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

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

26 **ABSTRACT**

27 The coupling of carbon cycle and nitrogen cycle drives food web structure and

28 biogeochemistry of an ecosystem. However, across precipitation gradients, there may be

29 a shift in C pool and N pool from above- to below-ground because of shifting plant

30 stoichiometry and allocation. Based on previous evidence, biomass allocation to roots

31 should increase with aridity, while leaf [N] should increase. If their effect sizes are equal,

32 they should cancel each other out, and the above- and below-ground proportions of the

33 N would remain constant. Here, we present the first study to explicitly compare above-

34 and below-ground pool sizes of N and C within predominant plant species along

35 precipitation gradients. Biomass and nutrient concentrations of leaves, stems and roots

36 of three predominant species were measured along two major precipitation gradients in

37 Inner Mongolia, China. Along the two gradients, the effect sizes of the biomass shifts

38 were remarkably consistent among three predominant species. However, the size of the

39 shift in aboveground [N] was not, leading to a species-specific pattern in above- and

40 below-ground pool size. In two species (*Stipa grandis* and *Artemisia ordosica*) the effect

41 sizes of biomass allocation and [N] were equal and the proportion of N of above- and

42 below-ground did not change with aridity, but in *S. bungeana* the increase in leaf [N]

43 with aridity was much weaker than the biomass shift, leading to a decrease in the

44 proportion of N aboveground at dry sites. We have found examples of consistent N pool

45 sizes above- and belowground and a shift to a greater proportion of belowground N in

46 drier sites depending on the species. We suggest that precipitation gradients do

47 potentially decouple the C and N pool, but the exact nature of the decoupling depends on

48 the dominant species' capacity for intraspecific variation.

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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.

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79   2003), which may compensate for prolonged periods of stomatal closure. Going from

80   mesic to dry sites, species commonly allocate more N per leaf area partially by

81   increasing N per unit leaf mass and partially by increasing the leaf mass per area (Wright

82   et al. 2002). This pattern has been documented both among species in Australia (Wright

83   et al. 2001) and across China (Han et al. 2011), and within species in Hawai'i (Cornwell

84   et al. 2007).

85   Interestingly, aridity creates a condition under which biomass may be allocated in

86   greater quantities belowground, but N is needed aboveground to facilitate greater water

87   use efficiency. This suggests a potential decoupling of pool sizes for C and N, above- and

88   belowground, with the pattern in pool size determined by the relative effect sizes of the

89   trends in biomass allocation and [N]. These shifts could have implications for

90   biogeochemical functions—especially the residence time of C in the biosphere, both via

91   leaf quality to herbivores and litter quality to decomposers. Both herbivory and

92   decomposition are known to be at least in part a function of tissue C:N ratio (Swift et al.

93   1979, Austin & Vitousek 2000, Perez-Harguindeguy et al. 2000). Here we argue that a

94   particular consequence of increasing divergence of above versus belowground N and C

95   pool with increasing aridity could be accelerated by land degradation; as many semi-arid

96   and arid lands are grazed by livestock, the proportional removal of a plant's

97   aboveground N would increase with aridity, thereby potentially leading to faster

98   exhaustion of whole-plant N to support productivity. Such positive feedback to land

99   degradation by livestock would be a significant and previously unrecognized

100 consequence of increased allocation of N to leaves to increase water use efficiency.

101   We investigate the above- and belowground pool sizes for C and N in the

102 predominant plant species across two precipitation gradients in the semiarid to arid

103 region of northern China. We then decompose the pool size patterns into the respective

104   drivers — shifts in both the allocation of biomass and in the concentration of

105   macronutrients. Our approach is to use three predominant species, which together

106   represent much of the biomass along these gradients. Our hypothesis is that, from mesic

107   towards dry sites, above and belowground C pool and N pool will diverge as a

108   consequence of increasing biomass allocation belowground combined with greater leaf

109   N concentration (Figure 1). To our knowledge, this is the first large-scale field study to

110   explicitly dissect carbon pool and nitrogen pool both between and within organs of

111   whole plants.

