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Plant volatiles inhibit restoration of plant species communities in dry grassland

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Abstract

Benefits from livestock grazing have declined in regions where vegetation has been degraded by overgrazing. The vegetation can be restored by excluding livestock for a period, but it takes longer in drier regions. Here we propose a possible mechanism for delays in the recovery of poor vegetation for livestock grazing in dry grassland, introducing a case in Mongolia where steppe vegetation dominated by *Stipa krylovii*, a palatable grass, can become dominated by *Artemisia adamsii*, an unpalatable forb, when the grassland is overgrazed. Our long-term field experiment shows that the exclusion of livestock has not enhanced the recovery of palatable species in 6 years, indicating that *A. adamsii* is a strong competitor in the plant community. To understand why livestock exclusion is ineffective, we examined the ecological significance of volatile organic compounds (VOCs) released by *A. adamsii*. In *ex situ* experiments, the VOCs promoted photosynthesis of *S. krylovii* with enhanced stomatal conductance, and *S. krylovii* grew faster and consumed more water when exposed to the VOCs even with water deficiency. These findings imply that *S. krylovii* would be more likely to face severe drought before the next rain falls. We therefore conclude that plant volatiles may reduce the resilience of overgrazed vegetation in arid environments.

Zusammenfassung

Die Erträge der Viehbeweidung sind in Regionen zurückgegangen, in denen die Vegetation durch Überweidung geschädigt wurde. Die Vegetation kann sich erholen, wenn das Vieh für eine gewisse Zeit ausgeschlossen wird, was aber in trockenen Gebieten länger dauert. Wir schlagen hier einen möglichen Mechanismus vor, der für die Verzögerung bei der Erholung spärlicher Vegetation für die Viehbeweidung in trockenen Steppen verantwortlich ist, indem wir einen Fall in der Mongolei vorstellen, bei dem die Steppenvegetation, die durch das fressbare Gras *Stipa kryvlovii* dominiert wird, bei einer Überbeweidung des Graslandes durch *Artemisia adamsii* dominiert wird, das ein nicht fressbares Kraut ist. Unsere langfristigen Freilandexperimente zeigen, dass der Ausschluss des Viehs die Erholung der fressbaren Arten in 6 Jahren nicht gefördert hat, und weisen darauf hin, dass *A. adamsii* in der Pflanzengemeinschaft ein starker Konkurrent ist. Um zu verstehen, warum der Ausschluss des Viehs nicht effektiv ist, untersuchten wir die Bedeutung von flüchtigen organischen Substanzen (VOCs), die von *A. adamsii* freigesetzt werden. In Laborexperimenten förderten die VOCs die Photosynthese von *S. kryvlovii* über eine stärkere Durchlässigkeit der Stomata, und *S. kryvlovii* wuchs schneller und verbrauchte mehr Wasser, wenn es den VOCs ausgesetzt war, selbst wenn es Wassermangel

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gab. Diese Ergebnisse lassen vermuten, dass *S. kryvlovii* mit größerer Wahrscheinlichkeit vor dem nächsten Regen ernste Austrocknungserscheinungen zeigen würde. Wir schließen daraus, dass flüchtige Pflanzensubstanzen die Widerstandfähigkeit einer überweideten Vegetation in trockenen Umgebungen reduzieren können.

Keywords: Allelopathy; *Artemisia adamsii*; Dryland; Hormesis; Overgrazing; *Stipa krylovii*

Introduction

Vegetation maintains an equilibrium with wild animals but can be disturbed by domestic livestock. Continuous overgrazing can debase vegetation, leading to the dominance of unpalatable species over palatable species. Further, overgrazing may result in a catastrophic shift of vegetation (Scheffer, Carpenter, Foley, Folke, & Walker, 2001; Van de Koppel, Rietkerk, & Weissing, 1997) and soil loss (Belnap, 1995). To reduce the risk of land degradation such as loss of soil organic matter, the best option is to reduce anthropogenic effects; the reduction or exclusion of livestock can allow palatable species to be restored in short periods in semi-arid and dry sub-humid regions (Harrison & Shackleton, 1999; Walker, Langridge, & McFarlane, 1997). Although the resilience of degraded land is relatively high in such regions, erratic rainfall causes primary production to vary greatly from year to year (Milchunas & Lauenroth, 1993; O'Connor, Haines, & Snyman, 2001). In arid regions, the resilience is much lower, so long-term exclusion of livestock will be required to return poor vegetation for livestock grazing to its original state (Lovich & Bainbridge, 1999).

