Plant Nutrients Appears Decoupled from Soil: Increasing Influences from Changing Climate in the Grassland's of Inner Mongolia, China

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Research Article

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Abstract

Extremes in weather episodes seem to be the new normal. We need to better understand how changing climatic conditions alter plant growth in grasslands, especially macro nutrient uptake and stoichiometry. However, few studies have examined how warmer/colder or wetter/drier climates influence the nutrient decoupling between plants and soils at the ecosystem level. Here, we investigated the changes in carbon (C), nitrogen (N), and phosphorus (P) concentrations and their stoichiometric ratios in plants and soils from 65 grassland sites along a geographic gradient of temperature and aridity in northern China. Often, we saw inverse responses between plant and soil nutrients with respect to temperature and aridity. Soil C and N were negatively correlated with temperature and aridity. Soil P was negatively correlated with aridity. Plant N was positively correlated with aridity and plant P was negatively correlated with temperature, while plant C had no relationship with either. Temperature and aridity were positively correlated with C:N and negatively correlated with C:P and N:P ratios in soils. However, aridity was negatively correlated with plant C:N ratios. Plant N:P ratios were positively correlated with temperature and aridity, whereas plant C:P ratios had no relationship with either. Our findings suggest at a broad geographic scale, plant nutrients do not always reflect soil nutrient availability. It is conceivable that rapid climate shifts and the resulting changes in element availability, turnover rates, absorption, and use efficiency might cause decoupling of C, N, and P cycles between plants and soils.

Introduction

Plant stoichiometry among carbon (C), nitrogen (N), and phosphorus (P) is the main factor affecting ecosystem productivity (Chapin et al. 2011). C:N:P ratios reflect ecosystem structure and function (Sterner and Elser 2002; Yuan and Chen 2015). The dynamic balance of C, N, and P in soils and plants directly affect soil fertility, plant nutrient uptake, and plant productivity. Plant C:N:P ratios exhibits the relative intensity of C, N and P metabolism. Plants adjust growth rate to adapt to the surrounding environment by regulating C:N:P ratios (Marschner 1995). It reasons that this adaptive ability in C, N, and P stoichiometries can predict plant growth and development (Elser et al. 2010).

All metabolic processes that drive stoichiometry in plants are temperature-dependent (Luo et al. 2015). Temperature variation may have direct and indirect consequences on C storage in soils (Sanaullah et al. 2014). Similarly, aridity influences the balance between C, N, and P in soils (Wardle 2013; Liu et al. 2019), and it may also affect plant metabolic processes, such as photosynthesis, respiration (Sanaullah et al. 2014), atmospheric N fixation, and subsequent microbial mineralization (Dai 2013; Liu et al. 2013; Wardle 2013). The *dilution effect hypothesis* suggests that both high soil fertility and high precipitation increase plant C uptake, growth rate, and plant size (Luo et al. 2013). This result might reduce plant nutrient concentrations (Jarrell and Beverly 1981). Therefore, study of the variation in stoichiometric ratios of plant and soil nutrients is key to understanding the impact of climate change on ecosystems. However, it remains unclear whether processes related to plant and soil nutrients are affected by predicted warming and drought.

Geographic gradients provide an opportunity to learn how plant and soil nutrient processes might respond to changes in temperature, precipitation, and aridity (Yuan and Chen 2009; Liu et al. 2013). Many factors along a geographical gradient can affect ecosystems, but variations in temperature and aridity have the greatest influence on plants and soils. In particular, grassland ecosystems are very likely to be impacted by changing temperature and aridity (Zavaleta et al. 2003; Hoeppner and Dukes 2012). Our transect gave ideal opportunity to study these issues. Such patterns may help to better understand the underlying mechanisms of plant and soil nutrients under the ongoing global environmental changes.

Although recent studies have examined how plant and soil nutrients respond to changes in temperature (Reich and Oleksyn 2004) and precipitation (Austin and Vitousek 1998; Yuan et al. 2011), further research is needed for a better understanding of how climate change affects the plant-soil nutrient cycle. Given that climate change induces various responses in plants and soils with respect to nutrient use, we hypothesized that with the increasing temperature and aridity, nutrient patterns between plants and soils are not necessarily the same, meaning that plant and soil nutrients may be decoupled.

In this study, we investigated how soil and plant nutrients responded to changes in temperature and aridity along a geographic gradient in northern China's grasslands. We aimed to determine: (1) how plant and soil nutrients and their stoichiometric ratios responded to macroclimates, and (2) whether plants and soils responded similarly to macroclimates along this geographic gradient.

Material And Methods

Study area and sampling sites

We collected plant and soil samples from a longitudinal range ~14° and latitudinal range ~12° (lat 37°48'-49°30' N and long 107°18'-121°6' E), located in semi-arid, arid and hyper-arid areas (Fig. 1). This region is characterized by a temperate continental monsoon climate, with mountain and tableland topography. The mean annual low temperature varies from -2°C (east) to 8°C (west), and mean annual precipitation ranges from 421 mm (east) to 183 mm (west). In this transect, temperature and precipitation range widely with little human interference. The dominant species along the transect are *Stipa capillata, Cleistogenes squarrosa, Carex* spp, and similar species. Soil types are predominantly Phaeozems, Chernozems, and Kastanozems.

Plant and soil sample collection and measurement

In the middle of July 2013, we established 65 sample sites along the transect and verified their latitude and longitude coordinates by GPS. At each site a 30 m × 30 m plot was set up with three sub-quadrats (0.5 m × 0.5 m) for collecting plant and soil samples. We collected intact and healthy aboveground parts of plants at each site to determine C, N, and P concentrations. Sampled plants were cleaned with deionized water to remove soil and then dried at 65°C to a constant weight. The plant samples were weighed and ground to pass a 100 mesh sieve and digested by H_2SO_4-H_2O_2. We measured plant contents of C using the potassium dichromate titrimetric method, total P by molybdenum blue colorimetry, and total N by Kjeldahl acid-digestion method. The C, N, and P contents in plants were expressed as mass-based nutrient concentration.