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114   **METHODS**

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116   **Study area and species**

117   This study was conducted along two transects, each following a major precipitation

118   gradient, in the Inner Mongolia Autonomous Region (hereinafter, Inner Mongolia),

119   N-China (Figure 2). The North-East China Transect (NECT) ranges from Erenhot to

120   Chifeng city (longitude 112.12 to 117.42 °E, latitude 43 to 44 °N, altitudes 920 to 1300

121   m), with mean annual precipitation (MAP) ranging from approx. 200mm to 400mm; The

122   Ordos Transect (OT) stretches also from the west to east in Ordos City, (longitude

123   107.00 to 111.31 °E, latitude 38 to 39 °N, altitudes 1200 to 1500 m), with MAP ranging

124   from 160mm to 440mm. Along the west of NECT, temperature only shows a modest

125   trend, with mean annual temperature (MAT) from 1 to 3 °C, mean temperature of the

126   coldest month (CMT) from -20 to -12 °C (January), and mean temperature of the

127   warmest month (WMT) from 19 to 24 °C (July). The precipitation from May through

128   September accounts for almost 80% of MAP (Zhang et al. 1997). The warmest sites have

129   the lowest relative inner-annual variability in temperature and the coldest sites have the

130   highest variability, while the driest sites have the highest seasonality in precipitation

131   and the wettest sites have the lowest variability along NECT (Ni & Zhang 2000). The

132   Ordos Transect, about 450 km south of NECT, features a weak east-to-west temperature

133   gradient (MAT from 6 to 9 °C, CMT from -13 to -10 °C (January), and WMT from 20 to

134   23 °C (July)) and a strong east-to-west precipitation gradient, with June through

135   September accounting for 60-80% of MAP (Niu & Li 1992).

136   *Artemisia ordosica* Krasch (Asteraceae) is a deciduous semi-shrub with plumose,

137   linearly lobate leaves, occurring in the Inner Mongolia Autonomous Region, Ningxia

138   Autonomous Region, and Shanxi Province of N-China. Its root system is mainly

139 distributed in the upper 30 cm of sandy soils. This species is overwhelmingly dominant

140 in the semi-fixed and fixed dune landscape of the Mu Us Sandland, which is the main

141 body of the Ordos Plateau (Zhang 1994). *Stipa grandis* P. Smim is a tall bunchgrass and

142 can grow to almost 1 m at the peak of the growing season (late August). Its aboveground

143 parts die off in autumn and new growth is in spring. It often forms nearly pure stands in

144 the semi-arid region of N-China. *Stipa bungeana* Trin. is smaller than *S. grandis*, with

145 height ranging from 20 to 60 cm. It is distributed in N, SW and SE China as well as in

146 Mongolia and Japan. Both *Stipa* species predominate on the loamier soils in the region,

147 as opposed to *A. ordosica* on the sandy substrates.

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149 **Field sampling and laboratory analysis**

150 The field investigation was conducted from 6 August to 18 September, 2006, i.e. the

151 first three weeks along NECT and the latter three weeks along OT. Along each transect

152 this was during the peak biomass period and well before the onset of senescence (which

153 is in September at NECT; end of September/early October at OT). In total 46 sites were

154 chosen along NECT and 41 sites along OT (Figure 2), each two adjacent sites at intervals

155 of more than 10 km. MAP at each site was extracted from the interpolated climate grids

156 (New et al. 2002), using the Raster package in R (Hijmans & van Etten 2011). The site

157 values closely matched previous estimates based on regional regressions with altitude,

158 latitude and longitude for NECT (Zhang et al. 1997) and OT (Niu & Li 1992), respectively.

159 Three 1m×1m quadrats for grass and/or 2m×2m quadrats for semi-shrub were

160 measured at each site. Within each quadrat, all living biomass was harvested, separated

161 into species and oven-dried at 70 °C for ≥ 24 h to constant mass before they were

162 weighed. For each species, cover %, height and number of individuals were also

163 measured within each quadrat at the same time. Leaves of *S. grandis* in NECT and of *S.*

164   *bungeana* and *A. ordosica* in OT were collected for lab analyses within each quadrat, as

165   well as the stems of *A. ordosica* in OT. For each species roots were collected by taking

166   three 10-cm diameter soil cores from 0-40cm depths, mixed in situ into one composite

167   sample. Roots of *S. grandis* in NECT and roots of *S. bungeana* and *A. ordosica* in OT were

168   hand-sorted and washed clean for lab analyses. It is often difficult to differentiate

169   between the roots of different species, but it was perfectly doable to differentiate

170   between the roots of the three target species in this study. Both *S. grandis* and *S.*

