Linking stoichiometric homeostasis with ecosystem structure, functioning, and stability

Qiang Yu1,*, Quanzheng Chen1, James J. Elser2, Ariane Cease3, Nanpeng He2, Honghui Wu2, Guangming Zhang2, Jianguo Wu4, Yongfei Bai4, Xingguo Han1,5

1State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China 2Graduate University of Chinese Academy of Sciences, Beijing 100049, China 3Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China 4School of Life Science, Arizona State University, Tempe, AZ 85287, USA

Introduction

The ecosystems upon which humans rely have been altered in unprecedented ways by human population expansion and industrialization, making it critical to understand the mechanisms that underlie ecosystem structure, functioning, and stability. Many studies have shown that greater ecological diversity leads to greater ecosystem production and stability but the topic remains controversial. The diversity of species traits present, especially in natural use strategies, is likely to play a fundamental role in modulating the relationship between biodiversity and ecosystem structure, functioning, and stability because these traits link organismal functioning to ecological sustainability and to key environmental factors such as biogeochemical nutrient supplies.

Stoichiometric homeostasis is the ability of an organism to maintain a given elemental composition despite variation in the elemental composition of its environment or diet and reflects the set of many underlying physiological and biochemical adjustments as organisms respond to their surroundings. Indeed, stoichiometric homeostasis is a fundamental concept of ecological stoichiometry as applied to trophic interactions. While early studies have emphasized strong physiological variations in elemental composition to phosphorus, especially algae and cyanobacteria, only a few studies have actually quantified the degree of stoichiometric homeostasis in terrestrial vascular plants. To our knowledge, no studies have examined the relationships between stoichiometric homeostasis and key aspects of ecological performance, such as species dominance, ecosystem function, and stability. In this study we examined these associations.

Methods

Our exploration of these patterns took place in the Inner Mongolia grassland of China, the largest contiguous grassland in the world. First, we examined the strength of stoichiometric homeostasis by measuring the stronger (N) and phosphorus (P) contents and N:P ratios in two different species (Leymus chinensis and Cenchrus ciliaris) and an annual species, the field N addition experiment is given in Figure 1. Species-level H was consistently positively correlated with dominance and stability on both the 20-year and 64-year scales and over a 200-km linear transect (Figure 1). At the community-level, H was also positively correlated with ecosystem function and stability in most cases (Figure 1).

Results

In this study, we estimated H of twelve species in a two-year field N and P addition experiment and found positive relationships between H and species dominance. Using these H values we subsequently documented positive patterns of species dominance over a 27-year seasonal scale and a 1200-km spatial scale. Overall, these positive association indicate that species with higher H are more dominant than those with lower H, supporting the view that stoichiometric homeostasis is an important mechanism underlying community structure. If we also positively associated with species utility in terms of these data sets. Thus, H predicted species stability not only in relation to short-term variation in nutrient supply (Figure 2A) but also in the context of long-term temporal dynamics (i.e. changes due to temperature or precipitation) (Figure 3A) and large-scale spatial variation (Figure 3C). Our experimental results suggest that the higher and more stable biomass-production of dominant perennial grass species is associated with their hauing of key limiting nutrients as indexed by H.

In meadow grassland (triangles), typical steppe (squares), and meadow-steppe (circles) communities. H in meadow grassland was higher than in the other two vegetation types: meadow-steppe and typical steppe. Species richness was measured by rarefaction. a, The 20-year monitoring study. c, The 27-year monitoring study. c, The 300-year monitoring study. a, The 20-year monitoring study. b, The 27-year monitoring study. c, The 300-year monitoring study.

Conclusion and Discussion

This study, in which we achieved H of twelve species in a two-year field N and P addition experiment and found positive relationships between H and species dominance. Using these H values we subsequently documented positive patterns of species dominance over a 27-year seasonal scale and a 1200-km spatial scale. Overall, these positive association indicate that species with higher H are more dominant than those with lower H, supporting the view that stoichiometric homeostasis is an important mechanism underlying community structure. If we also positively associated with species utility in terms of these data sets. Thus, H predicted species stability not only in relation to short-term variation in nutrient supply (Figure 2A) but also in the context of long-term temporal dynamics (i.e. changes due to temperature or precipitation) (Figure 3A) and large-scale spatial variation (Figure 3C). Our experimental results suggest that the higher and more stable biomass-production of dominant perennial grass species is associated with their hauing of key limiting nutrients as indexed by H.