We also collected 15 soil core samples (5-cm in diameter) from the 0-30 cm layer at each site. Soil samples were dried in the laboratory and ground to pass a 100 mesh sieve. We determined soil contents of organic C by colorimetry after dichromate oxidation by boiling with a mixture of potassium dichromate and sulfuric acid. Total N content in soils was determined by Kjeldahl acid-digestion method. Total P in soils was determined by the sulfuric acid hydrolysis procedure. We used total N and total P content in soils as surrogates for N, and P availability because they are in general highly related to available C, N, and P (Delgado-Baquerizo et al. 2013a). The ratios of soil C:N, C:P, and N:P were calculated based on total N and P concentrations in soils along the studied aridity gradient. The determination methods of plant and soil nutrients have been described in details by Bao (2000).

Climatic data

First, we obtained the daily average temperature of the closest meteorological stations from National Oceanic and Atmospheric Administration (ftp://ftp.ncdc.noaa.gov/pub/data/gsod). Then we derived the mean temperature of the growth season from May to July in 2013. To better interpret our results, we substituted the aridity index (AI) with aridity, estimated as [1-AI] (Delgado-Baquerizo et al. 2013b; Yuan and Chen 2015). Our studied transect covers an aridity gradient from 0.40 to 0.83. Both temperature and aridity increased from east to west in the study region. AI is the ratio of mean annual precipitation (MAP) to mean annual potential evapotranspiration (MAE). MAP was determined from the global Worldclim data set (http://www.worldclim.org). MAE was calculated via monthly mean potential evapo-transpiration and derived from the Global-PET (http://www.cgiar-csi.org).

Data analysis

All plant and soil measurements (n=3 per site) were averaged for each site to conduct site-level statistical analyses. One-way analysis of variance was used to test the effect of climate types on plant and soil C, N and P concentrations. We used ordinary least squares (OLS) regression to determine the effect of temperature and aridity on C, N, and P concentrations in plants and soils. The relationships between plant C, N and P concentrations and their ratios and soil C, N and P concentrations and their ratios were explored by using Pearson correlation analysis. We defined an 'observed relationship' between two variables when the *p*-value was less than 0.001. The stoichiometric ratios of plants and soils were $\log_{10}$ transformed to meet normality assumptions. OLS regression and Pearson correlation analysis were conducted with the software program R version 4.0.3 (R Development Core Team 2011).

We used structural equations modeling (SEM) to evaluate the direct and indirect effects of aridity, temperature and soil C-N-P on the C, N, and P and their ratios of plants. The first step in SEM requires establishing a priori model (Fig. S1) based on the known effects and relationships among the climate factors and nutrients of plants and soils (Fig. 2-5 and Figs. S2 and S3). However, due to the small data size of this study, we used chi-square and comparative fit index as the standard of model fitness test (Bentler and Yuan 1999; Kenny et al. 2014). We fitted the different models using the *lavaan* package in R (Rosseel 2012).

Results

Table 1 presents the ranges in temperature, aridity, precipitation, soil organic C, total N, total P, plant C, N and P in 2013. Both soil C and N decreased as temperature (Fig. 2d and Fig. 2e) and aridity (Fig. 3d and Fig. 3e) increased across the studied geographic gradient. Soil P decreased as aridity (Fig. 2f) increased, but it was not significantly corelated to temperature (Fig. 3f). We found that soil C:P and N:P ratios were negatively correlated but soil C:N ratios were positively correlated with temperature and aridity (Figs. 4 and 5).

Table 1

Plant and soil nutrients among three climate types

Climate type	AI	Precipitation (mm)	Temperature (°C)	Soil nutrients			Plant nutrients		
				Carbon (%)	Nitrogen (%)	Phosphorus (%)	Carbon (%)	Nitrogen (%)	Phosphorus (%)
Semi-arid	0.40 - 0.58	318 - 421	18.06 - 19.94	0.61±0.06a	0.51±0.04a	0.05±0.01a	38.37±0.4a	1.04±0.08a	0.19±0.01a
Arid	0.53 - 0.77	202 - 355	17.63 - 21.37	0.22±0.02b	0.17±0.01b	0.03±0.002b	37.98±0.6a	1.22±0.05b	0.16±0.01a
Hyper-arid	0.75 - 0.83	183 - 243	19.28 - 20.80	0.10±0.01c	0.07±0.01c	0.03±0.003b	38.44±0.8a	1.53±0.2b	0.16±0.02a

Data are means ± SE. The climate types are classified according to the aridity index of UNEP (LeHouerou 1996). Different letters indicate significant ($p < 0.05$) differences among climate types. Abbreviations: AI, aridity index; Precipitation, mean annual precipitation in 2013-2014; Temperature, mean temperature in May to July 2013.

Plant nutrients tended to show opposite relationships to temperature and aridity compared to soil nutrients. For example, we did not find a significant relationship between plant C and temperature or aridity (Fig. 2a and Fig. 3a). N and P showed similar results as C (Figs. 2 and 3). Stoichiometric ratios also showed variable responses to temperature and aridity (Figs. 4 and 5). Correlation analyses found that plant C/N/P were not significantly correlated with soil C/N/P. Similar relationships were found between plant C:P ratios and soil C:P ratios (Figs. S2 and S3). The remarkable negative correlation was found between biomass and aridity, but not for temperature (Figs. S2 and S3).

