Dear Editor,
We were very pleased with the positive and constructive comments on our manuscript. Below we explain how in the main text (indicated with track changes there) we have addressed the remaining queries point by point.
We hope that this has taken our manuscript up to *Biogeosciences* publication standard.
Yours sincerely, on behalf of the coauthors,
Ming Dong and Xuehua Ye

Response to referees

Anonymous Referee #1

Reported is an investigation into C and N allocation above- and belowground in three dominant plant species along two precipitation gradients in north China. The working hypothesis was that smaller proportions of aboveground biomass in drier environments would be offset by higher concentrations of N in leaves, so that the aboveground proportion of N would remain unchanged across precipitation gradients. This hypothesis was confirmed for two species. In the third species, leaf-N concentrations changed too little to offset the decrease in aboveground biomass at arid sites.
I find this a very interesting, thought-provoking study. It contains new results, is well done and clearly written. The last paragraph of the Discussion section explores possible implications of the results. Here, I would like to see a few more sentences on the possible interaction between leaf N concentrations and grazing behavior. Are grazers, large mammals, but also insects, attracted by higher leaf N concentrations? If so, how would an increasing grazing pressure affect the composition of the three species studied along the precipitation gradient?

Authors: thanks! It's a good idea. To raise this point we have added the following sentence to the end of the Discussion (before Conclusion):

It would also be important to test whether and how the possible feedback suggested above might be influenced by possible changes in preference of livestock for different food plants as related to changing leaf nutritional value for the different species, with consequences for their abundance hierarchies at different points along the precipitation gradient.

Apart from this suggestion, I have only a few minor suggestions for improving the manuscript:
Abstract, line 19: should it not "aboveground" instead of "belowground"? This would be logically consistent with the preceeding part of the sentence and also with the statement made in the last sentence on page 14184.

Authors: thanks! In our investigation, *S. bungeana* had no significantly increasing leaf N concentration but significantly increasing aboveground biomass along precipitation gradient, leading to a decrease in the proportion of nitrogen aboveground at dry sites. It should be "aboveground", and we have changed "belowground" to "aboveground".

page 14182, lines 10, 23, 24: replace "Steam" with "Stem".

Authors: thanks! We have replaced "steam" with "stem".

page 14183, line 12: replace ": : :there were a significant positive relationships: : :" with": : :there was a significant positive relationship: : :"

Authors: thanks! We have replaced "...there were a significant positive relationships...." with "...there were significant positive relationships...".

Anonymous Referee #3

Review of Ye et al., "Divergence of above and belowground C and N pool within predominant plant species along two precipitation gradients in North China" Ye et al. investigate a potential decoupling between aboveground and belowground C and N cycling with increasing aridity. They hypothesize plants allocate a greater fraction of biomass to roots while increasing the N content of aboveground biomass in drier conditions. This could be important because grazing would have a larger impact on plants with a smaller but N-enriched aboveground component. They tested this effect by measuring above- and belowground C and N in 3 plants along 2 MAP transects in Inner Mongolia. They found the different species showed different responses to increasing aridity, with one spicies increasing belowground biomass allocation and another increasing leaf N content.

I found the paper to be generally well written, and the hypothesis and potential implications were clearly stated. The data collected address an interesting and important problem and should be published in principle. However, I have some issues with the interpretation of the data, as discussed below. I therefore recommend publication of the manuscript after major revisions.

General comments:

-The conclusion discussed starting on line 325 (decreasing aboveground allocation to biomass that is richer in N as aridity gets more severe) is not supported by the data. Only A. ordosica had significantly decreasing aboveground biomass, and only S. grandis had significantly increasing leaf [N] with increasing aridity. None of the 3 plants showed both decreasing aboveground biomass and higher leaf [N] with aridity. Statements that the effects were "balanced" (eg line 318) to maintain a constant %N aboveground are similarly problematic, as one or both effects were not significant.

Authors: Actually, our results showed that there was a shift from more aboveground towards more belowground biomass allocation with decreasing precipitation in *S. bungeana* (Figure 3b). Also consistent with our expectation, there was a significant increase in leaf N concentration in the drier versus the more mesic site in *S. grandis* and *A. ordosica*, and a weaker increase in leaf N concentration in *S. bungeana* (r2=0.167, p=0.059) (Figure 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 (Figure 4d). To make it clearer, we changed the figures, removed the insignificant trend lines, and provided r^2 and p values for the significant trend lines.

-Please address potential effects of differences in nutrient availability. Any systematic difference in N availability among the sites would also affect [N] in both leaves and roots. You would also expect greater belowground biomass allocation with greater N limitation to aid in nutrient acquisition. This possibility should be discussed in the manuscript.

