

**Divergence of above- and belowground C and N pool along precipitation gradients**

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# Divergence of above- and belowground C and N pool within predominant plant species along two precipitation gradients in north China

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Received: 3 July 2014 – Accepted: 22 September 2014 – Published: 2 October 2014

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Published by Copernicus Publications on behalf of the European Geosciences Union.

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## Abstract

The coupling of carbon cycle and nutrient cycle drives food web structure and biogeochemistry of an ecosystem. However, across precipitation gradients, there may be a shift in C pool and N pool from above- to belowground because of shifting plant stoichiometry and allocation. Based on previous evidence, biomass allocation to roots should increase with aridity, while leaf [N] should increase. If their effect sizes are equal, they should cancel each other out, and the above- and belowground proportions of the N would remain constant. Here, we present the first study to explicitly compare above- and belowground pool sizes of N and C within predominant plant species along precipitation gradients. Biomass and nutrient concentrations of leaves, stems and roots of three predominant species were measured along two major precipitation gradients in Inner Mongolia, China. Along the two gradients, the effect sizes of the biomass shifts were remarkably consistent among three predominant species. However, the size of the shift in aboveground [N] was not, leading to a species-specific pattern in above- and belowground pool size. In two species (*Stipa grandis* and *Artemisia ordosica*) the effect sizes of biomass allocation and [N] were equal and the proportion of N of above- and belowground did not change with aridity, but in *S. bungeana* the increase in leaf [N] with aridity was much weaker than the biomass shift, leading to a decrease in the proportion of N belowground at dry sites. We have found examples of consistent N pool sizes above- and belowground and a shift to a greater proportion of belowground N in drier sites depending on the species. We suggest that precipitation gradients do potentially decouple the C and N pool, but the exact nature of the decoupling depends on the dominant species' capacity for intraspecific variation.

## 1 Introduction

Plant carbon economy and nitrogen economy are closely coupled (Shaver and Chapin, 1991; Aerts and Chapin, 2000), and this coupling has important feedbacks to terres-

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trial carbon budgets and climate (IPCC, 2007; Chapin et al., 2009). To capture and utilize light, nutrients, carbon and water, plants allocate resources both to aboveground shoots and belowground roots. Nitrogen is obtained belowground via roots and partly transported to the aboveground shoots to support photosynthesis principally through the enzyme Rubisco and other parts of the photosynthetic systems, while carbon is obtained aboveground via photosynthesis and partly transported to belowground roots to support both acquisition of water and mineral nutrients. Important differences in allocation strategy occur both among species and among abiotic environments within species (Lambers et al., 1998; Poorter and Nagel, 2000). When a given resource is in short supply, plants typically allocate resources differently to compensate. If the resource in short supply is belowground, for example limited water, species and populations within species typically will allocate more resources belowground to compensate (Brouwer, 1963; Tilman, 1991; Gleeson and Tilman, 1992; Reynolds and Chen, 1996; Craine et al., 2002). So comparing dry vs. mesic sites, it is well documented that the allocation of biomass shifts to a higher proportion of roots vs. leaves (Orians and Solbrig, 1977; Mooney et al., 1978).

There is a key shift in the use of nitrogen when water is in short supply. Increased N allocation to leaves can support greater Rubisco-N investment per unit leaf area, which in turn can drive a greater photosynthetic capacity per unit transpiring area (Field and Mooney, 1986). Faster photosynthetic production at a given stomatal conductance increases intrinsic water use efficiency (Field et al., 1983; Buckley et al., 2002; Wright et al., 2003), which may compensate for prolonged periods of stomatal closure. Going from mesic to dry sites, species commonly allocate more N per leaf area partially by increasing N per unit leaf mass and partially by increasing the leaf mass per area (Wright et al., 2002). This pattern has been documented both among species in Australia (Wright et al., 2001) and across China (Han et al., 2011), and within species in Hawai'i (Cornwell et al., 2007).