Community production and stability was positively correlated with community H both in the short-term and the long-term experiments. However, the strength of the relationship between community production and stability and community H declined substantially from short-term to long-term studies. This suggests that linking short-term species with long-term ecosystem production and stability requires careful consideration of more fluctuating environmental factors, particularly rainfall and temperature. No significant relationships were found in typical steppe and desert steppe across the large-scale transect (a significant relationship was only found in meadow grassland). This may reflect the fact that community structure and soil fertility differed considerably across the spatial transect as suggested by previous studies. More importantly, grazing was not excluded at sites along the transect. It is likely that grazing was heavier in the desert grassland and typical grassland sites relative to the meadow grassland sites we sampled, which could be seen clearly from the biomass data (Figure 3C). Nevertheless, these results suggest that aggregated community stoichiometric homeostasis can predict ecosystem functioning and stability at the local scale in grasslands.

Our data suggest that stoichiometric homeostasis is a key species trait linked to ecosystem functioning and stability. In this study, the species with high H are potential genets with high root : shoot ratios. This suggests that the resource scavenging and storage functions of root allow these species to buffer the metabolism and production of aboveground biomass against environmental variation, promoting community stability. While additional research is needed to establish the underlying mechanisms by which H is related to important aspects of ecological dynamics, the predictive ability of H likely reflects the fact that many intrinsic properties of individual species, including their physiological adaptations to abiotic environmental factors, are embodied in it. Thus, the strength of stoichiometric homeostasis is not only a key concept for understanding the nature of trophic interactions at the landscape level but also an important characteristic of species utility in terms of these data sets. Thus, H predicted species stability not only in relation to short-term variation in nutrient supply (Figure 2A) but also in the context of long-term temporal dynamics (i.e. changes due to temperature or precipitation) (Figure 3A) and large-scale spatial variation (Figure 3C). Our experimental results suggest that the higher and more stable biomass-production of dominant perennial grass species is associated with their hauing of key limiting nutrients as indexed by H.

The stoichiometric regulation of each plant species was estimated by calculating the stoichiometric regulation coefficient (H) according to the following equation: y = a + bx, where y is the N or P content (% dry mass) and x is the N or P available (N or P) content or N:P ratio in the soil, x is a constant. Community H was calculated by the ratio of H across all species weighted by species x's relative (functional) contribution in overall biomass. In the N and P addition experiment, associations of plant N and P contents and N:P ratio with soil nutrient contents and N:P ratio could be rigorously described by the stoichiometric homeostasis model (Sterner & Elser 2002): y = ax + bx^2. Exemplary data for strong N homeostasis in Leymus chine (a dominant species in the steppe), N homeostasis in Cenchrus ciliaris-panicles, an annual species, from the N additions experiment are given in Figure 1.

Conclusion and Discussion

In this study, we estimated H of twelve species in a two-year field N and P addition experiment and found positive relationships between H and species dominance. Using these H values we subsequently documented positive patterns of species dominance over a 27-year seasonal scale and a 1200-km spatial scale. Overall, these positive associations indicate that species with higher H are more dominant than those with lower H, supporting the view that stoichiometric homeostasis is an important mechanism underlying community structure. If we also positively associated with species utility in terms of these data sets. Thus, H predicted species stability not only in relation to short-term variation in nutrient supply (Figure 2A) but also in the context of long-term temporal dynamics (i.e. changes due to temperature or precipitation) (Figure 3A) and large-scale spatial variation (Figure 3C). Our experimental results suggest that the higher and more stable biomass-production of dominant perennial grass species is associated with their hauing of key limiting nutrients as indexed by H.

Community production and stability was positively correlated with community H both in the short-term and the long-term experiments. However, the strength of the relationship between community production and stability and community H declined substantially from short-term to long-term studies. This suggests that linking short-term species with long-term ecosystem production and stability requires careful consideration of more fluctuating environmental factors, particularly rainfall and temperature. No significant relationships were found in typical steppe and desert steppe across the large-scale transect (a significant relationship was only found in meadow grassland). This may reflect the fact that community structure and soil fertility differed considerably across the spatial transect as suggested by previous studies. More importantly, grazing was not excluded at sites along the transect. It is likely that grazing was heavier in the desert grassland and typical grassland sites relative to the meadow grassland sites we sampled, which could be seen clearly from the biomass data (Figure 3C). Nevertheless, these results suggest that aggregated community stoichiometric homeostasis can predict ecosystem functioning and stability at the local scale in grasslands.