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CONCEPTS & THEORY

Is relative Si/Ca availability crucial to the performance of grassland ecosystems?

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Abstract. Species composition of grasslands and pastures is an important control on biomass production and ecological functioning, with a significant role of grasses and legumes. A change in composition of legumes/grasses abundance and biomass ratio results in altered nutrient cycling and composition of higher trophic-level communities (e.g., grazers). However, in addition to pasturing and fire effects, other parameters may also potentially affect grassland composition. Grasses are known as silicon (Si) accumulators and legumes as calcium (Ca) accumulators. We propose a new testable hypothesis, and a conceptual model, on the role of Si/Ca availability in controlling legume/grass dominance/competition in grassland systems. Based on available literature, we argue that Si/Ca availability is an important trigger for shifts in abundance of both plant families. The differential uptake of Si and Ca by legumes and grasses affects grassland biogeochemistry and microbial (fungal) biomass. In addition, altered litter stoichiometry, through impact of Ca and Si uptake on N, C, and P turnover, affects the decomposition processes.

Key words: biodiversity; biomass production; competition; nutrients; organic matter decomposition; species richness; turnover.

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Introduction

Grassland ecosystems have been in the focus of biodiversity research during the last few decades. Grassland biodiversity and species composition are important for ecosystem processes and grassland properties such as biomass production, carbon (C) sequestration, nutrient cycling and storage, as well as litter quality and decomposition (Balvanera et al. 2006). Plant composition and diversity in grasslands further affect cycling of important nutrients such as phosphorus (P) and nitrogen (N; Abbas et al. 2013). Hence, many researchers have focused on the mechanisms driving species turnover processes and biodiversity in these ecosystems. Pasturing/herbivory (Milchunas et al. 1988, Olff and Ritchie 1998) and fire (DeBano et al. 1998) have been particularly well studied, but there are many other factors that may affect community shifts.

Legumes are an important plant group in this context. They can increase the biomass production of grass ecosystems by increasing N accumulation and acquisition (Bruning and Rozema 2013), induced by the symbiotic bacteria associated with the plants' roots and root nodules. Over longer time periods, grasses can benefit from the N fixation of legumes, leading to a dominance of grasses (Ledgard and Steele 1992) and a reduction in legume abundance. The relative proportion of legumes in grassland biomass and biodiversity is hence strongly dependent on the availability of N to the grasses, with high N availability negatively affecting legume abundance. The role of P in the interaction can happen in two different ways. High P availability can induce N limitation, while a limitation of P (or molybdenum or iron) negatively affects the colonization/activity of N fixers (Vitousek and Howarth 1991). P can therefore shift the legume/grass balance in both directions. In fact P, N, soil pH, precipitation, water content, and warmth holding capacity have all been shown to affect the interaction between grasses and legumes in pasture (Tyler and Ström 1995, Ström et al. 2005). Here, we hypothesize that the capability of grasses to accumulate silicon (Si) also strongly impacts on the relationship between legumes and grasses in mixed grasslands (Ma and Takahashi 1990, Schaller et al. 2012, 2016*b*).

Silicon is taken up by plants as monosilicic acid: Some plant families including grasses have active Si transporters (Ma and Yamaji 2006). The mechanisms behind the uptake of Si by plants have only really been studied in the last ten years, following the extensive work of Jian Feng Ma and his group (Ma and Yamaji 2015). Most work has concentrated on cereals and particularly rice. Rice is an effective Si accumulator: Rice plants have a series of "Si-pumps." But also a lot of other grasses are able to actively take up Si (Ma and Yamaji 2015). Active uptake of Si into root xylem occurs via the transporters Lsi1 and Lsi2 (Ma et al. 2008). Part of the intracellular Si can be effluxed back to the rhizosphere through Lsi1 (Zhao et al. 2010), but probably also through yet unidentified transporters (Clemens and Ma 2016). The transporter Lsi6 is involved in directing Si transport toward the panicles (Ma and Yamaji 2015).