Interestingly, aridity creates a condition under which biomass may be allocated in greater quantities belowground, but N is needed aboveground to facilitate greater wa-

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ter use efficiency. This suggests a potential decoupling of pool sizes for C and N, above- and belowground, with the pattern in pool size determined by the relative effect sizes of the trends in biomass allocation and [N]. These shifts could have implications for biogeochemical functions – especially the residence time of C in the biosphere, both via leaf quality to herbivores and litter quality to decomposers. Both herbivory and decomposition are known to be at least in part a function of tissue C : N ratio (Swift et al., 1979; Austin and Vitousek, 2000; Perez-Harguindeguy et al., 2000). Here we argue that a particular consequence of increasing divergence of above- vs. belowground N and C pool with increasing aridity could be accelerated by land degradation; as many semi-arid and arid lands are grazed by livestock, the proportional removal of a plant's aboveground N would increase with aridity, thereby potentially leading to faster exhaustion of whole-plant N to support productivity. Such positive feedback to land degradation by livestock would be a significant and previously unrecognized consequence of increased allocation of N to leaves to increase water use efficiency.

We investigate the above- and belowground pool sizes for C and N in the predominant plant species across two precipitation gradients in the semiarid to arid region of northern China. We then decompose the pool size patterns into the respective drivers—shifts in both the allocation of biomass and in the concentration of macronutrients. Our approach is to use three predominant species, which together represent much of the biomass along these gradients. Our hypothesis is that, from mesic towards dry sites, above- and belowground C pool and N pool will diverge as a consequence of increasing biomass allocation belowground combined with greater leaf N concentration (Fig. 1). To our knowledge, this is the first large-scale field study to explicitly dissect carbon pool and nitrogen pool both between and within organs of whole plants.

## 2 Methods

### 2.1 Study area and species

This study was conducted along two transects, each following a major precipitation gradient, in the Inner Mongolia Autonomous Region (hereinafter, Inner Mongolia), N-China (Fig. 2). The North-East China Transect (NECT) ranges from Erenhot to Chifeng city (longitude 112.12–117.42° E, latitude 43–44° N, altitudes 920–1300 m), with mean annual precipitation (MAP) ranging from  $\approx$  200–400 mm; The Ordos Transect (OT) stretches also from the west to east in Ordos City, (longitude 107.00–111.31° E, latitude 38–39° N, altitudes 1200–1500 m), with MAP ranging from 160–440 mm. Along the west of NECT, temperature only shows a modest trend, with mean annual temperature (MAT) from 1 to 3°C, mean temperature of the coldest month (CMT) from –20 to –12°C (January), and mean temperature of the warmest month (WMT) from 19 to 24°C (July). The precipitation from May through September accounts for almost 80% of MAP (Zhang et al., 1997). The warmest sites have the lowest relative inner-annual variability in temperature and the coldest sites have the highest variability, while the driest sites have the highest seasonality in precipitation and the wettest sites have the lowest variability along NECT (Ni and Zhang, 2000). The Ordos Transect, about 450 km south of NECT, features a weak east-to-west temperature gradient (MAT from 6 to 9°C, CMT from –13 to –10°C (January), and WMT from 20 to 23°C (July)) and a strong east-to-west precipitation gradient, with June through September accounting for 60–80% of MAP (Niu and Li, 1992).

*Artemisia ordosica* Krasch (Asteraceae) is a deciduous semi-shrub with plumose, linearly lobate leaves, occurring in the Inner Mongolia Autonomous Region, Ningxia Autonomous Region, and Shanxi Province of N-China. Its root system is mainly distributed in the upper 30 cm of sandy soils. This species is overwhelmingly dominant in the semi-fixed and fixed dune landscape of the Mu Us Sandland, which is the main body of the Ordos Plateau (Zhang, 1994). *Stipa grandis* P. Smim is a tall bunchgrass and can grow to almost 1 m at the peak of the growing season (late August). Its above-

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ground parts die off in autumn and new growth is in spring. It often forms nearly pure stands in the semi-arid region of N-China. *Stipa bungeana* Trin. is smaller than *S. grandis*, with height ranging from 20 to 60 cm. It is distributed in N, SW and SE China as well as in Mongolia and Japan. Both *Stipa* species predominate on the loamier soils in the region, as opposed to *A. ordosica* on the sandy substrates.

## 2.2 Field sampling and laboratory analysis

The field investigation was conducted from 6 August–18 September 2006, i.e. the first three weeks along NECT and the latter three weeks along OT. Along each transect this was during the peak biomass period and well before the onset of senescence (which is in September at NECT; end of September/early October at OT). In total 46 sites were chosen along NECT and 41 sites along OT (Fig. 2), each two adjacent sites at intervals of more than 10 km. MAP at each site was extracted from the interpolated climate grids (New et al., 2002), using the Raster package in R (Hijmans and van Etten, 2011). The site values closely matched previous estimates based on regional regressions with altitude, latitude and longitude for NECT (Zhang et al., 1997) and OT (Niu and Li, 1992), respectively.

