mammalian herbivores decrease N cycling and abundance (Fig. 1A), when they prefer to eat faster decomposing plants, and this finding suggested that this could be a general outcome if the same plant traits leading to faster decomposition also are sought in food. In contrast, McNaughton et al. (1988) demonstrated that mammalian herbivores increase N cycling and abundance (Fig. 1B) when they prefer to eat slower decomposing plants. Belovsky and Slade (2000, 2002) experimentally demonstrated in the field that grassland grasshoppers (Acrididae) can decrease or increase N cycling in different habitats.

Grasshoppers and locusts (Acrididae) are likely candidate herbivores for strongly affecting N cycling and abundance in herbaceous-dominated ecosystems. First, grasshoppers are not efficient digesters, producing large quantities of excrement that is deposited in a fine-grained fashion, unlike mammalian herbivore excrement (Belovsky 2000). Second, grasshoppers are short-lived, so nutrients in their bodies are recycled quickly compared to mammals. Third, other than cutting plants, grasshoppers are environmentally “soft”: i.e., do not compact, dig or burrow in the soil. Finally, grasshoppers are abundant and can consume or cut large proportions of the vegetation in herbaceous natural ecosystems (Table 1), especially in seasonally-warm semi-arid herbaceous communities with short vegetation (Table 1). In these ecosystems, grasshoppers and locusts often reduce vegetation as much or more than mammalian herbivores (1–3 times) (Morton 1936; Drake & Decker 1937; Parker & Connin 1964; Bullen 1966; Sinclair 1975; Belovsky 2000; Roberts 2015). In moister herbaceous ecosystems, grasshoppers reduce vegetation less, as taller plants may be poorer quality food (coarser and less nutritious) and may shade insects, so that feeding time is reduced due to cooler conditions.

We experimentally examined how the same grasshopper (*Melanoplus sanguinipes*) affected N cycling and thereby annual primary production (ANPP) at two bunchgrass prairie sites (National Bison Range, MT, USA) with similar vegetation (grasses: *Pascopyrum smithii* and *Poa pratensis*). One site was examined for 21 years (4 years: manipulated grasshopper density, then 17 years of un-manipulated density, a recovery period); the other site for 15 years (5 years: manipulated density, then 10 years of recovery). Increased grasshopper feeding at one site should increase N cycling and the subsequent year’s ANPP by preferential feeding on slower decomposing plants, while diminishing N cycling and the subsequent year’s ANPP at the other site by preferential feeding on faster decomposing plants (Belovsky & Slade, 2000, 2002). We expected that recovery from manipulations at both sites would be slow due to positive feedbacks created by the grasshopper manipulations. Finally, we provide insight into how often grasshoppers enhance or diminish N cycling and primary production by monitoring 20 sites to determine whether grasshoppers preferentially consume faster or slower decomposing plants at each and whether consistent changes in N availability and ANPP are observed.

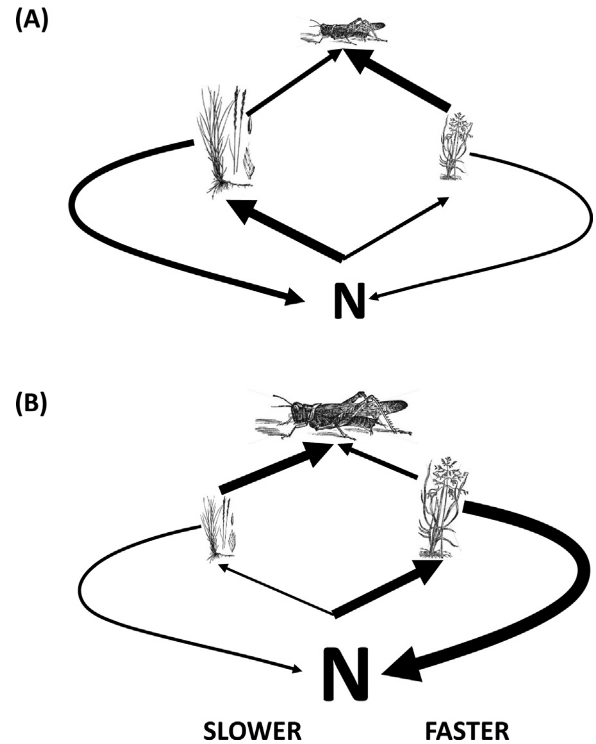

Fig. 1. Alternative ways that herbivory affects ecosystem functioning. (A) When herbivores preferentially feed on faster decomposing plants, the abundance of slower decomposing plants increases, which reduces nutrient availability and primary production. Herbivore abundance is likely to decline. (B) When herbivores preferentially feed on slower decomposing plants, the abundance of faster decomposing plants increases, which increases nutrient availability and primary production. Herbivore abundance is likely to increase. In either case, changing relative abundances of faster/slower decomposing plants, and herbivore abundance create a positive feedback perpetuating or enhancing herbivore-induced changes. Picture and arrow size reflect abundances and fluxes.

Materials and Methods

Studies were conducted in bunchgrass prairie at the National Bison Range (NBR), Montana (USA) between 1994

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