The concentration of Si in plants varies considerably: Dicotyledons are generally lower Si accumulators than monocots (Trembath-Reichert et al. 2015). Poales, which include grasses, are among the highest Si accumulators, while Fabales, including legumes, are low accumulators (White and Broadley 2003, Hodson et al. 2005, Schaller et al. 2016*b*). Solid amorphous silica (often termed biogenic silica) is deposited in many species, but most particularly in the heavy Si accumulators such as the grasses. It is deposited in the endodermis of roots of, for example, wheat (Hodson and Sangster 1989). Heavier deposits can be found in most aerial organs including the culm, leaves, and inflorescence bracts of grasses (Piperno 1988). The deposits, known as phytoliths, take the shapes of the cells in which the deposition occurs, and are often used in archaeological and paleoecological research (Hodson 2016). Another form of Si deposit in aboveground tissues is the Si-double layer, which together with the phytoliths controls the condensation state of the Si compounds (Schaller et al. 2013*a*). A higher condensation state decreases the Si mobilization from plant material during decomposition (Schaller et al. 2013*b*). Silicon availability during plant growth can affect grass biomass production, grass nutrient content, and grass nutrient stoichiometry (Neu et al. 2017). Silicon acts as an anti-herbivore defense by increasing tooth and mandible wear and reducing the digestibility of plant material from grasses (Massey and Hartley 2009), and at least partly controls P availability (Seyfferth and Fendorf 2012) and P uptake by plants (Neu et al. 2017). After grass decay, Si affects carbon and nutrient recycling during organic matter decomposition by increasing decomposition rates and decreasing nutrient mobilization, as recently shown for *Phragmites australis* in a pot experiment (Schaller et al. 2012, Schaller and Struyf 2013). This research is at its infancy, and the mechanisms whereby Si controls P at both the species and community levels are unknown.

Interestingly, for legumes calcium (Ca) is known to positively affect N and P supply and in turn biomass production (Andrew and Johnson 1976, Jakobsen 1993). Ca concentrations in plant biomass vary considerably, but are generally lower in orders of commelinoid monocots (including the grasses) than other monocot or eudicot orders (Broadley et al. 2003). On entering the root, most Ca is transported passively in the apoplast (cell walls and intercellular spaces). Some Ca moves across the plasma membranes of the root cells through Ca^{2+}-permeable ion channels, but Ca concentrations in the cytoplasm are strictly controlled at low (submicromolar) levels (White and Broadley 2003). Although Ca has an important role in cell signaling, it is toxic to plant cells at moderate concentrations. Therefore, excess Ca is removed from the cytoplasm by Ca^{2+}-ATPases and H^{+}/Ca^{2+} antiporters, and is either pumped from the cytoplasm into the apoplast or into the vacuole and other membrane-bound cellular organelles. Calcium must enter the protoplasts at the level of the root endodermis in the root, as the Casparian strips block the apoplastic route at that point. This means that delivery of Ca to the xylem is restricted mostly to the tips of roots and areas where lateral roots are emerging. Long-distance transport of Ca is exclusively in the xylem and is thus unidirectional. The element is carried passively in the transpiration stream and tends to accumulate at the end of the stream in the leaves. Presumably because of its toxicity to the cytoplasm, Ca is not re-translocated in the phloem, a living tissue, but increases in concentration over time in leaves. Furthermore, Ca is incorporated by Ca-accumulating plants as Ca oxalate crystals for defense against herbivory (Nakata 2003). For a more detailed overview on soil Si and Ca availability and distribution, please see Bear and Toth (1948), Haynes (2014).

While grasses are known as Si accumulators (Epstein 1994), many legumes are Ca accumulators (Broadley et al. 2004, Bauer et al. 2011). Consequently, the dominance of a particular plant group (e.g., grasses, legumes) is likely to be partly related to the ecosystem processes affecting Si and Ca availability, which differs depending on the bedrock or soil diagenesis stage (Derry et al. 2005, Bothe 2015). We therefore argue that the interactions between Si and Ca cycling can play a role in structuring grassland communities, and the feedbacks that exist between their relative availability and grass/legume dominance remain to be determined.