Three 1 m × 1 m quadrats for grass and/or 2 m × 2 m quadrats for semi-shrub were measured at each site. Within each quadrat, all living biomass was harvested, separated into species and oven-dried at 70 °C for ≥ 24 h to constant mass before they were weighed. For each species, cover %, height and number of individuals were also measured within each quadrat at the same time. Leaves of *S. grandis* in NECT and of *S. bungeana* and *A. ordosica* in OT were collected for lab analyses within each quadrat, as well as the stems of *A. ordosica* in OT. For each species roots were collected by taking three 10 cm diameter soil cores from 0–40 cm depths, mixed in situ into one composite sample. Roots of *S. grandis* in NECT and roots of *S. bungeana* and *A. ordosica* in OT were hand-sorted and washed clean for lab analyses. It is often difficult to differentiate between the roots of different species, but it was perfectly doable to differentiate between the roots of the three target species in this study. Both *S. grandis*

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and *S. bungeana* are bunch-grasses and could be identified visually; their roots are fibrous and shallow. Confusion with *Leymus* can be excluded, as this grass is rhizomatous and has its root distribution much deeper in the soil profile than *Stipa*. The roots of the shrub *A. ordosica* were easily recognized by their strong and typical aroma as well as by their morphology. Most other species in NECT and OT were non-grass herbaceous species, such as *Allium*, *Carex*, *Euphorbia*, *Iris*, *Potentilla* and *Taraxacum*. Only roots of the three target species were hand-sorted and washed clean for lab analyses, and all other roots in NECT were mixed into one composite sample.

Leaf, stem and root biomass of the three species were measured after  $\geq 24$  h oven-drying at 70 °C. Leaf, stem and root potassium (K) concentration was determined using Atomic Absorption Spectrophotometry (Model-932, GBC Scientific Equipment, Melbourne, Australia), while nitrogen (N) and phosphorus (P) concentrations were analyzed according to the micro-Kjeldahl method (Kjeltec 2300 Analyzer Unit, Sweden), and total carbon (C) concentration was determined using the method of  $K_2Cr_2O_7$ - $H_2SO_4$  solution digestion with oil-bath heating (Dong et al., 1996). The  $K_2Cr_2O_7$ - $H_2SO_4$  method was extensively calibrated against an elemental analyzer method (Vario Macro Cube, Elementar, Hanau, Germany) in our lab. Also, standard reference materials were used throughout to guarantee the measurement accuracy and repeatability.

In total, 15 of the sites provided data for plant aboveground and underground biomass and element contents for *A. ordosica* in OT, 22 sites for *S. bungeana* in OT, and 35 sites for *S. grandis* in NECT.

### 2.3 Data analysis

Statistical analyses were performed using SPSS13.0 software (2004, SPSS Inc., USA). We analyzed variation in each trait for the effect of species and precipitation using ANCOVA, with species as an independent variable and precipitation as a covariate. And we analyzed relationship between each trait and precipitation for each species using Linear Regression. Data for leaf [P], leaf [K], root [P], root [K], and proportion of



aboveground N, C, P and K content were log-transformed before analyses in order to meet the assumptions of normality.

### 3 Results

The relative contribution of *A. ordosica* to the plant community biomass ranged from 13–86 % (mean 52.6 %) and increased with higher precipitation within the sandy region in OT ( $r^2 = 0.319$ ,  $P = 0.035$ ) (Fig. 3a). *S. bungeana* made up a higher proportion of the total biomass (range 10–91 %, mean 36.8 %) on the loamier OT sites where *A. ordosica* did not dominate. *S. bungeana* on the OT achieved a greater dominance compared to *S. grandis* in NECT (range 1–80 %, mean 29.8 %). For neither *Stipa* species was the proportion correlated with precipitation ( $P > 0.1$ ).