Authors: thanks! We agree that this is a shortcoming in our study, but we have now added some text about this in the methods, explaining why we think this issue has not had a large effect on our results: "Unfortunately, it was not logistically possible to measure soil nutrient availabilities simultaneously and repeatedly at so many points along the two gradients, given that nutrient availability is notoriously variable in time. However, we expect nutrient availabilities to have varied little over each of the transects for given species, as both *Stipa* species were generally sampled from unfertilized loamy soils and *A. ordosica* generally from unfertilized sandy soils, The remarkably flat pattern for root N content with MAP for all three species (see Results, Fig. 4b) strongly suggests that there was no correspondence between soil nutrient availability and precipitation regime, although we cannot exclude effects of nutrient availability on intra-specific variability in nutrient-related traits at finer spatial scale."

-It appears from the figures that overall, the %biomass and %N aboveground is actually higher at low MAP, due to higher %aboveground biomass in *S. grandis* compared to other species. Could a shift in the plant community toward more drought-tolerant plants like *S. grandis* produce the opposite of the hypothesized effect?

Authors: we don't think so. If there is a shift in the plant community toward more drought-tolerant plants like *Stipa*, the relative contributions of *Stipa* to the plant community biomass may increase in dry sites. However, out results showed that both the relative contributions of *S. bungeana* in OT and of *S. grandis* in NECT to the plant community biomass were not significantly correlated with mean annual precipitation (Figure 3A). And because our study was focused on one or two predominant plant species but not on the plant community composition, it would be difficult to extrapolate any shift in plant community based on our present results.

-The figures are cluttered with unnecessary and insignificant trend lines, complicating their interpretation. I suggest removing the insignificant lines and providing r2 and p values for the significant trends on the figure or in the caption.

Authors: we have removed the insignificant trend lines, and provided r^2 and p values for the significant trend lines on the figure.

Specific comments:
Line 84: Increasing biomass but decreasing N allocation- you are basically hypothesizing increased C:N in the roots. Has this been observed? Roots are still living cells and have N requirements of their own. How elastic can the C:N be?

Authors: this is an interesting point. Actually, in our investigation, all three plant species along the two transects had no significantly changing root N concentration and root C concentration, meaning a stable C:N in the roots along the precipitation gradient.

Line 120, 122: “Mean annual precipitation” should be abbreviated “MAP”

Authors: thanks! We have changed “Mean annual precipitation” to “MAP” excepted the first time it appeared.

Line 184: I’m not familiar with the method used for C analysis, and the citation provided is to a book that’s not immediately available. Please provide an additional sentence or two about the method, and consider including the calibration vs. the elemental analyzer as supplementary material with the manuscript.

Authors: thanks! The method of K2Cr2O7-H2SO4 solution digestion with the oil-bath heating is a common method to determine the soil and plant carbon, and is widely used in carbon studies, such as:

Zheng SX, Ren HY, Lan ZC et al., 2010. Effects of grazing on leaf traits and ecosystem functioning in Inner Mongolia grasslands: scaling from species to community. *Biogeosciences*, 7, 1117-1132.

We have added this reference as the citation for the method.

Line 212: This statement is not clear and doesn’t appear to be supported by the data. S. bungeana vs. MAP is the only significant relationship shown in Fig. 3B.

Authors: this statement is based on the results of ANCOVA with species as an independent variable and precipitation as a covariate, which showed that the proportion of aboveground biomass increased linearly with mean annual precipitation (df=1, F=8.135, P=0.006). We have changed this sentence as “The ANCOVA results showed that the proportion of aboveground biomass increased linearly with MAP in all three species (df = 1, F = 8.135, P = 0.006);...”

Line 232: Leaf C content appears to be constant with MAP in Fig. 4. Please cite statistics showing significant relationship.

Authors: thanks! We have changed figure 4, removed the insignificant trend lines, and provided r^2 and p values for the significant trend lines.

Line 256: “Similar” should read “smaller”

Authors: thanks. We have corrected “similar” to “weaker”, which we think is even better than “smaller”.

Line 295: This effect was only significant in 1 of the 3 species tested.

Authors: Yes, we have make it clear by changing the sentence to “there was a shift from more aboveground towards more belowground biomass allocation with decreasing precipitation in *S. bungeana* (Figure 3b). Also consistent with our expectation, there was an significant increase in leaf N concentration from the drier towards the more mesic sites in *S. grandis* and *A. ordosica*, and a weaker increase in leaf N concentration in *S. bungeana* (r^2=0.167, p=0.059) (Figure 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 (Figure 4d).”

Line 323: I don’t understand where the statement “There was much more C aboveground in mesic vs. dry place” is coming from. That relationship does not appear to be significant.

Authors: this statement is based on the results of ANCOVA with species as an independent variable and precipitation as a covariate, which showed that the proportion of aboveground biomass increased linearly with mean annual precipitation (df=1, F=8.135, P=0.006), and there was a significant difference in elevation of these regressions among species (df = 2, F = 6.521, P = 0.003).

Figure 2: Define the criteria used for determining “similar annual and seasonal patterns of precipitation and temperature” used in the inset.