Silicon/calcium interactions in plants

There have been few studies on the interaction between Si and Ca uptake in plants. Ma and Takahashi (1993) reported that at a concentration of 1.66 mmol/L in hydroponic culture, Si decreased Ca uptake in rice plants. This was related to decreased transpiration caused by silica deposition in the leaves. However, increased Ca in the nutrient solution did not affect Si uptake and deposition. Hammond et al. (1995) found that concentrations of Si up to 2 mmol/L had little effect on Ca content of barley seedlings, but 2.8 mmol/L caused a decrease in Ca content. More recently, Brackhage et al. (2013), working on common reed in a pot experiment, showed that increased Si availability (through addition of solid amorphous silica) decreased Ca uptake and transport to the shoot. It is thus clear that Si availability decreases Ca uptake in grasses in experimental setups at high concentrations. We have been unable to locate any evidence for other plant groups. We also found one study (Ma and Takahashi 1993) suggesting that Ca has no effect on Si uptake.

To further investigate the interactions between Si and Ca in shoot concentrations across multiple plant groups, we therefore carried out a comparative analysis of the data obtained by Hodson et al. (2005) for Si and Broadley et al. (2003) for Ca for grassland species. In both papers, a detailed literature survey identified suitable data, and this was then subjected to a meta-analysis to give relative elemental contents (relative Si and relative Ca). A residual maximum-likelihood (REML) procedure was used to adjust for differences in shoot Si and Ca concentrations between studies.

Hodson et al. (2005) presented data on 44 angiosperm clades (orders or unassigned families). Of these, 18 were also considered by Broadley et al. (2003). Fig. 1a shows the relative Si and Ca values plotted against each other for the 18 orders. There is no clear relationship between Si and Ca (no significant correlation). It is, however, immediately apparent how different the Poales (circled) are from all other orders. Fig. 1b shows the same plot excluding the Poales. The remaining data points are all dicots. Within the dicots, there does appear to be a weak positive correlation (0.379) between relative Si and Ca, but narrowly below the 95% significance level ($P = 0.06$). This could indicate that some dicot orders that accumulate higher Si also accumulate higher Ca. This is different from the Poales, where Si was found to decrease Ca uptake in the experimental studies mentioned earlier.

We also tested whether there was a relationship between Ca and Si in grasses using the data from Hodson et al. (2005) and Broadley et al. (2003); 27 grass species were common to both