#### 3.1 Plant biomass and its allocation along transects

The proportion of aboveground biomass increased linearly with MAP in all three species ( $df = 1$ ,  $F = 8.135$ ,  $P = 0.006$ ); the slope of proportion of aboveground biomass as a function of MAP was not heterogeneous across species. The size of the trend, the crucial element affecting pool sizes, was a mean of 7.0 % additional allocation aboveground for every 100 mm  $yr^{-1}$  of additional rainfall. There was a significant difference in elevation of these regressions among species ( $df = 2$ ,  $F = 6.521$ ,  $P = 0.003$ ); *S. grandis* in NECT had the largest proportion aboveground biomass allocation, followed by *A. ordosica* and *S. bungeana* in OT. Only the latter species by itself increased aboveground biomass with MAP ( $r^2 = 0.497$ ,  $P < 0.001$ , Fig. 3b).

#### 3.2 Effects of species and precipitation on plant element concentrations

Precipitation had a negative and significant relationship with leaf nitrogen concentration (LNC) and leaf phosphorus concentration (LPC), as well as significant overall effects

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on proportion of aboveground C, P and K content (Table 1). There were significant interactions for species by precipitation on most plant traits analyzed (Table 1).

Although LNC decreased along a gradient of MAP for all three species, the effect was stronger in *S. grandis* (slope  $-1.24 \text{ mg g}^{-1}$  per  $100 \text{ mm yr}^{-1}$ ,  $r^2 = 0.718$ ,  $P < 0.001$ ) and *A. ordosica* (slope  $-0.79 \text{ mg g}^{-1}$  per  $100 \text{ mm yr}^{-1}$ ,  $r^2 = 0.426$ ,  $P = 0.011$ ) than in *S. bungeana* (slope  $-0.22 \text{ mg g}^{-1}$  per  $100 \text{ mm yr}^{-1}$ ,  $r^2 = 0.167$ ,  $P = 0.059$ ). All three species had similar leaf carbon concentration (LCC) values, which increased steadily with MAP (Fig. 4a). MAP had no significant effect on root carbon concentration (RCC) or root nitrogen concentration (RNC). The three species had similar RNC, while *A. ordosica* had a higher RCC than the two *Stipa* species (Fig. 4b). Steam nitrogen concentration (SNC) of *A. ordosica* showed no trend with increasing MAP in OT (Fig. 4c,  $r^2 = 0.011$ ,  $P = 0.719$ ).

*A. ordosica* had higher LPC and leaf potassium concentration (LKC) than the two *Stipa* species. MAP decreased LPC in all three species (but only significantly in *S. grandis*, slope  $-0.175 \%$  LPC per  $100 \text{ mm yr}^{-1}$ ,  $r^2 = 0.343$ ,  $P < 0.001$ ), and had no significant negative effect on LKC in any species (Supplement Fig. S1a). MAP had a significant positive effect on root phosphorus concentration (RPC) in *S. grandis* (slope  $0.125 \%$  RPC per  $100 \text{ mm yr}^{-1}$ ,  $r^2 = 0.128$  and  $P = 0.038$ ), a marginal negative effect in *A. ordosica* (slope  $-0.224 \%$  RPC per  $100 \text{ mm yr}^{-1}$ ,  $r^2 = 0.205$ ,  $P = 0.10$ ) and no effect in *S. bungeana* (Fig. S1b,  $r^2 = 0.084$ ,  $P = 0.189$ ). With increasing MAP, root potassium concentration (RKC) appeared to decrease in *S. bungeana* (slope  $0.082 \%$  RKC per  $100 \text{ mm yr}^{-1}$ ,  $r^2 = 0.151$ ,  $P = 0.074$ ) but showed no clear trend in *S. grandis* or *A. ordosica* (Fig. S1a). Steam phosphorus concentration (SPC) of *A. ordosica* showed no trend ( $r^2 = 0.039$ ,  $P = 0.50$ ), while steam potassium concentration (SKC) significantly decreased with increasing MAP in OT (Fig. S1, slope  $-2.904 \%$  SKC per  $100 \text{ mm yr}^{-1}$ ,  $r^2 = 0.248$  and  $P = 0.070$ ).

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### 3.3 Proportion of aboveground plant N, C, P and K pools

Precipitation had a significant effect on the proportion of N and C pool aboveground, and this effect differed among species (significant interactions see Table 1). *S. grandis* had the highest proportion of N and C pool aboveground, followed by *A. ordosica* and *S. bungeana* respectively. There was a significant positive relationship between MAP and proportion of N (slope 0.129 % per 100 mm yr<sup>-1</sup>,  $r^2 = 0.315$ ,  $P = 0.007$ ) and C aboveground content (slope 0.239 % per 100 mm yr<sup>-1</sup>,  $r^2 = 0.583$  and  $P < 0.001$ ) in *S. bungeana*, while *A. ordosica* showed only a similar trend and *S. grandis* none at all (Fig. 4d).