Authors: thanks! We have defined it in the inset as: (with similar annual and seasonal pattern of precipitation and temperature, that is, with mean annual precipitation ranging from 160mm to 440mm, and most of MAP occurring from May through September, and with mean annual temperature from 1 to 9 ℃, mean temperature of the coldest month from -20 to -12 ℃ (January), and mean temperature of the warmest month from 19 to 24 ℃ (July)).

Short comments from JF. Liu

The paper found that a shift of C/N pool between above- and belowground was not depending on the precipitation gradient, but species-specific. I think the results will be of important significance as a case study in developing or improving related processed model(s).

Authors: thanks!

Short comments from J. Liu

The study found that the effect sizes of the biomass shifts were consistent among three predominant species and the size of the shift in aboveground [N] was not, suggesting that precipitation gradients might potentially decouple the C and N pool. I think the results are very interesting and should be considered in understanding the effects of changing precipitation on ecosystems.

Authors: thanks!

Changes made in the manuscript

Page 2, line 27

Page 2, line 44

Page 9, line 85

Page 10, line 190-199

Page 11, line 222

Page 11, line 227

Page 12, line 245, 257 and 258

Page 13, line 269

Page 13, line 273

Page 15, line 308

Page 15, line 309-311

Page 15, line 314, 315

Page 15, line 315-316

Page 17, line 357-361

Page 22, line 506-508

Page 24, legend of figure 2

Page 28, figure 3

Page 29, figure 4

Page 30, figure 5

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

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Author contributions: MD directed, coordinated and funded this study with intellectual input from JHCC, WKC and XY; XY, XP, SG and MD carried out the fieldwork and lab analyses; XY, WKC and JHCC did the data analysis and wrote the first manuscript draft. All authors commented on the manuscript and consent with the submitted version.

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Running title: Divergence of above- and belowground C and N pool along precipitation gradients

ABSTRACT

The coupling of carbon cycle and nitrogen 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 below-ground 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 below-ground proportions of the N would remain constant. Here, we present the first study to explicitly compare above- and below-ground 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 below-ground 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 below-ground 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 aboveground 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.

Key words: aridity, biomass allocation, climate gradient, desertification, intra-specific variation, grassland, leaf nitrogen, plant trait, root, shrubland

INTRODUCTION

Plant carbon economy and nitrogen economy are closely coupled (Shaver & Chapin 1991, Aerts & Chapin 2000), and this coupling has important feedbacks to terrestrial 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 & 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 & Tilman 1992, Reynolds & Chen 1996, Craine et al. 2002). So comparing dry versus mesic sites, it is well documented that the allocation of biomass shifts to a higher proportion of roots versus leaves (Orians & 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 & 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 water 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 & Vitousek 2000, Perez-Harguindeguy et al. 2000). Here we argue that a particular consequence of increasing divergence of above versus 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 (Figure 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.

METHODS

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 (Figure 2). The North-East China Transect (NECT) ranges from Erenhot to Chifeng city (longitude 112.12 to 117.42 °E, latitude 43 to 44 °N, altitudes 920 to 1300 m), with mean annual precipitation (MAP) ranging from approx. 200mm to 400mm; The Ordos Transect (OT) stretches also from the west to east in Ordos City, (longitude 107.00 to 111.31 °E, latitude 38 to 39 °N, altitudes 1200 to 1500 m), with MAP ranging from 160mm to 440mm. 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 & 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 & 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 aboveground 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.

Field sampling and laboratory analysis

The field investigation was conducted from 6 August to 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 (Figure 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 & 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 & Li 1992), respectively. Three 1m×1m quadrats for grass and/or 2m×2m 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 0-40cm 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* 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 ≥ 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; Zheng et al. 2010). 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. Unfortunately, it was not logistically possible to measure soil nutrient availabilities simultaneously and repeatedly at so many points along the two gradients, given that nutrient availability is notoriously variable in time. However, we expect nutrient availabilities to have varied little over each of the transects for given species, as both *Stipa* species were generally sampled from unfertilized loamy soils and *A. ordosica* generally from unfertilized sandy soils, The remarkably flat pattern for root N content with MAP for all three species (see Results, Fig. 4b) strongly suggests that there was no correspondence between soil nutrient availability and precipitation regime, although we cannot exclude effects of nutrient availability on intra-specific variability in nutrient-related traits at finer spatial scale.

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.

RESULTS

The relative contribution of *A. ordosica* to the plant community biomass ranged from 13 to 86% (mean 52.6%) and increased with higher precipitation within the sandy region in OT ($r^2 = 0.319$, $P = 0.035$) (Figure 3a). *S. bungeana* made up a higher proportion of the total biomass (range 10 to 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 to 80%, mean 29.8%). For neither *Stipa* species was the proportion correlated with precipitation ($P > 0.1$).

Plant biomass and its allocation along transects

The ANCOVA results showed that 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 percent additional allocation aboveground for every 100 mm/yr of additional rainfall. Also, 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 ($r^2 = 0.497$, $P < 0.001$, Figure 3b).