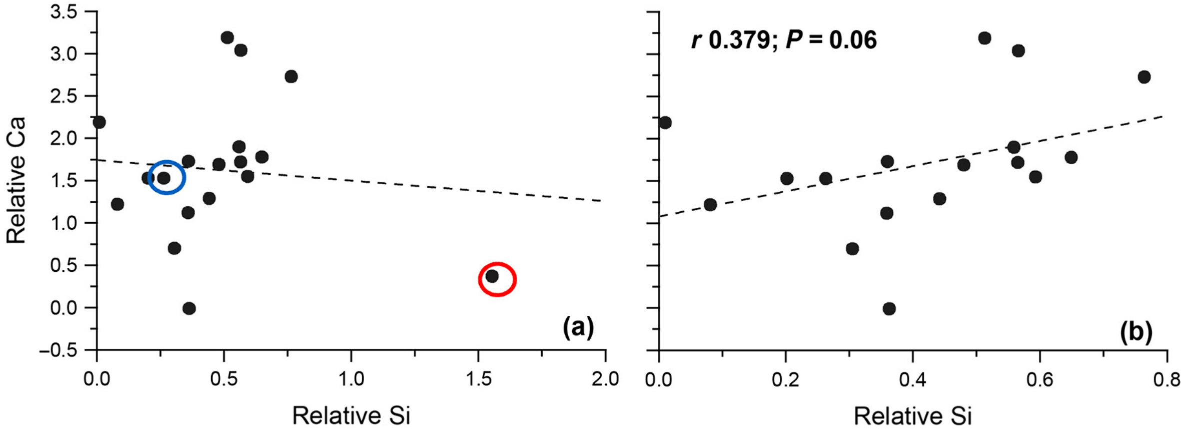

Fig. 1. Relative Si vs. Ca content of (a) shoot values of 18 angiosperm orders (Poales circled in red, Fabales in blue) and (b) shoot values of 17 dicot orders. The data were obtained by Hodson et al. (2005) for Si and Broadley et al. (2003) for Ca in grassland species. In both papers, a detailed literature survey identified suitable data, and this was then subjected to a meta-analysis to give relative elemental contents (relative Si and relative Ca). A residual maximum-likelihood (REML) procedure was used to adjust for differences in shoot Si and Ca concentrations between studies.

studies. Fig. 2a shows no significant correlation between the relative Si and Ca values for these 27 species. As we have noted above, the Poales are active accumulators of Si. While previous research mainly identified a negative relationship between Si and Ca content, our data indicate the absence of any relationship between Si and Ca concentration in the Poales. The concentration range of monosilicic acid in soil is from 0.01 to 2.0 mmol/L (Haynes 2014), but is more usually in the range between 0.1–0.6 mmol/L (Haynes 2014). For soils, the Si concentration is thus below the level that would be likely to decrease Ca uptake in the majority of the cases. Within the dataset, there are some species (e.g., rice, *Oryza sativa*) that accumulate relatively high amounts of both Ca and Si, while some like *Juncus effusus* are relatively low in both elements.

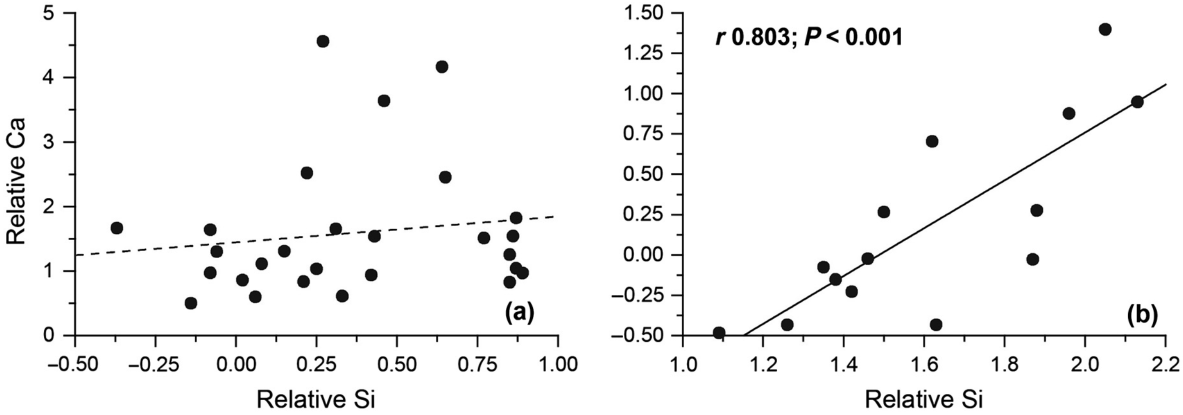

Fig. 2. Relative Si vs. Ca content of (a) Poales and (b) Fabales. The data were obtained by Hodson et al. (2005) for Si and Broadley et al. (2003) for Ca in grassland species. In both papers, a detailed literature survey identified suitable data, and this was then subjected to a meta-analysis to give relative elemental contents (relative Si and relative Ca). A residual maximum-likelihood (REML) procedure was used to adjust for differences in shoot Si and Ca concentrations between studies.