Both species and precipitation had significant effects on the proportion of P and K pool aboveground and also the interactions were significant (Table 1). Comparable with N pool, there were a significant positive relationships between MAP and proportion of P (slope 0.212 % per 100 mm yr<sup>-1</sup>,  $r^2 = 0.631$ ,  $P < 0.001$ ) and K aboveground content (slope 0.239 % per 100 mm yr<sup>-1</sup>,  $r^2 = 0.620$ ,  $P < 0.001$ ) in *S. bungeana*, but not in the other two species (Fig. S1d).

## 4 Discussion

The aboveground vs. belowground pool size and concentrations of carbon and nitrogen are linked, and understanding the shifts across a precipitation gradient requires a whole-plant perspective (Van der Putten et al., 2001; Wardle et al., 2004; Bardgett et al., 2005; De Deyn et al., 2008). Because of the many fungi and animals associated with the plants – mutualists, pathogens, herbivores, decomposers – the whole plant C and N strategy is crucial for carbon storage, food webs, soil water and nitrogen retention and cycling (Hooper et al., 2000; Bardgett and Wardle, 2003). Changes in the stoichiometry and balance between these pools owing to differences or changes in precipitation regime are therefore likely to impact greatly on ecosystem function and biodiversity.

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Two quantities affect the proportion of N above- vs. belowground: the relative allocation of biomass and the concentration of N in that biomass. *A priori* we expected the proportion of biomass aboveground to be greater in mesic vs. dry place (Orians and Solbrig, 1977; Mooney et al., 1978). We also expected Inner Mongolia to show similar tissue N concentration patterns to China at larger scale (Han et al., 2011), Australia (Wright et al., 2001, 2002), Hawaii (Cornwell et al., 2007), Panama (Santiago et al., 2005), and western North America (Maherali and DeLucia, 2001), that is, the concentration of N in leaves would be greater in dry vs. mesic environment. For the pool size of N, because these two components were expected to change in opposing directions, we expected the result to be a function of the relative effect sizes of the two trends. Because, to the best of our knowledge, the effect sizes for biomass and N concentration have not previously been measured in one system, we started from the null hypothesis that the two trends would cancel each other out, resulting in similar proportions of N aboveground vs. belowground pool size across aridity gradients.

We found that like other aridity gradients across the world (Maherali and DeLucia, 2001; Austin and Sala, 2002; Santiago et al., 2005; He et al., 2008), there was a shift from more aboveground towards more belowground biomass allocation with decreasing precipitation (Fig. 3b). Also consistent with our expectation, there was an increase in leaf N concentration in the drier vs. the more mesic site (Fig. 4a). Integrating both patterns, we found that for one species, *S. bungeana*, there was a significant positive trend in proportion of N aboveground with precipitation. The other two species did not show relationships that differed significantly from flat. This was not due to differing biomass allocation – the slopes of those relationships were very similar (Fig. 3b). Instead, *S. bungeana* did not increase leaf N concentration in response to aridity to nearly the extent that the other two species did (Fig. 4a). This meant that unlike in the two other species where N and biomass shifts came close to equal effect sizes, in *S. bungeana* the biomass effect dominated and the proportion of N aboveground increased with precipitation.



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are grazed by livestock, often heavily, the dominant vegetation could drive a positive feedback on land degradation by livestock at low precipitation regimes. This situation will not be unique to Inner Mongolia, as extensive regions in a similar climate zone in at least West, Central and East Asia and North America (Fig. 2, insert) host similar vegetation types and similarly heavy use by livestock. This possibility may deserve in depth study that would have to extend to vegetation regrowth patterns and N and C pathway and pool via livestock at different animal densities.

## 5 Conclusions

The C and N cycle are usually tightly coupled, because the proportion of N that is needed in specific tissue types is relatively constrained – N is usually low in structural tissue and high in absorbing (roots) and photosynthetic (leaves) tissue (Sterner and Elser, 2002). Therefore, decoupling of the C and N pool across different climates is a paradox. Changing water availability potentially decouples the C and the N pool because of greater allocation to high N leaves in dry sites. Here we have fully decomposed above- and belowground C and N allocation and stoichiometry. We have found examples of consistent N pool sizes above- and belowground and a shift to a greater proportion of belowground N in drier sites depending on the species. We suggest that precipitation gradients do potentially decouple the C and N pool, but the exact nature of the decoupling depends on the dominant species' capacity for intraspecific variation. Even in cases where the above- vs. belowground N and C pool themselves do not change proportionally, smaller biomass allocation to shoots with higher N concentrations in drier areas might facilitate a positive feedback to land degradation by livestock.