Our SEM analysis explained 96, 97 and 97% of plant C:N, C:P and N:P ratios of the research data sets, respectively. (Fig. 6). Aridity had a strong direct negative effect on soil nutrients. Temperature had a weak direct negative effect on soil C and N but no effect on soil P. Soil nutrients had strong direct effects on soil stoichiometry. Temperature a direct positive effect on soil C:N, but a negative effect on soil C:P and N:P. Fig. 6 showed that plant N was strongly dependent on aridity, soil C:N and N:P ratios and weakly dependent on soil N. Plant P was strongly dependent on temperature, soil C:P and N:P ratios. Plant nutrients were the most important predictor of plant stoichiometry.

Discussion

Our findings suggest that soil nutrient concentrations increased from west to east. However, the spatial changes in plant nutrient concentrations from west to east were not distinct along the 3500-km transect. Our hypothesis is supported by the result that plant nutrient concentrations do not always agree with soil nutrient concentrations. The inconsistent nutrient patterns observed between plants and soils may be the consequence of the dilution effect. It has a greater influence than soil nutrient supply on plant nutrient concentrations in cooler and wetter areas. Our SEM analysis suggests that soil nutrient concentrations may not have a direct effect on plant nutrient concentrations because the effect of soil nutrients tend to be overwhelmed by macroclimates changes (temperature and aridity). Our analyses highlight that severe warming and droughts in drylands might lead to out-of-sync nutrient cycles between plants and soil under rapid change of global climate.

Climatic controls on soil and plant nutrients

Soil C and N increased while temperature and aridity decreased from west to east. This response could be due to the simultaneous decreased water availability and vegetation that likely intensifies soil drying and erosion. In fact, these events may compound and lead to further loss of soil C and N. Unlike the spatial patterns of soil C and N, soil P in our study was not strongly affected by temperature and it was negatively correlated with aridity (Fig. 7). Given that an increase of soil P in arid areas is mainly caused by rock weathering (Delgado-Baquerizo et al. 2013b), the decline of total soil P as aridity increased suggests that rock weathering products are readily available. Although previous studies showed that temperature affected soil P by influencing weathering (Reich and Oleksyn 2004), we did not found a relationship between total soil P and temperature in our study. This probably resulted from the relatively little change in temperature (Table 1). This indicated that total soil P depends more on aridity than on temperature in the grasslands of northern China. In addition, our result of SEM (Fig. 6) implied that increases in aridity in drylands were expected to lead to severe nutrient depletion.

C is the most abundant element in plants and plays a major role in supporting plant structure. Photosynthesis, not soil, is the main source for C in plants, by transforming atmospheric carbon dioxide into plant C (Hamerlynck et al. 2000; Huxman and Smith 2001; Tissue et al. 2010).

Therefore, plant C is relatively stable and does not change as much as soil C (Fig. 7). Across the geographic gradient we studied, plant N was positively correlated with aridity. This result was consistent with the findings by Luo et al. (2015) who reported a negative correlation between plant N and precipitation in northern China. Aridity is thought to cause N in plant cells to be allocated to enzyme proteins that maintain photosynthetic rate (Reich and Oleksyn 2004; Hikosaka and Shigeno 2009; Reich et al. 2009). These findings may also be due to the effect of humidity on promoting plant growth rate and increasing plant biomass, as our findings show in drylands (Fig. S4). Therefore, the accelerated growth may account for the “dilution effect” and lead to decreased plant N (Wang et al. 2019). In our study, temperature did not correlate with plant N. This result conflicts with the *°T-Plant Physiological hypothesis* proposed by Reich and Oleksyn (2004). They suggest that the dynamic processes of plant N are very sensitive to temperature, and the physiological acclimation makes plants have higher N concentration in cold climate. Our findings indicate that increasing aridity may stimulate the rates of decomposition and mineralization, as well as enhancing the soil N (Luo et al. 2015) and promoting N absorption by plants in drylands.

Climatic controls on stoichiometry of soils and plants

Soil stoichiometry reflects soil C decomposition and mineralization rates and nutrient balance (Bronson et al. 2004; Tian et al. 2010). We found that decreased temperature and aridity reduced soil C:N ratios but enhanced C:P and N:P ratios from west to east. We believe this indicates that soil C had a higher mineralization rate than that of N, and the mineralization rate of P was higher than that of C (Fig. 7). Several studies have shown that decreased temperature and aridity decelerated the mineralization of soil C and N (Schlesinger and Andrews 2000) by reducing soil respiration rate (Savage and Davidson 2001) and soil enzyme activity (Burns et al. 2013). Decreased aridity exacerbated the P leaching from soils. This is possibly the main reason for different mineralization rates along our studied geographic gradient.

Plant C:P ratios mainly depend on plant species characteristics (Zheng and Shangguan 2007), rather than temperature and aridity. That is likely the reason why we observed no correlations between plant C:P ratios and temperature/aridity in our study. Plant C:N ratios were negatively correlated with aridity (Fig. 7). According to the *Growth Rate hypothesis* (Elser et al. 2003; Makino et al. 2003), plant stoichiometry patterns are generally considered to reflect the acclimation and adaptation of macroclimate. Aridity decreased from west to east in the study region and humid conditions can stimulate plant growth rate (Luo et al. 2013). Thus, fast growing plants have higher C:N ratios in drylands than in humid systems.

In general, environmental changes and the resulting decoupling of plant N and P status may interrupt dryland nutrient cycles and further affect ecosystem functions like primary production, decomposition and others controlled by biogeochemical reactions (Delgado-Baquerizo et al. 2013b). Precipitation decreased along our study region from semi-arid to hyper-arid areas, and we found that aridity did not affect plant P while increased temperature reduced plant P. The plant N trends were not consistent with plant P trends and resulted in increased plant N:P ratios along the transect. Given that plant N:P ratios are an indicator of nutrient limitation for plant growth (Koerselman and Meuleman 1996; Aerts and Chapin 2000), the temperature- and aridity-related plant N:P ratios in this study indicate that plant growth is more limited by P than N in the grasslands of northern China.