Fourteen species in the Fabales were considered by both Hodson et al. (2005) and Broadley et al. (2003). In these species, we observe a strong positive correlation (0.803, $P < 0.001$) between the relative Si and Ca values (Fig. 2b). As far as we are aware, this relationship has not been identified previously. Although based on a fairly small sample size, it does suggest that both Si and Ca have passive uptake mechanisms in the Fabales (and to a lesser extent other dicots) and that those species that accumulate more of the one element also accumulate more of the other. Species like *Glycine max* and *Phaseolus vulgaris*, which accumulate relatively high levels of both Si and Ca, would be expected to increase biogeochemical cycling of both elements if they were present in pasture. Conversely, species like *Glycine wightii* and *Desmodium uncinatum*, which accumulate relatively low levels of both Si and Ca, would be expected to have little effect.

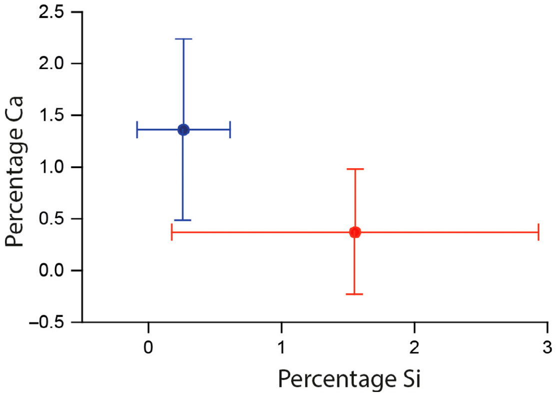

Fig. 3. Mean (±SD) Si and Ca concentrations in the Poales (red) and Fabales (blue). Si data (Poales n = 394 and Fabales n = 45) in Supplementary data from Hodson et al. (2005) and Ca data (Poales n = 403 and Fabales n = 646) courtesy of Martin Broadley and Philip White.

Silicon and calcium in pasture vegetation

A typical pasture is dominated by grasses and legumes with smaller amounts of other dicot species. Legumes are excellent pioneer species on infertile substrates, principally because they are not reliant on N in the soil, as they have symbiotic bacteria in nodules in their roots which fix N from the atmosphere (Vitousek and Howarth 1991). In contrast, grasses are not as well adapted to infertile soil, but as legumes fertilize N-poor substrates, they render them more suitable for grass growth. Once the grasses become established, they tend to grow faster than the legumes, partly because they do not need to provide sugars as an energy source for symbiotic partners (Vitousek and Howarth 1991). As such, they outcompete legumes in mature pasture and become dominant.

To gain an appreciation of Si and Ca in pasture, we again turned to Hodson et al. (2005) for Si data, but this time to the supplementary data which give Si concentrations as percentages of biomass. Martin Broadley and Philip White kindly provided the percentage Ca data which lay behind much of the relative data presented in Broadley et al. (2003). We then combined the data from their experimental and literature survey approaches. Ca was higher in the Fabales than in the Poales and, as expected, Si is considerably higher in the Poales than in the Fabales (Fig. 3). Mean Si is quite variable, particularly in the Poales. The original data came from many studies conducted worldwide, but should give a reasonable estimate for our purposes. The pattern of grasses accumulating more Si than legumes was also apparent in a biodiversity experiment where all plants were grown in the same soil (Schaller et al. 2016*b*). In this case, Si content in the Poales was ~1% and for the Fabales it was ~0.3%, being within the range of the abovementioned literature. The Ca content in this experiment was 0.8% for Poales and 1.6% for Fabales. These values are comparable with those from the literature mentioned above.

Having obtained estimates of percentage Si and Ca in the Poales and Fabales, it is then possible to create a "virtual pasture" in which the yields of both orders varied between 0% and 100% (Fig. 4). This illustrates the large differences in Si and Ca taken up by the pasture vegetation during grass/legume succession and soil development.