The steppes of Mongolia and Inner Mongolia (China), which have a long history of livestock grazing, feature xerophytic plant communities that are adapted to severe cold winters. Distinct wet and dry seasons, corresponding to the growing season and the off-season, respectively, typify the climate. Yet dry spells often occur during the growing season; accordingly, plant growth is interrupted from time to time. *Stipa krylovii*, a palatable perennial grass, shares the community with small colonies of *Artemisia adamsii*, an unpalatable perennial forb. The grass generally predominates under low grazing pressure, but there is a clearly perceptible extreme of community structure across the steppe, typified by *A. adamsii*-dominated communities under high grazing pressure (Hilbig, 1995). *Artemisia frigida*, a palatable semi-shrub, also predominates under high grazing pressure in some cases (Cheng, Tsendeekhuu, Narantuya, & Nakamura, 2008).

Annual species (e.g., *Chenopodium album* and *Salsola collina*) are relatively abundant in both *S. krylovii*- and *A. adamsii*-dominated communities, but *S. krylovii* cannot coexist evenly with *A. adamsii*. *Artemisia* spp. are well known to emit large quantities of volatile organic compounds (VOCs). For example, *Artemisia californica* released 47 μg (monoterpenes) g^{-1} (dry leaf weight) h^{-1} (Arey, Crowley, Crowley, Resleto, & Lester, 1995). These species release constitutive and low-level VOCs when healthy, and large quantities of inducible VOCs when damaged (Holopainen, 2004). On the steppe, *A. adamsii* is a major species that releases VOCs with a strong smell, so its effect is of interest.

To a greater or lesser degree, all plant species produce VOCs. A well-known paradigm is that plants emit VOCs to defend themselves against attack by insects and pathogens (Dudareva, Negre, Nagegowda, & Orlova, 2006; Shulaev, Silverman, & Raskin, 1997; Walling, 2000). Volatiles emitted by damaged plants can be detected by undamaged neighbors, which can then modify their own defenses for better protection against herbivores and pathogens (Baldwin, Halitschke, Paschold, von Dahl, & Preston, 2006; Farmer, 2001). However, the role of plant volatiles in ecosystems must be further elucidated.

Allelopathy is a function that can be additional to this paradigm (Kegge & Pierik, 2009). Plant volatiles have been shown to inhibit plant growth, and species that produce large quantities of VOCs can suppress coexisting species to some extent (Muller, Muller, & Haines, 1964; Rai, Gupta, & Singh, 2003; Tarayre, Thompson, Escarré, & Linhart, 1995). For example, *A. californica* emits several volatiles, such as camphor and 1,8-cineole, which inhibit seed germination of *Madia sativa*, a native forb of the west coast of North America (Halligan, 1975). VOCs in large amounts have been shown to cause inhibitory effects, but concentrations in nature are usually lower than those used in experiments (Cape, 2003). On the other hand, several studies have shown a prevalence of plant hormesis (or stimulatory allelopathy at low concentrations): a positive response to low levels of stressors (An, Johnson, & Lovett, 1993; Belz & Cedergreen, 2010; Calabrese & Blain, 2009; Stebbing, 1982; Vicherková & Polová, 1986).

In the process of vegetation degradation on the steppe, *S. krylovii* adjacent to *A. adamsii* is susceptible to grazing pressure as a result of the selective grazing habit of livestock, and the *Artemisia* colonies can proliferate. Although coexisting annual and perennial species play important roles in secondary succession from overgrazed vegetation, vigorous growth of *S. krylovii* after a cold and dry winter may be a prerequisite for restoration of the vegetation. This vigorous growth may also be susceptible to VOCs from the *Artemisia* plant residues remaining from the previous growing season, which might either stimulate or inhibit the growth of neighboring *S. krylovii* sprouts early in the growing season. In addition, older *A. adamsii* plants release more VOCs. An understanding of the survival strategy of unpalatable species that produce large quantities of VOCs is of importance to revealing their interaction with palatable species in the recovery of poor vegetation for livestock grazing. Here we show