Relationship between soil and plant nutrient status

Our study showed that environmental changes decoupled the nutrient status between plants and soils (Fig. 7). Soil nutrients increased as aridity decreased, while the nutrients of plants decreased along the transect. This finding diverges from the generally accepted view that plants in nutrient-rich soils tend to have high tissue nutrient concentrations (Koerselman and Meuleman 1996; Aerts and Chapin 2000; He et al. 2010). Presumably this is because increased soil nutrients may promote the nutrient uptake by plants. However, increased plant nutrient content and improved soil water conditions usually promote plant growth rate and biomass. Thus a “dilution effect” surfaces whereby decreased plant nutrient concentration leads to increased biomass (Jarrell and Beverly 1981; Elser et al. 2010). In this study, plant N was not correlated with soil N. We suggest the dilution effect had a greater influence on plant N uptake than increased soil N supply. We also did not observe a significant relationship between plant P and soil P. We think that the influence of the dilution effect and increased soil P supply on plant P uptake could be offset by climate change.

Our findings of decoupled plant and soil nutrient status may also be explained by how nutrient demand, rather than supply, drives plant nutrient concentrations. Specifically, plants in nutrient-rich soils have optimal growth conditions and may only absorb the nutrients that match their own growth demands, rather than match the soil nutrient supply (Prentice et al. 2014). In our study, increasing aridity reduced soil P, but did not affect plant P. This demonstrates that plant nutrient concentration mainly depends on plant nutrient utilization strategies and not soil nutrient supply (Fig. 7). The result of SEM (Fig. 6) also revealed that soil nutrients had a weak or no effect on plant nutrients under the board macroclimates. This further indicates the decoupling nutrient cycle between plants and soils in drylands.

Short-term manipulative experiments with N addition, however, often reveal that experimental N addition tends to enhance both plant and soil nutrients. For example, Han et al. (2013) and Vourlitis et al. (2007), indicated that plant-soil systems respond differently to short- and long-term nutrient changes. The contrasting findings between experimental studies with N addition and our study may be because plant nutrient concentrations are intricately linked to key ecosystem processes, including those involving soil nutrient concentrations. Those experiments only exerted a sudden change in soil nutrient concentrations on plants. However, the soil nutrient concentration effect tends to be overwhelmed by other changes (e.g., plant biomass, plant cover and soil properties) that can stem from climate shift on a large-scale climate gradient in our study. To summarize, the results of this study do not support the traditional view (Aerts and Chapin 2000; He et al. 2010) that plant nutrients always change in accordance with soil nutrient status. Our results imply that drought aggravation shifts the overall use strategy of these nutrients by the plant-soil system, potentially reducing the dependence of plants on soil nutrient supply in drylands.

Conclusion

In this study, we investigated the spatial patterns of C, N, and P concentrations and their stoichiometric ratios in plants and soils along a large geographic gradient of temperature and aridity in northern China. We found that

1) plant N was positively correlated with aridity, but negatively correlated with soil N. Soil P was also positively correlated with aridity. However, we did not observe a significant relationship between temperature and plant N or soil P.

2) These opposite spatial trends of plant and soil N:P ratios suggest a decoupling of plant nutrient uptake from soil supply. These results may be explained by the dependency of plant nutrient contents on a plant's nutrient utilization strategies, rather than the nutrient supply in the soil. Moreover, a “dilution effect” may decouple the nutrient link between plants and soils in cold and barren environments.

3) Our findings indicate that nutrient concentrations in plants may not always be positively correlated with soil nutrient availability under changing climatic conditions. Thus, plant nutrient uptake cannot be predicted simply using soil nutrient supply status, presenting challenges to large-scale biogeochemical modeling.

Declarations

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Authors' contributions: ZZY and XRS conceived the ideas and designed methodology; QD, LLC and GYL collected the data; XL analyzed the data; XL led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Figures