It is thus clear that we should expect the relative proportions of Poales and Fabales to significantly influence both Si and Ca cycling in pasture. Moreover, it is evident from our analysis that the presence/absence of certain plant species within the Poales and Fabales in the pasture system will also have an important effect. In the next section, we argue that the resultant

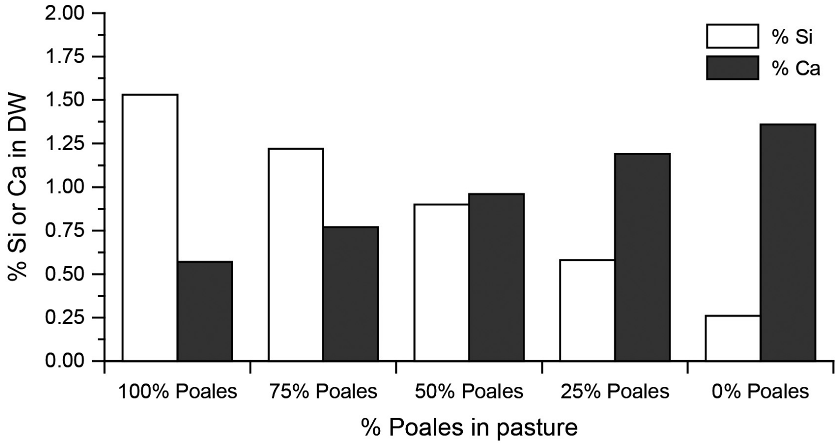

Fig. 4. Percentage Si and Ca content in dry weight (DW) in a "virtual pasture" of Poales and Fabales.

changes in Si–Ca availability in the soil could be important in pasture succession or oscillation of grasses and legumes.

A Conceptual Model for Si–Ca Interactions in Pasture Succession

Grass communities cycle large amounts of Si via plant root uptake and litter fall (Cornelis et al. 2010). Silicon stored in dead plant biomass has high dissolution rates in soils and sediments, in the same order of magnitude as Si-containing secondary reactive minerals, such as illite and kaolinite (Dixit and Van Cappellen 2002, Fraysse et al. 2009, Haynes 2014, Bélanger et al. 2015). Quartz and most primary minerals have a much lower solubility, suggesting that Si-accumulating plants can strongly influence turnover rates of Si in soils (Lucas 2001, Sommer et al. 2006).

On the one hand, Si in grasses can be beneficial for plant growth, resulting, for example, in better P status, biomass production, and nutrient-use efficiency (Neu et al. 2017). On the other hand, optimal Ca availability may increase nutrient uptake for legumes and herbs (Ma and Takahashi 1993, Zhao et al. 2012). Calcium is positively correlated with nodulation, resulting in better N supply and biomass production (Andrew and Johnson 1976). Calcium also increases legume P uptake and in turn biomass production (Jakobsen 1993). This supporting effect is due to the simultaneous uptake and translocation of Ca and P.

The Si/Ca availability ratio may consequently be important for the performance of particular plant functional groups (Si for grasses and Ca for legumes/herbs) in high-diversity grassland ecosystems (Fig. 5). An imbalance of Si/Ca may lead to suboptimal nutrition of one plant functional group resulting in a possible replacement by the functional group with a better nutrient state (e.g., poor Si nutrition resulting in more legumes). Under Si-rich and Ca-poor conditions, the dominance may shift to grasses; under Si-poor and Ca-rich conditions, the dominance may shift to legumes. This may lead to an altered plant community, which in turn may result in altered biomass production and nutrient turnover (e.g., N).

We propose a conceptual model for the role of Si/Ca availability in legume/grass dominance in pastures. Ca and Si differ in "weathering" mobility, that is, release from primary minerals. Earlier research has clearly shown that Ca is mobilized more rapidly from newly weathered soils compared to Si (Derry et al. 2005, Vitousek et al. 2014). During soil formation from bedrock or during other initial soil stages with low soil layer thickness, one could assume an overabundance of available Ca in soil compared to Si (Derry et al. 2005, Vitousek et al. 2014). This will be advantageous to legumes in the early stages of soil development. Furthermore, legumes have the advantage in this pioneer stage of creating their own N source, through the interaction with microorganisms (see *Silicon and calcium in pasture vegetation*). We assume a theoretical near 100% dominance of legumes in such an initial pasture, with grasses hampered in competitiveness by