**The Supplement related to this article is available online at doi:10.5194/bgd-11-14173-2014-supplement.**

*Author contributions.* M. D. directed, coordinated and funded this study with intellectual input from J. H. C. C., W. K. C. and X. Y.; X. Y., X. P., S. G. and M. D. carried out the fieldwork and lab analyses; X. Y., W. K. C. and J. H. C. C. did the data analysis and wrote the first manuscript draft. All authors commented on the manuscript and consent with the submitted version.

5 *Acknowledgements.* This research was supported by the “Strategic Priority Research Program” of the Chinese Academy of Sciences (CAS) (XDA05050406), the National Natural Science Foundation of China (30570296), and the Chinese Academy of Sciences Visiting Professorship for Senior International Scientists (2010T2S24). Many thanks to Renqiang Li for his help with our field work in NECT and Jianjiang Qiao in OT.

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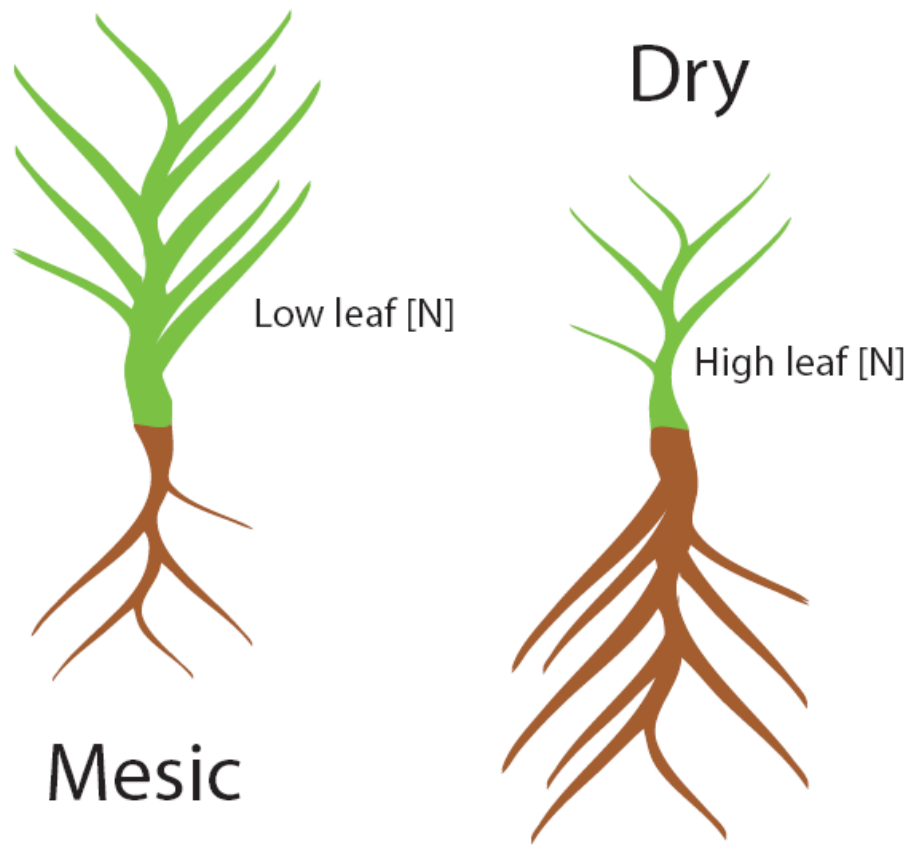
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**Table 1.** Effects of species and mean annual precipitation on each plant trait in the two transects. Bold values indicate  $P < 0.05$ .