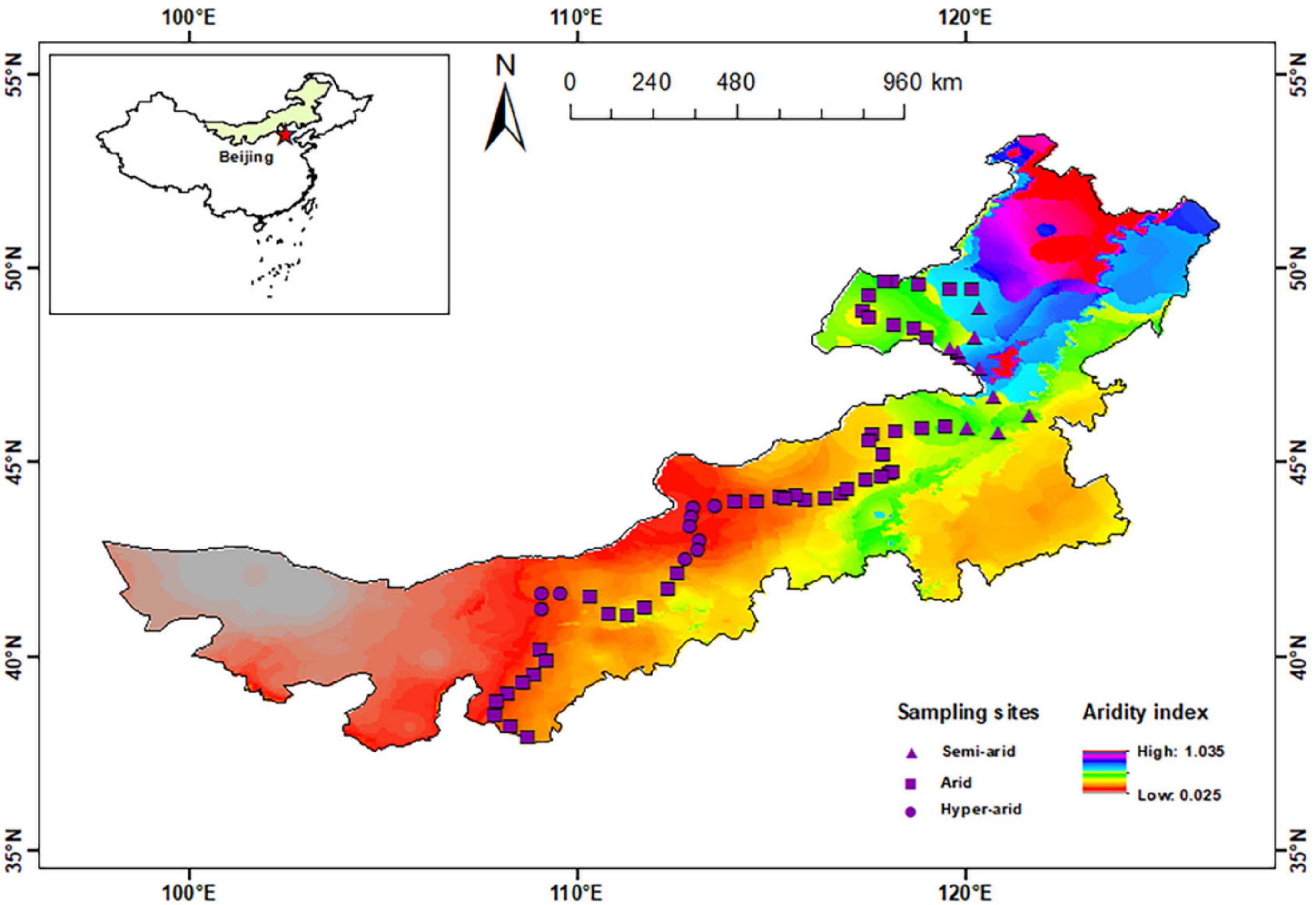

Figure 1

Sampling locations in this study.

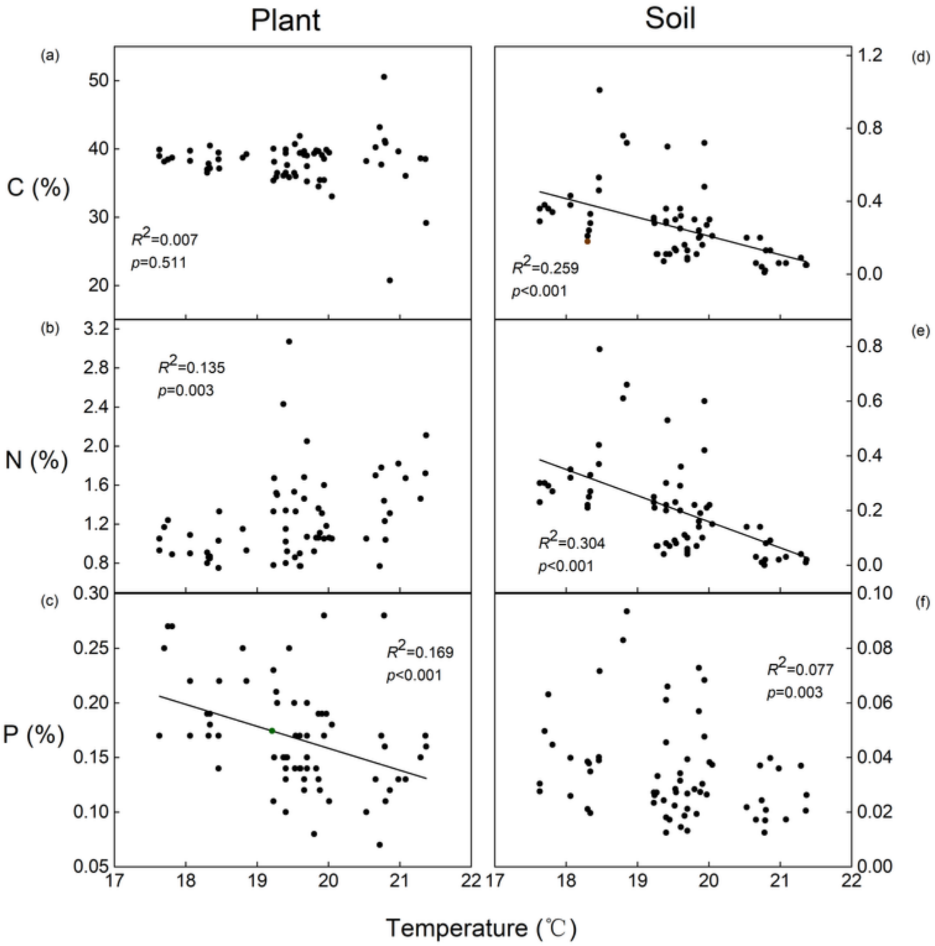

Figure 2

Changes in soil and plant nutrients in relation to mean temperature. (a-c) plant nutrients; (d-f) soil nutrients. The solid green and red lines represent the fitted linear regressions. R2, proportion of variance explained by regression line.