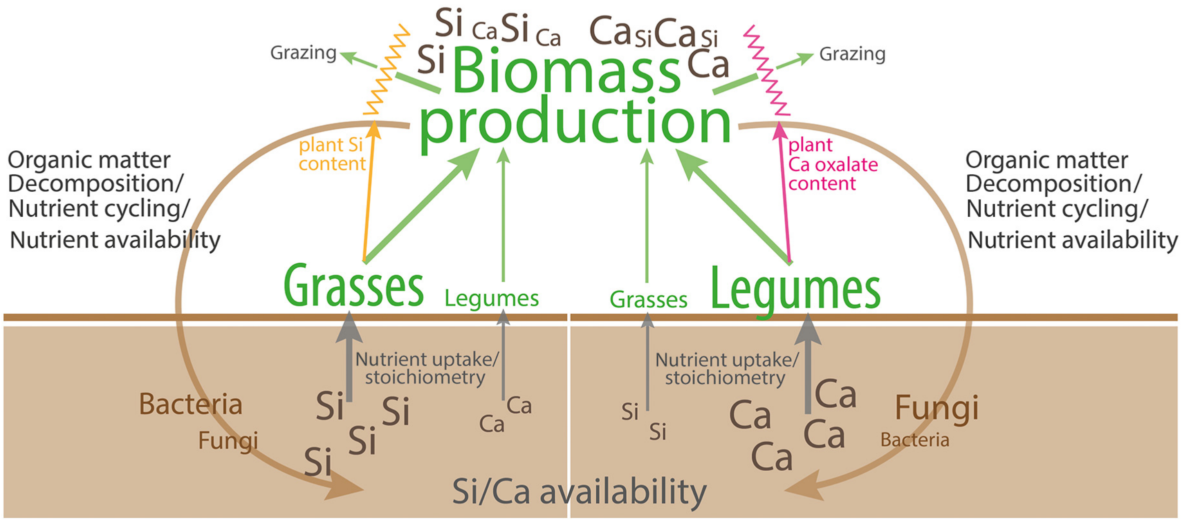

Fig. 5. Scheme showing the crucial role of Si/Ca availability in the dominance of grasses/legumes, biomass production, organic matter decomposition, microbial decomposer communities, nutrient cycling, and grazing.

low N and low Si availability. It is interesting to consider that grasses have been found to show lower N uptake under low Si conditions, potentially further hampering their ability to compete initially in a low Si, low available N environment (Schaller et al. 2012). This also increases the relative Ca in litter compared to Si, creating an even more favorable Ca environment for the legumes.

Gradually, however, the primary source of Ca from soil minerals may leach out over time, reducing availability of Ca. This might be compensated for initially by high Ca content in litter, but will still result in a gradually lower Ca availability. The soils also become richer in N, due to N-rich litter from legumes. This creates a more favorable environment for grasses, which at low Si availability, need more N to grow. As such, grasses may gradually constitute an ever larger part of the vegetation. Grasses will accumulate Si in their biomass, and upon decay, more Si-rich litter will become part of the soil. This could improve competitiveness of the grasses. At the same time, lower P availability may decrease legume competitiveness.

We thus propose a general mechanism where Si/Ca availability could be an important part of the frequently observed shift from legume to grass dominance in pasture (Fig. 5). Interestingly, this shift will also have strong biogeochemical and ecological implications, through the differential impacts of Si and Ca in litter on the decomposing community, through the effect of grass Si on grazers, and through the impact of Si on litter stoichiometry.

Implications

Grazing

With an estimated consumption of about 20% of total biomass (Cebrian 1999), grazing in grasslands has a high impact on ecosystem performance (Biondini et al. 1998). Besides herbivory changing plant morphology and nutrient accumulation pattern, also other factors may affect grazing (Bryant et al. 1983, Holland et al. 1992). In this context, the Si content of the plant material is important, because it acts as an anti-herbivore defense by increasing tooth and mandible wear and reducing the digestibility of plant material from grasses (Massey and Hartley 2009). However, some Ca accumulator plants incorporate Ca oxalate crystals for defense against herbivory (Nakata 2003). Hence, both Si and Ca are involved in strategies to reduce grazing.