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 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 mg/g per 100 mm/yr, r^2 = 0.718, *P* < 0.001) and *A. ordosica* (slope -0.79 mg/g per 100 mm/yr, r^2 = 0.426, *P* = 0.011) than in *S. bungeana* (slope -0.22 mg/g per 100 mm/yr, r^2 = 0.167, *P* = 0.059). All three species had similar leaf carbon concentration (LCC) values, which increased steadily with MAP (Figure 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 (Figure 4b). Stem nitrogen concentration (SNC) of *A. ordosica* showed no trend with increasing MAP in OT (Figure 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 percent LPC per 100 mm/yr, r^2 = 0.343, *P* < 0.001), and had no significant negative effect on LKC in any species (Supplementary Figure S1a). MAP had a significant positive effect on root phosphorus concentration (RPC) in *S. grandis* (slope 0.125 percent RPC per 100 mm/yr, r^2 = 0.128 and *P* = 0.038), a marginal negative effect in *A. ordosica* (slope -0.224 percent RPC per 100 mm/yr, r^2 = 0.205, *P* = 0.10) and no effect in *S. bungeana* (Supplementary figure S1b, r^2 = 0.084, *P* = 0.189). With increasing MAP, root potassium concentration (RKC) appeared to decrease in *S. bungeana* (slope 0.082 percent RKC per 100 mm/yr, r^2 = 0.151, *P* = 0.074) but showed no clear trend in *S. grandis* or *A. ordosica* (Supplementary Figure S1a). Stem phosphorus concentration (SPC) of *A. ordosica* showed no trend (r^2 = 0.039, *P* = 0.50), while stem potassium concentration (SKC) significantly decreased with increasing MAP in OT (Supplementary Figure S1, slope -2.904 percent SKC per 100 mm/yr, r2 = 0.248 and *P* = 0.070).

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 percent per 100 mm/yr, r2 = 0.315, *P* = 0.007) and C aboveground content (slope 0.239 percent per 100 mm/yr, r2 = 0.583 and *P* < 0.001) in *S. bungeana*, while *A. ordosica* showed only a weaker trend and *S. grandis* none at all (Figure 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 significant positive relationships between MAP and proportion of P (slope 0.212 percent per 100 mm/yr, r2 = 0.631, *P* < 0.001) and K aboveground content (slope 0.239 percent per 100 mm/yr, r2 = 0.620, *P* < 0.001) in *S. bungeana*, but not in the other two species (Supplementary Figure S1D).

DISCUSSION

The aboveground versus 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 & Wardle 2003). Changes in the stochiometry and balance between these pools owing to differences or changes in precipitation regime are therefore likely to impact greatly on ecosystem function and biodiversity.

Two quantities affect the proportion of N above versus 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 versus dry place (Orians & 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 & DeLucia 2001), that is, the concentration of N in leaves would be greater in dry versus 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 versus belowground pool size across aridity gradients.

We found that like other aridity gradients across the world (Maherali & DeLucia 2001, Austin & 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 in *S. bungeana* (Figure 3b). Also consistent with our expectation, there was a significant increase in leaf N concentration from the drier towards the more mesic sites in *S. grandis* and *A. ordosica*, and a weaker increase in leaf N concentration in *S. bungeana* (r^2=0.167, p=0.059) (Figure 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 (Figure 4d). The other two species did not show relationships that differed significantly from flat. This was neither due to differing biomass allocation, the slopes of which relationships were very similar (Figure 3b); nor to root N concentration, which also showed similar pattern for the three plant species (Figure 4b). Instead, *S. bungeana* did not increase leaf N concentration in response to aridity to nearly the extent that the other two species did (Figure 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.

Species differ in their intraspecific variation—both for biomass allocation and the extent to which they adjust their N concentration. While intraspecific variation in leaf traits (including N concentration and leaf mass per area) has been relatively widely studied (e.g. Shipley & Almeida-Cortez 2003, McGill et al. 2006, Ackerly & Cornwell 2007, Cornwell & Ackerly 2009, Albert et al. 2010, Messier et al. 2010), there is still no consensus on why species differ in the magnitude of their intraspecific variation. We suggest that intraspecific variation in a few key traits, especially N and C allocation, is crucial for understanding how much of N and biomass cycling occurs belowground versus above ground as living biomass and then on the surface of the soil as leaf and stem litter.

In our study of three predominant species in Inner Mongolia, in two cases (clearly in *S. grandis*, borderline in *A. ordosica*) intraspecific variation in biomass allocation balanced shifts in the concentration of leaf N. In the third species, *S. bungeana,* biomass allocation changed, but the shift in N concentration did not fully compensate. Where *S. bungeana* was predominant, a greater proportion of N was held aboveground in mesic versus dry place. In contrast, where *S. grandis* was predominant, the pool sizes of N above- versus belowground were similar in mesic versus dry place, but the pool size of C was not. There was much more C aboveground in mesic versus dry place, but that C was accompanied with a lower concentration of N.