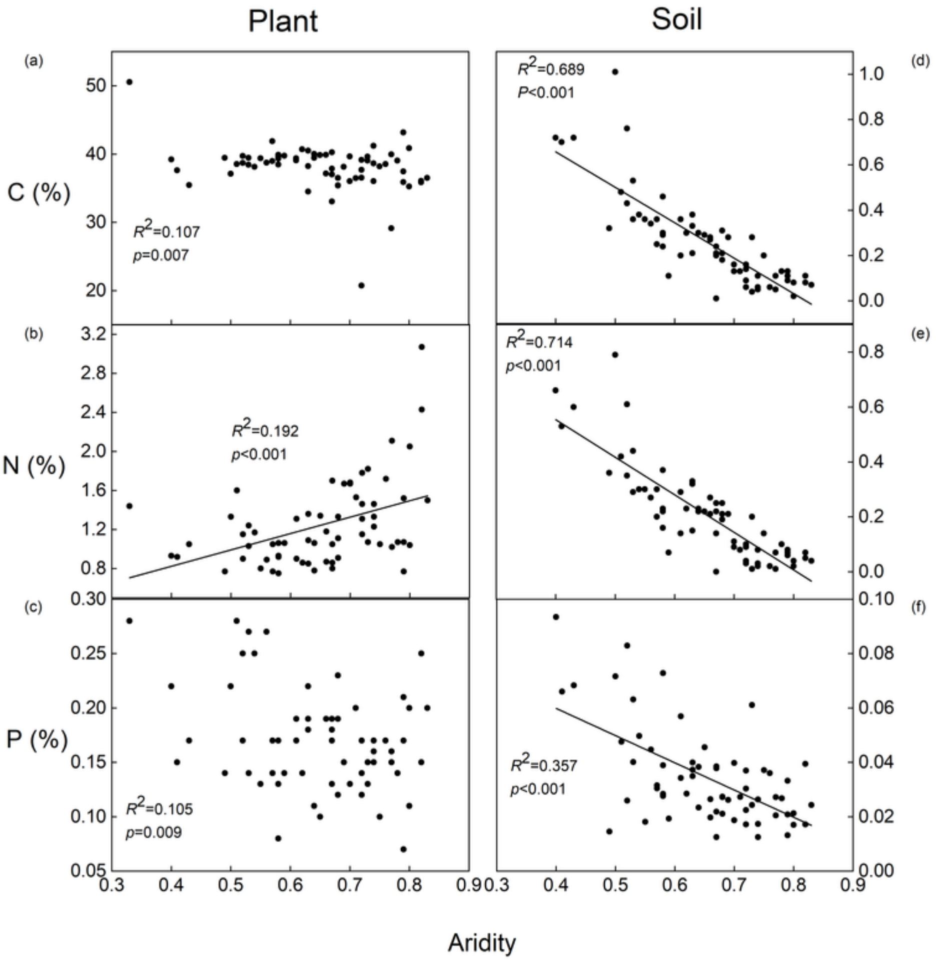

Figure 3

Changes in soil and plant nutrients in relation to aridity. (a-c) plant nutrients; (d-f) soil nutrients. Aridity refers to [1-AI], where AI is the aridity index, the ratio of precipitation to potential evapotranspiration. The solid green and red lines represent the fitted linear regressions. R2, proportion of variance explained by regression line.

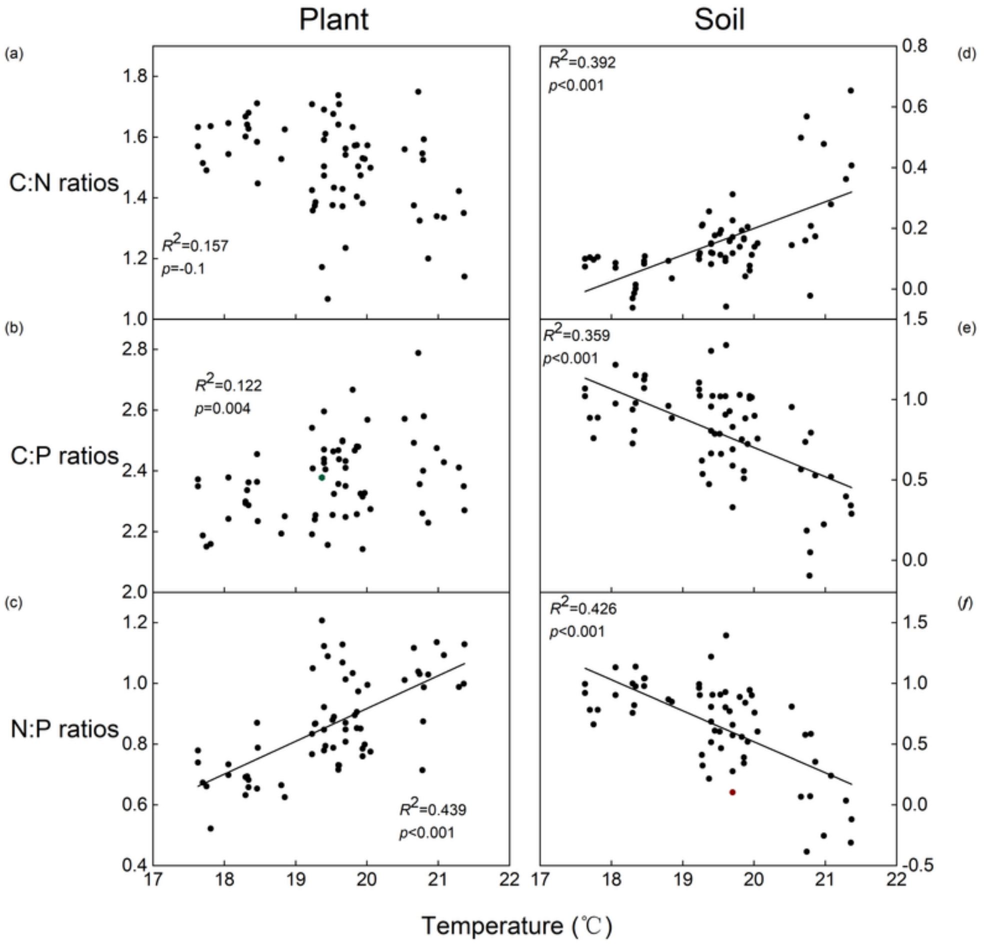

Figure 4

Changes in soil and plant stoichiometry in relation to mean temperature. (a-c) plant stoichiometry; (d-f) soil stoichiometry. The solid green and red lines represent the fitted linear regressions. R2 refers to proportion of variance explained by regression line. The values of stochiometric C:N:P ratio are log10-transformed.