Organic matter decomposition and nutrient cycling

The decomposer community in soils consists of bacteria, fungi, and invertebrates (Gessner et al. 2010). Microorganisms are, however, the most important agent for decomposition of organic material. The heterotrophic decomposer community of microbes was found to change with increasing organic matter Si content from grass litter, resulting in a significant decrease in fungi (Schaller et al. 2014). This decrease in fungal decomposers did not translate to reduced organic matter decomposition. On the contrary, the decomposition increased with increasing organic matter Si content (Schaller and Struyf 2013, Schaller et al. 2014). Bacteria are here prime candidates as alternative microbial decomposers. However, another study analyzing the effect of organic matter Si content on composition of the microbial decomposer community found a negative effect of Si on both gram-positive and gram-negative bacteria (Schaller et al. 2016*a*). Hence, Si may affect decomposition by altering the microbial decomposer community. Decomposition has also been found to positively correlate with (1) legume presence, as an effect of increasing N in the organic matter, decreasing the C/N ratio of the organic matter (Fog 1988), and (2) organic matter Ca content (Berg 2000). But in contrast to Si, Ca was found to increase fungal biomass during decomposition because fungi require much more Ca compared to bacteria (Lindeberg 1944, Berg 2000). Hence, the microbial decomposer community may be altered when grasslands shift between grasses and legumes.

Fungi are the most important agents in the process of dissolved organic carbon (DOC) production, probably because of their incomplete degradation of organic matter (Guggenberger et al. 1994). If fungi are important for DOC formation, the organic matter Si/Ca ratio may be significant as increasing Si decreases fungal biomass, while Ca increases fungal biomass (see last paragraph). Römkens and Dolfing (1998), however, found that Ca increases the precipitation of DOC, with the high molecular weight fraction of DOC preferentially precipitated and low molecular weight organic substances being unaffected. Hence, too much Ca in organic matter may lead to DOC decrease.

Grasses and legumes also influence the N and P cycle in grasslands (Spehn et al. 2002). Oelmann et al. (2011) found that legumes increase aboveground P storage in plant biomass and decrease the labile P concentrations in soils. Uptake of P and N by legumes is positively correlated with Ca and has an impact on biomass production (Andrew and Johnson 1976, Jakobsen 1993). The effect of legumes on both the N and the P cycle may therefore be influenced by Ca availability. Silicon has a strong effect on nutrient cycling and uptake by grasses, by increasing P uptake and nutrient-use efficiency, resulting in an altered litter stoichiometry and potentially altered decomposition rates (Schaller et al. 2012, Brackhage et al. 2013, Schaller and Struyf 2013, Neu et al. 2017).

SYNTHESIS AND CONCLUSIONS

We propose a conceptual model in which the role of Si/Ca availability is a potentially important factor for legume/grass dominance in pastures (Fig. 5). Depending on the bedrock or soil diagenesis stage, the Si/Ca availability is different. During soil diagenesis, the relative availability of Ca and Si shifts, with potential effects on the presence of certain plant species. The shift in the balance between legumes and grasses, and the resulting Si–Ca mobilization changes have multiple potential biogeochemical consequences. The grazing defense strategy of the plants alters: Legumes protect themselves using Ca oxalate compounds, whereas grasses use silica. Litter decomposition is also affected. High Ca content in litter favors heterotrophic fungi, whereas high Si content in litter suppresses fungi. Si and Ca uptake also impacts on the biological turnover of N and P. This overview thus provides evidence of substantial Si/Ca availability effects on ecosystem functioning in grasslands. Considering the processes discussed here in biogeochemical and ecological research will lead to a better understanding of nutrient cycles, shifts in biodiversity, and biomass production.

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