We propose one potentially important consequence of the decreasing aboveground allocation to biomass that is richer in N as aridity gets more severe. Logically, at the level of the plant individual, a given proportion of consumption of aboveground biomass by herbivores in a more arid site will remove a relatively large proportion of the plant's total N pool, which has to be compensated for to the extent possible by N uptake from the soil. Under strong grazing regimes, uptake may not keep up with N removal and this might lead to exhaustion of the aboveground N pool and eventually lead to shoot death, with consequences for the soil stabilizing function of the vegetation in these erosion-prone areas. Thus, increasing divergence of above- versus belowground N and C pool with increasing aridity could accelerate land degradation; as many semi-arid and arid lands 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 (Figure 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. It would also be important to test whether and how the possible feedback suggested above might be influenced by possible changes in preference of livestock for different food plants as related to changing leaf nutritional value for the different species, with consequences for their abundance hierarchies at different points along the precipitation gradient.

Conclusion

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 below ground 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- versus 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.

Acknowledgement

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Tables and Figures, Ye *et al.*

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	**<0.001**	1	52.915	**<0.001**	2	16.711	**<0.001**
	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	**<0.001**	1	2.540	0.116	2	3.336	**0.042**
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	**0.002**	1	9.185	**0.004**	2	1.141	0.326
P	Leaf P conc.	2	6.122	**0.004**	1	7.860	**0.007**	2	2.927	0.061
	Stem P conc.	-	-	-	1	0.481	0.501	-	-	-
	Root P conc.	2	7.158	**0.002**	1	1.325	0.254	2	5.448	**0.007**
	Prop. of P aboveground	2	23.905	**<0.001**	1	8.187	**0.006**	2	7.930	**0.001**
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	**0.001**	1	1.602	0.210	2	3.833	**0.027**
	Prop. of K aboveground	2	22.785	**<0.001**	1	12.185	**0.001**	2	5.272	**0.008**

Figure legends

Fig. 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 versus leaves and higher leaf N concentrations.

Fig. 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, that is, with mean annual precipitation ranging from 160mm to 440mm, and most of MAP occurring from May through September, and with mean annual temperature from 1 to 9 ℃, mean temperature of the coldest month from -20 to -12 ℃ (January), and mean temperature of the warmest month from 19 to 24 ℃ (July)).

Fig. 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

Fig. 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.

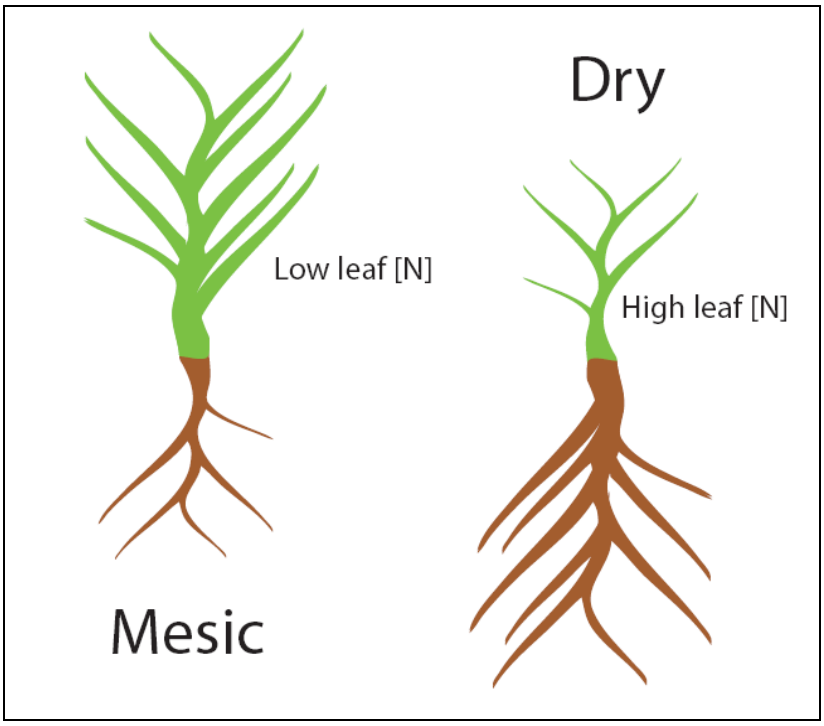
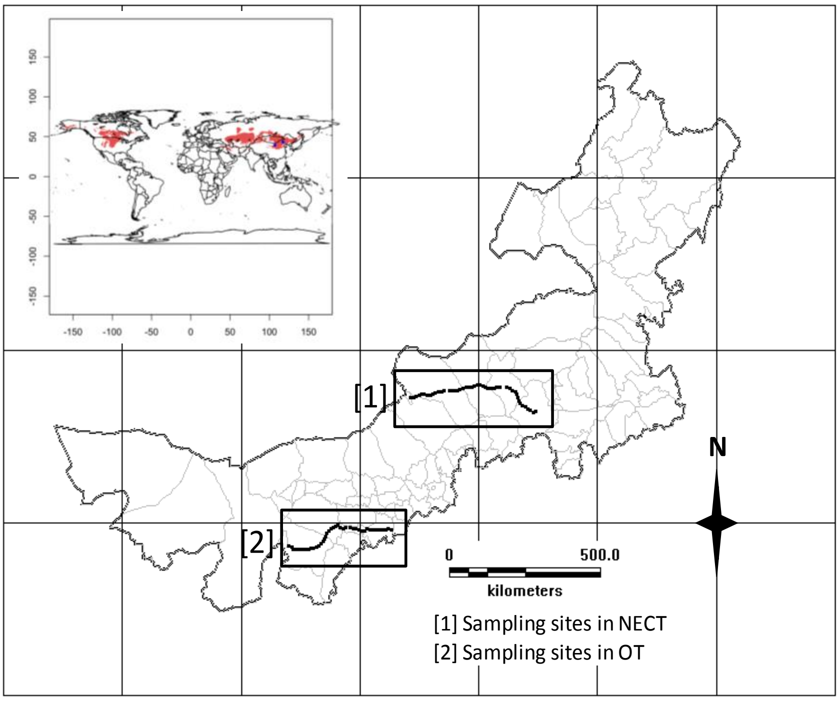