Plant traits		Species			Precipitation			Interaction		
		df	F	P	df	F	P	df	F	P
N	Leaf N conc.	2	14.665	<b>&lt; 0.001</b>	1	52.915	<b>&lt; 0.001</b>	2	16.711	<b>&lt; 0.001</b>
	Stem N conc.	–	–	–	1	0.136	0.719	–	–	–
	Root N conc.	2	0.598	0.553	1	0.360	0.550	2	0.393	0.677
	Proportion of N aboveground	2	10.543	<b>&lt; 0.001</b>	1	2.540	0.116	2	3.336	<b>0.042</b>
C	Leaf C conc.	2	0.581	0.562	1	1.031	0.314	2	0.703	0.499
	Stem C conc.	–	–	–	1	0.406	0.536	–	–	–
	Root C conc.	2	0.147	0.864	1	0.705	0.404	2	0.397	0.674
	Proportion of C aboveground	2	6.774	<b>0.002</b>	1	9.185	<b>0.004</b>	2	1.141	0.326
P	Leaf P conc.	2	6.122	<b>0.004</b>	1	7.860	<b>0.007</b>	2	2.927	0.061
	Stem P conc.	–	–	–	1	0.481	0.501	–	–	–
	Root P conc.	2	7.158	<b>0.002</b>	1	1.325	0.254	2	5.448	<b>0.007</b>
	Prop. of P aboveground	2	23.905	<b>&lt; 0.001</b>	1	8.187	<b>0.006</b>	2	7.930	<b>0.001</b>
K	Leaf K conc.	2	1.978	0.147	1	0.921	0.341	2	0.056	0.945
	Stem K conc.	–	–	–	1	3.96	0.07	–	–	–
	Root K conc.	2	7.414	<b>0.001</b>	1	1.602	0.210	2	3.833	<b>0.027</b>
	Prop. of K aboveground	2	22.785	<b>&lt; 0.001</b>	1	12.185	<b>0.001</b>	2	5.272	<b>0.008</b>



**Figure 1.** The allocation of biomass under different water regimes. Going from mesic to dry sites, the allocation of biomass shifts to a higher proportion of roots vs. leaves and higher leaf N concentrations.

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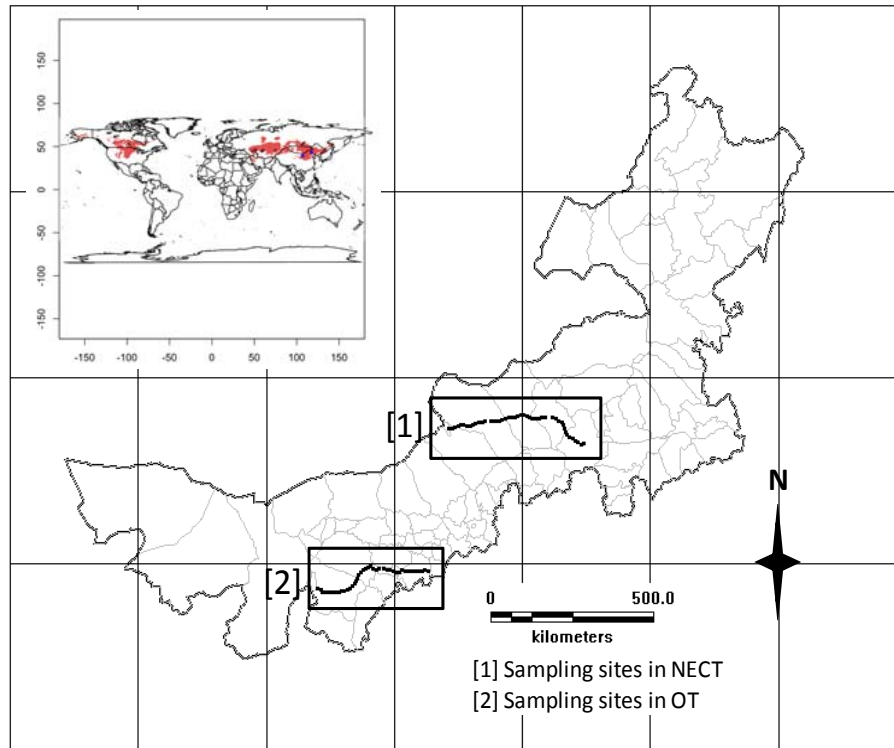
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**Figure 2.** The sampling sites in Inner Mongolia, China. The 46 northern sites (1) were along the North-East China Transect (NECT), and the 41 southern sites (2) were along the Ordos Transect (OT). The map in the upper left corner shows places in the world with a similar climatic regime to the study area (with similar annual and seasonal pattern of precipitation and temperature).