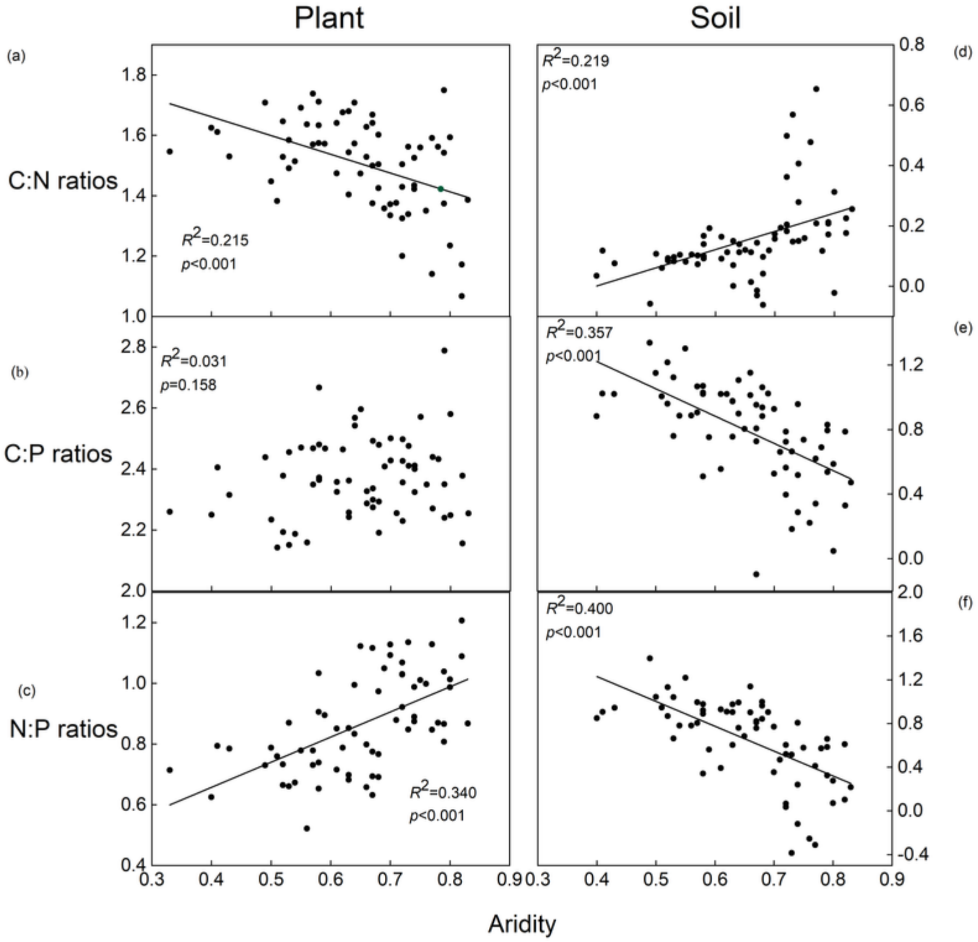

Figure 5

Changes in soil and plant stoichiometry in relation to aridity. (a-c) plant stoichiometry; (d-f) soil stoichiometry. Aridity refers to [1-AI], where AI is the aridity index, the ratio of precipitation to potential evapotranspiration. The solid green and red lines represent the fitted linear regressions. R2 refers to proportion of variance explained by regression line. The values of stochiometric C:N:P ratio are log10-transformed.