Figure 1


150
100
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-50
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kilometers
[1] Sampling sites in NECT
[2] Sampling sites in OT

Figure 2

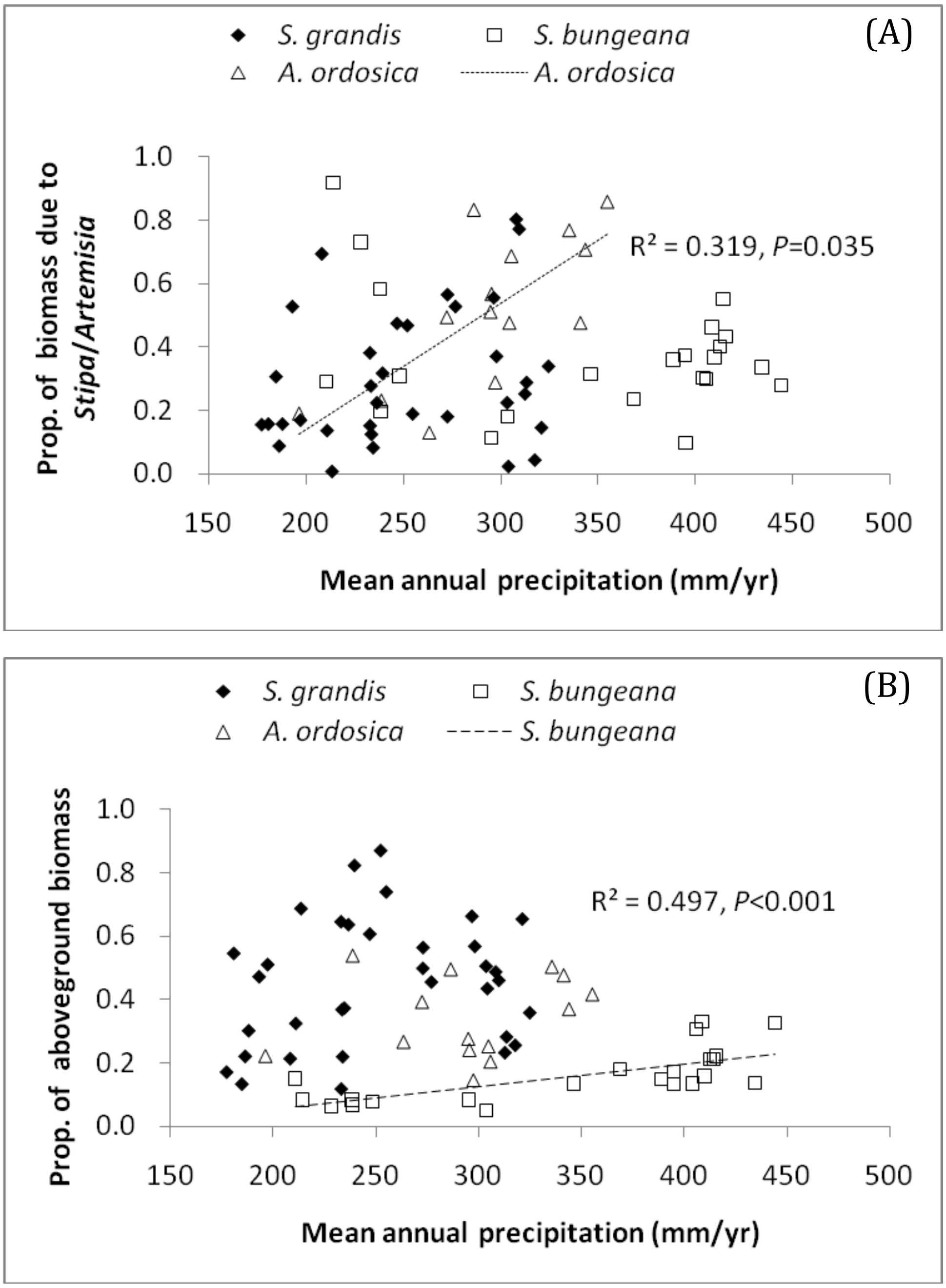

S. grandis
S. bungeana
A. ordosica
A. ordosica
(A)
Prop. of biomass due to Stipa/Artemisia
1.0
0.8
0.6
0.4
0.2
0.0
R² = 0.319, P=0.035
150
200
250
300
350
400
450
500
Mean annual precipitation (mm/yr)
S. grandis
S. bungeana
A. ordosica
S. bungeana
(B)
Prop. of aboveground biomass
R² = 0.497, P<0.001
Mean annual precipitation (mm/yr)

