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Granivory reduces biomass and lignin concentrations of plant tissue during grassland assembly

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Abstract

Small mammals can influence grassland assembly by selecting against palatable plants – the community can become dominated by the plants they avoid. This predation-based selection could have indirect effects on community biomass and tissue quality, especially given how untasty plants may have higher concentrations of recalcitrant carbon compounds including lignin. We tested small mammal effects on biomass and tissue quality of roots and shoots in a two-year-old 18 ha restored tallgrass prairie with established zones of high and low plant predation. We focused on the three dominant herbaceous functional groups of tallgrass prairie (perennial forbs, C_3 and C_4 grasses), and targeted the early stages of assembly given that plant predation by small animals can unfold quickly and is difficult to subsequently quantify. We predicted rodent predation to create communities with reduced biomass but an increased abundance of lignin-rich plants; we only observed the former. Rodents reduced aboveground biomass by 46% but preferentially targeted lignin-rich plants, with the latter result explained by the predominance of granivory over herbivory – there was no opportunity for selection based on tissue palatability. Based strictly on aboveground biomass, we estimated small mammals reduced standing stocks of recalcitrant carbon by 65 kg ha^{-1}, with reductions in belowground stocks almost certainly higher given that root:shoot ratios averaged 21:1. Given that the quantity and quality of plant production can affect ecosystem functions including decomposition and the regulation of soil carbon stocks, our work suggests that non-random plant predation may substantially affect rates of soil carbon accumulation in the early stages of grassland development.

Zusammenfassung

Kleinsäuger können die Zusammensetzung von Grasländern beeinflussen, indem sie gegen schmackhafte Pflanzen selektieren, so dass die Gemeinschaft von den verschmähten Pflanzen dominiert wird. Diese Selektion könnte indirekten Einfluss auf die Biomasse der Gemeinschaft und die Gewebequalität haben, insbesondere angesichts der hohen Konzentrationen von schwer abbaubaren Kohlenstoffverbindungen (z.B. Lignin), die bei nichtschmackhaften Pflanzen vorkommen können. Wir untersuchten den Einfluss von Kleinsäugern auf die Biomasse und Gewebequalität von Wurzeln und Sprossen auf einer zwei Jahre alten, wiederhergestellten Tallgrass-Prärie mit Zonen hohen und geringen Räuberdrucks auf die Pflanzen. Wir konzentrierten uns auf drei dominante krautige funktionelle Gruppen (ausdauernde Kräuter, C3- und C4-Gräser) und betrachteten die frühen Stadien der Gemeinschaftsbildung, da sich der Pflanzenfraß durch Kleinsäuger schnell aufbauen kann, später aber schwer zu quantifizieren ist. Wir sagten voraus, dass Fraß durch Kleinsäuger Gemeinschaften mit verringerter Biomasse aber erhöhter Abundanz von Lignin-reichen Pflanzen entstehen lassen sollte. Wir beobachteten nur das Erste. Kleinsäuger reduzierten die oberirdische Biomasse um 46%, attackierten aber vorzugsweise Lignin-reiche Pflanzen, wobei sich der zweite Befund dadurch

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erklärt, dass die Kleinsäuger überwiegend Samen und nicht Pflanzen fraßen. Damit gab es keine Gelegenheit für eine Selektion aufgrund der Genießbarkeit der Pflanzen. Basierend auf der oberirdischen Biomasse, kalkulierten wir, dass die Kleinsäuger den Vorrat an schwer abbaubarem Kohlenstoff um 65 kg ha^{-1} verringerten, wobei die Verringerungen der unterirdischen Vorräte fast sicher noch höher sein sollten, da die Wurzel:Spross-Verhältnisse im Schnitt 21:1 betrugen. Da die Quantität und Qualität der Pflanzenproduktion Ökosystemfunktionen (darunter Dekomposition und Regulation von Kohlenstoffvorräten im Boden) beeinflussen kann, legt unsere Studie nahe, dass nicht-zufälliger Räuberdruck auf Pflanzen die Raten der Kohlenstoffakkumulation im Boden in den frühen Stadien der Graslandentwicklung entscheidend bestimmen könnte.
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Keywords: Granivory; Herbivory; Small mammals; Grasses; Forbs; Ecosystem function; Grassland; Tallgrass prairie