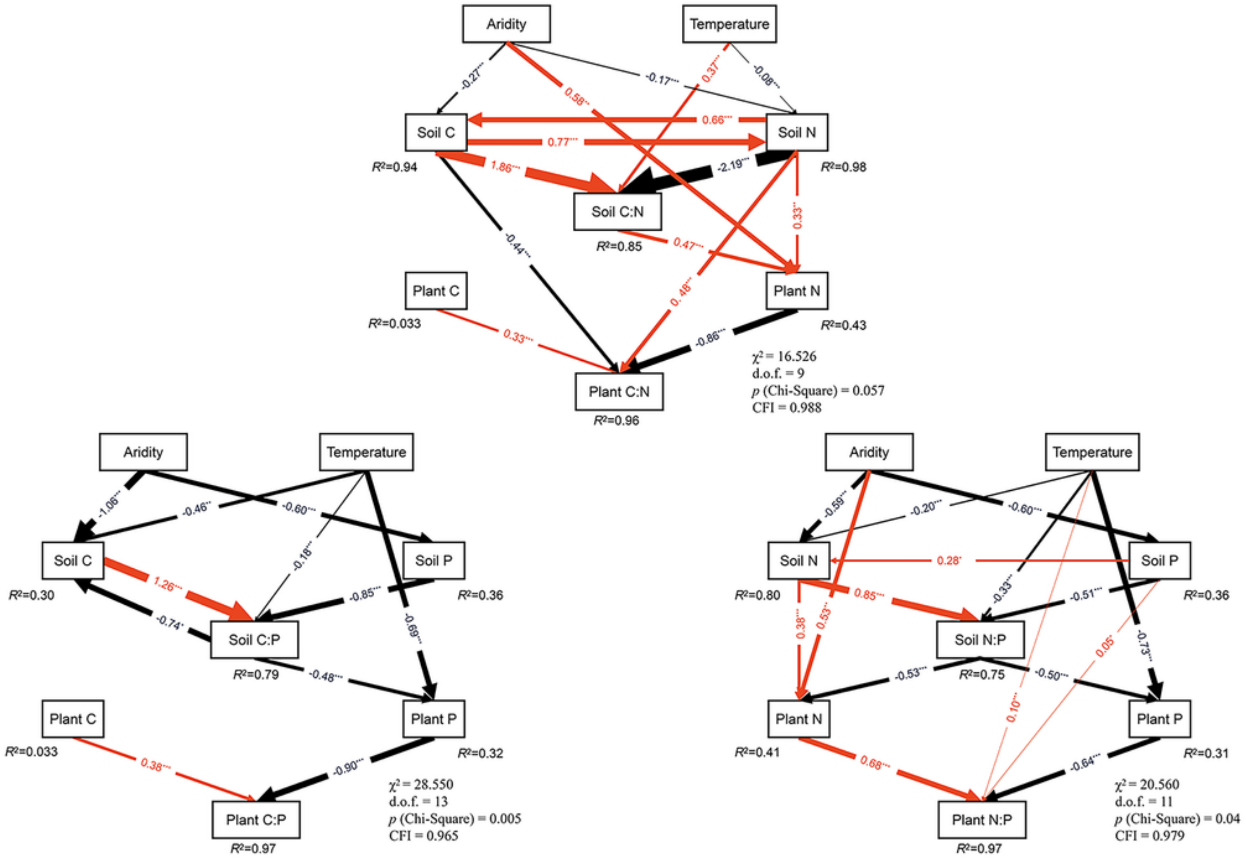

Figure 6

Diagrams of the structural equation models to explain the maximum variance in the aridity, temperature, plant/soil nutrients and stoichiometries. Red and black arrows indicate positive and negative relationships, respectively. Arrow width is proportional to the strength of the relationship. The proportion of variance explained (R2) appears alongside every response variable in the model. Numbers on arrows indicate likelihood estimates between the two corresponding variables and the corresponding level of significance (p-value). *p < 0.1, ** p < 0.05, ***p < 0.01. d.o.f., degrees of freedom. CFI, comparative fit index.

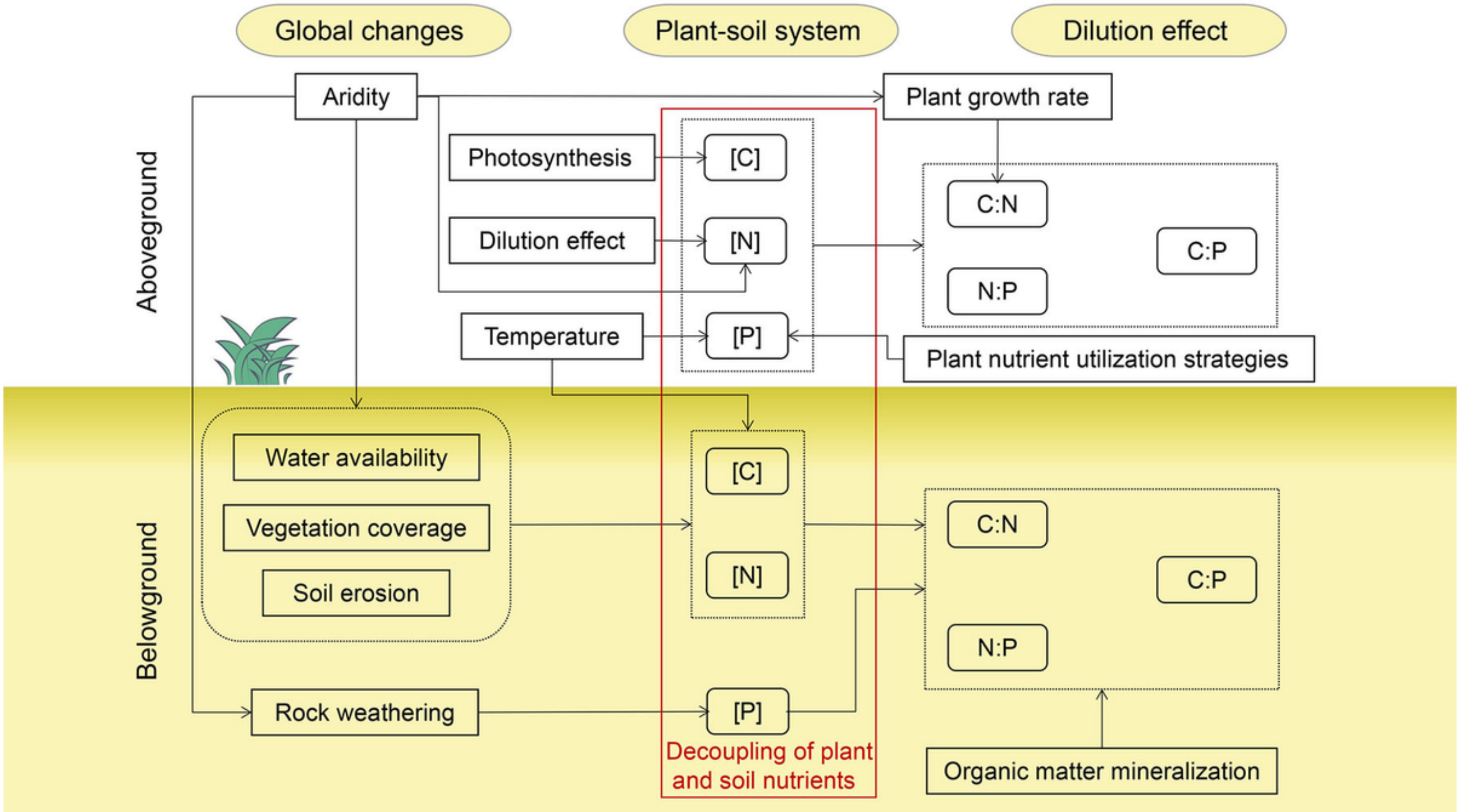

Figure 7

Conceptual diagram of the impacts of aridity on ecosystem processes that control plant and soil nutrients and their stoichiometry.

Supplementary Files

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