Figure 3

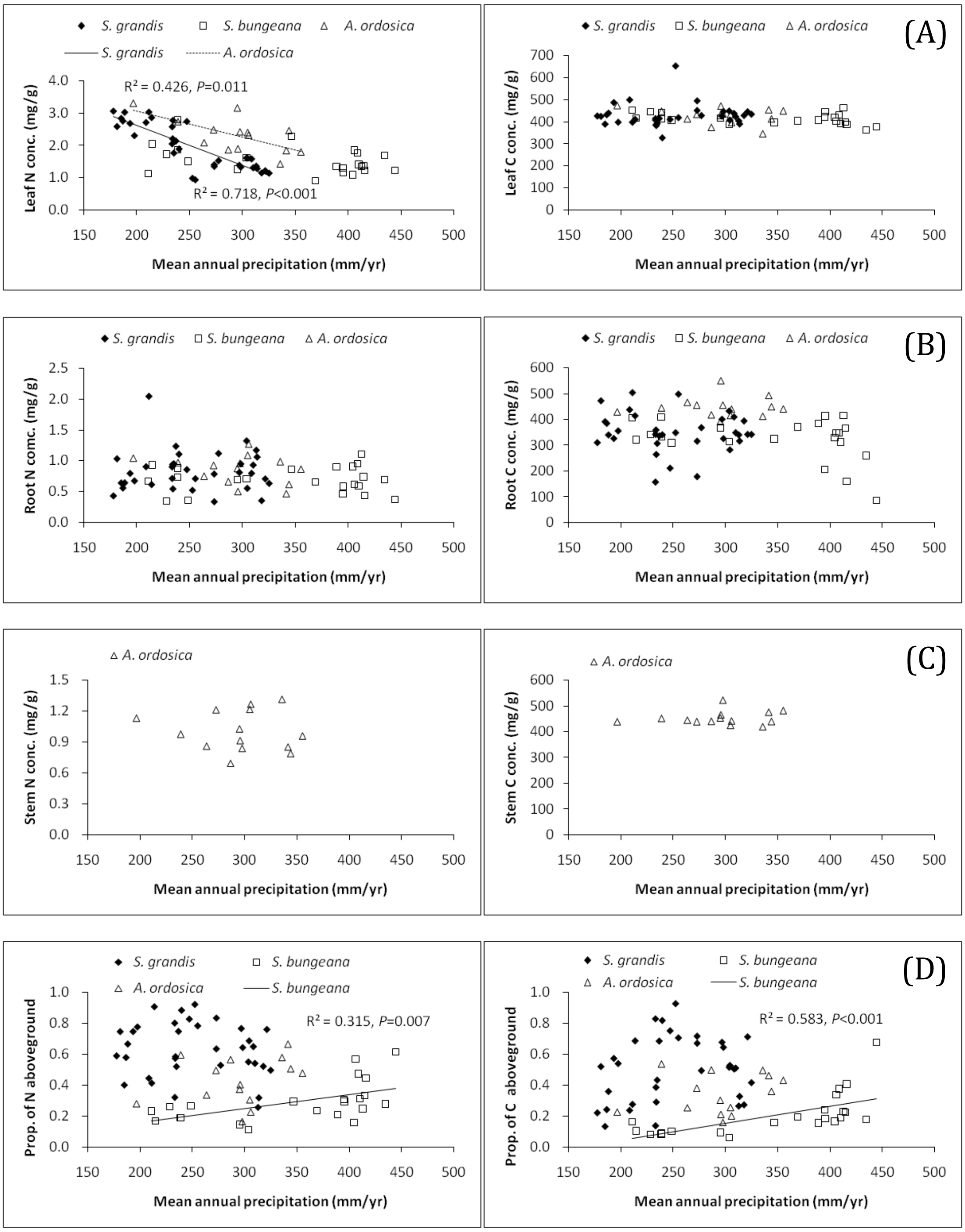
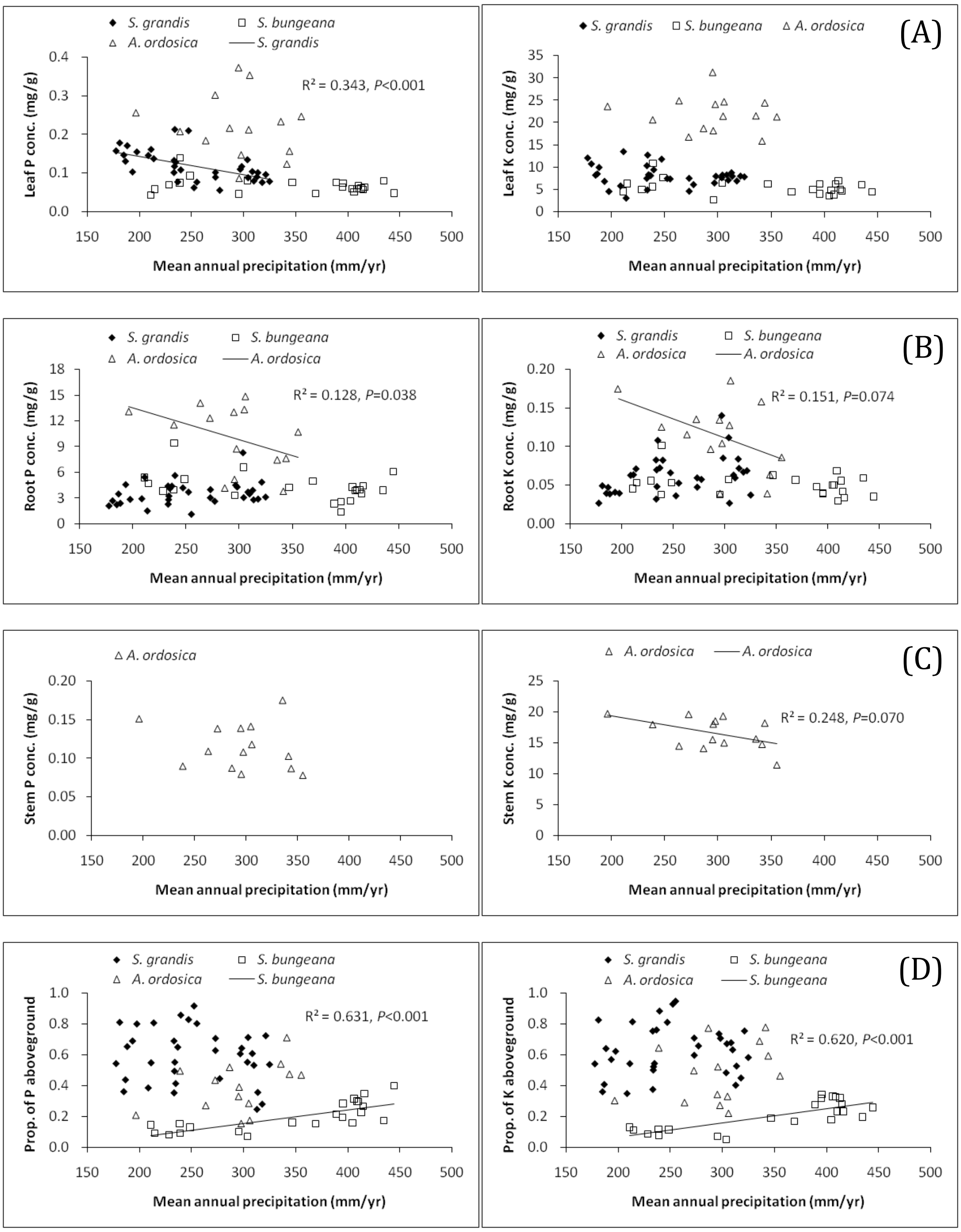

(A)
(B)
(C)
(D)
S. grandis
S. bungeana
A. ordosica
R² = 0.426, P=0.011
R² = 0.718, P<0.001
R² = 0.315, P=0.007
R² = 0.583, P<0.001
Leaf N conc. (mg/g)
Leaf C conc. (mg/g)
Root N conc. (mg/g)
Root C conc. (mg/g)
Stem N conc. (mg/g)
Stem C conc. (mg/g)
Prop. of N aboveground
Prop. of C aboveground
Mean annual precipitation (mm/yr)
150
200
250
300
350
400
450
500

Figure 4

Supplementary materials



Supplementary Materials Figure S1: The relationship between precipitation and plant traits, (A) LPC and LKC, (B) RPC and RKC, (C) SPC and SKC, and (D) proportion of P and K aboveground. LPC, leaf phosphorus concentration; LKC, leaf potassium concentration; RPC, root phosphorus concentration; RKC, root potassium concentration; SPC, stem phosphorus concentration; SKC, stem potassium concentration.