Introduction

Substantial small mammal effects on herbaceous plant communities, via granivory and herbivory, have been described in many of the world's grasslands (Batzli & Pitelka 1970; Noy-Meir 1988; Howe & Brown 1999; Maron & Vilà 2001; Howe, Brown, & Zorn-Arnold 2002; Howe, Zorn-Arnold, Sullivan, & Brown 2006; MacDougall & Wilson 2007; Orrock, Witter, & Reichman 2009; Germain, Johnson, Schneider, Cottenie, Gillis, et al. 2013). These effects can deterministically drive assembly trajectories, via trait-based differences among plants in the palatability of seeds, plant tissue, or both, sometimes leading to communities dominated by unconsumed species (Howe et al. 2002, 2006). The end result can include dramatic reductions in plant diversity favoring a small subset of unpalatable species (Howe et al. 2002; MacDougall & Wilson 2007).

Plant predation by rodents may also have substantial effects on ecosystem function within plant communities, via the influence on two factors: biomass production and the tissue quality of plants (e.g., Bryant, Chapin, & Klein 1983; Tracy & Frank 1998; Sirotnak & Huntly 2000). Small mammals can influence biomass production by reducing stem density at the community level (fewer individuals per area – Weltzin, Archer, & Heitschmidt 2007), by reducing the amounts of foliage on individual plants by browsing (browsed individuals growing smaller – MacDougall, Duwyn, & Jones 2010), or by preferentially removing large-seeded species given the positive correlation between seed mass and standing biomass in many plants (Lönnberg & Eriksson 2013). Tissue quality can be influenced by the targeting of palatable species, resulting in a community of individuals with potentially higher concentrations of recalcitrant compounds such as lignin. Lignin restricts digestion in herbivores but also has spin-off effects on slowing decomposition (Tracy & Frank 1998; Cornelissen, Pérez-Harguindeguy, Díaz, Grime, Marzano, et al. 1999; Cornwell, Cornelissen, Amatangelo, Dorrepaal, & Eviner 2008), suggesting the rodent impacts on tissue quality could indirectly influence carbon (C) accumulation in soils of assembling grasslands. The negative effects of rodents on grassland plant diversity are commonly reported; the hypothesis that rodent-influenced prairies could have less production but more lignin-rich biomass has not been directly tested although it would be consistent with other systems (e.g., boreal systems – Bryant et al. 1983).

Here, we describe rodent impacts on biomass and tissue quality in the early stages of assembly of a species-rich 18 ha planted tallgrass prairie in southwestern Ontario, Canada. We focus our analysis on three dominant herbaceous functional groups associated with tallgrass prairie in North America (C_3 grasses, C_4 grasses, and perennial forbs), with known differences in sensitivity to rodent granivory and herbivory (Howe & Brown 1999; Germain et al. 2013). We focus on the early stages of assembly (year 2 after planting) because species loss from small animals can unfold quickly in planted prairie and is difficult to quantify after-the-fact; prairie assembly usually peaks in diversity and biomass 4–5 years after planting due to the slow maturation of C_4 grasses (Collins & Adams 1983). The study area is spatially differentiated into two zones, based on the presence or absence of intense small mammal predation on plants that occurred immediately after planting (Germain et al. 2013). A zone of high predation extended 30–50 m into the prairie from bordering oldfield grassland, with the oldfield providing protective cover for the small mammals; prairie diversity in the high-predation area is low and mostly dominated by species avoided by small mammals especially C_4 grasses. A zone of low predation occurred in areas beyond 50 m from the oldfield boundary, presumably due to the complete absence of protective cover that reduced visitation by rodents; prairie diversity is high, with mixtures of all three functional groups.

We quantified differences between the two zones in the quantity of biomass production and the quality of plant tissue, for both shoots and roots. Roots are not directly browsed by small mammals but production and tissue quality of belowground tissues can differ substantially from patterns observed aboveground (e.g., >90% of plant biomass can occur belowground in prairie – Mokany, Raison, & Prokushkin 2006) and can be strongly linked with the impacts of herbivory on aboveground tissues (Milchunas & Lauenroth 1993; Frank, Pontes, Maine, Caruana, Raina, et al. 2010; Balogianni, Wilson, Vaness, MacDougall, & Pinno 2014; Ziter & MacDougall 2013). We quantified differences in tissue quality in roots and shoots of the three functional groups, including lignin content which, as a form of recalcitrant carbon, can influence both herbivory and decomposition (e.g., Bontti, Decant,

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