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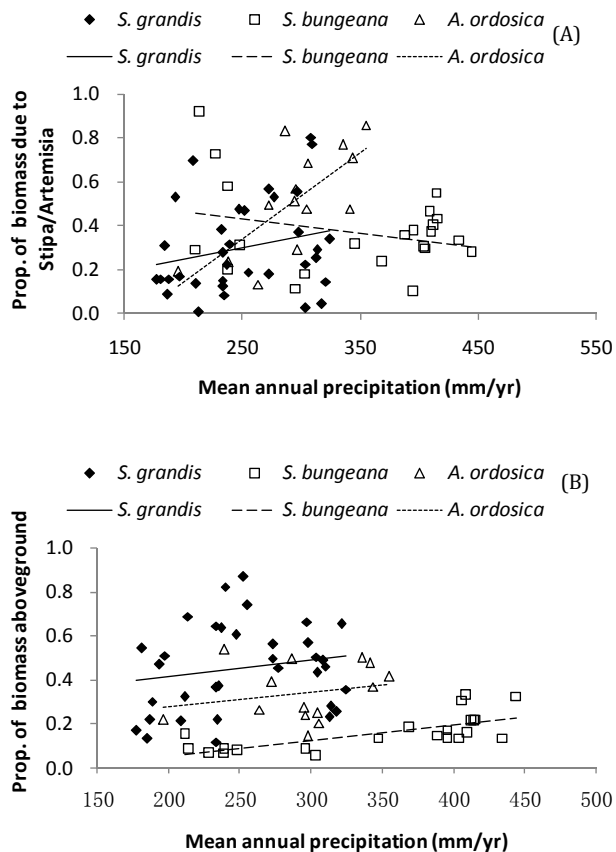
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**Figure 3.** Relationship between percentage of vegetation biomass due to *Stipa/Artemisia* and mean annual precipitation (A), percentage of biomass aboveground in *Stipa/Artemisia* and mean annual precipitation (B), both along the two transects.

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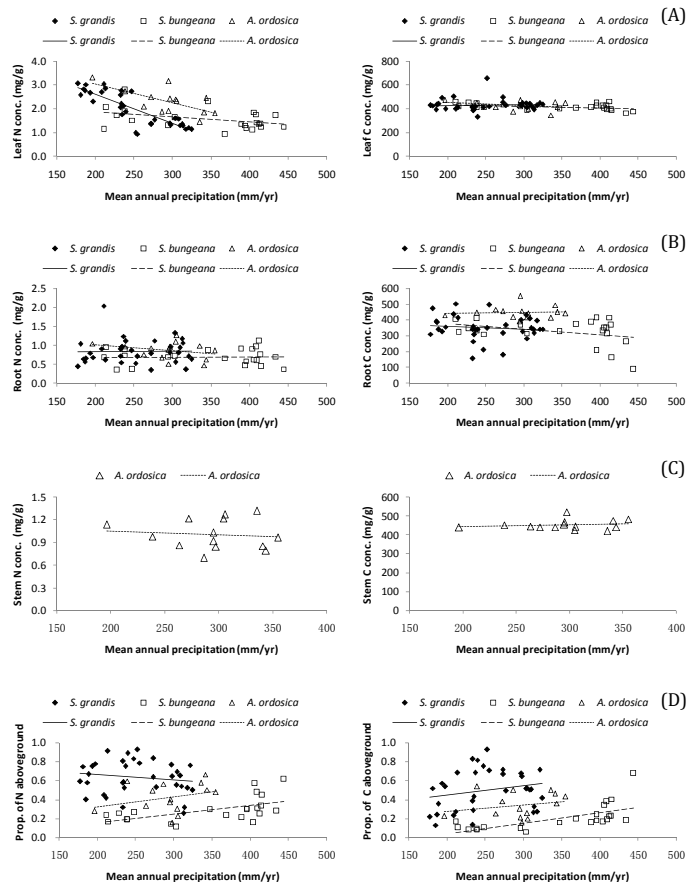
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**Figure 4.** The relationship between mean annual precipitation and plant traits: **(A)** leaf nitrogen (LNC) and leaf carbon concentration (LCC), **(B)** root nitrogen (RNC) and root carbon concentration (RCC), **(C)** stem nitrogen (SNC) and stem carbon concentration (SCC), and **(D)** proportion of N and C aboveground.

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