171   *bungeana* are bunch-grasses and could be identified visually; their roots are fibrous and

172   shallow. Confusion with *Leymus* can be excluded, as this grass is rhizomatous and has its

173   root distribution much deeper in the soil profile than *Stipa*. The roots of the shrub *A.*

174   *ordosica* were easily recognized by their strong and typical aroma as well as by their

175   morphology. Most other species in NECT and OT were non-grass herbaceous species,

176   such as *Allium*, *Carex*, *Euphorbia*, *Iris*, *Potentilla* and *Taraxacum*. Only roots of the three

177   target species were hand-sorted and washed clean for lab analyses, and all other roots in

178   NECT were mixed into one composite sample.

179   Leaf, stem and root biomass of the three species were measured after $\geq$ 24 h

180   oven-drying at 70°C. Leaf, stem and root potassium (K) concentration was determined

181   using Atomic Absorption Spectrophotometry (Model-932, GBC Scientific Equipment,

182   Melbourne, Australia), while nitrogen (N) and phosphorus (P) concentrations were

183   analyzed according to the micro-Kjeldahl method (Kjeltec 2300 Analyzer Unit, Sweden),

184   and total carbon (C) concentration was determined using the method of $K_2Cr_2O_7$-H_2SO_4

185   solution digestion with oil-bath heating (Dong et al. 1996; Zheng et al. 2010). Also,

186   standard reference materials were used throughout to guarantee the measurement

187   accuracy and repeatability.

188   In total, 15 of the sites provided data for plant aboveground and underground

189 biomass and element contents for *A. ordosica* in OT, 22 sites for *S. bungeana* in OT, and

190 35 sites for *S. grandis* in NECT. Unfortunately, it was not logistically possible to measure

191 soil nutrient availabilities simultaneously and repeatedly at so many points along the

192 two gradients, given that nutrient availability is notoriously variable in time. However,

193 we expect nutrient availabilities to have varied little over each of the transects for given

194 species, as both *Stipa* species were generally sampled from unfertilized loamy soils and

195 *A. ordosica* generally from unfertilized sandy soils, The remarkably flat pattern for root N

196 content with MAP for all three species (see Results, Fig. 4b) strongly suggests that there

197 was no correspondence between soil nutrient availability and precipitation regime,

198 although we cannot exclude effects of nutrient availability on intra-specific variability in

199 nutrient-related traits at finer spatial scale.

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202 **Data analysis**

203 Statistical analyses were performed using SPSS13.0 software (2004, SPSS Inc., USA).

204 We analyzed variation in each trait for the effect of species and precipitation using

205 ANCOVA, with species as an independent variable and precipitation as a covariate. And

206 we analyzed relationship between each trait and precipitation for each species using

207 Linear Regression. Data for leaf [P], leaf [K], root [P], root [K], and proportion of

208 aboveground N, C, P and K content were log-transformed before analyses in order to

209 meet the assumptions of normality.

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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

236   significant interactions for species by precipitation on most plant traits analyzed (Table

237   1).

238   Although LNC decreased along a gradient of MAP for all three species, the effect was

239   stronger in *S. grandis* (slope -1.24 mg/g per 100 mm/yr, r^2 = 0.718, *P* < 0.001) and *A.*

240   *ordosica* (slope -0.79 mg/g per 100 mm/yr, r^2 = 0.426, *P* = 0.011) than in *S. bungeana*

241   (slope -0.22 mg/g per 100 mm/yr, r^2 = 0.167, *P* = 0.059). All three species had similar

242   leaf carbon concentration (LCC) values, which increased steadily with MAP (Figure 4a).

243   MAP had no significant effect on root carbon concentration (RCC) or root nitrogen

244   concentration (RNC). The three species had similar RNC, while *A. ordosica* had a higher

245   RCC than the two *Stipa* species (Figure 4b). Stem nitrogen concentration (SNC) of *A.*

246   *ordosica* showed no trend with increasing MAP in OT (Figure 4c, r^2 = 0.011, *P* = 0.719).

247   *A. ordosica* had higher LPC and leaf potassium concentration (LKC) than the two

248   *Stipa* species. MAP decreased LPC in all three species (but only significantly in *S. grandis*,

249   slope -0.175 percent LPC per 100 mm/yr, r^2 = 0.343, *P* < 0.001), and had no significant

250   negative effect on LKC in any species (Supplementary Figure S1a). MAP had a significant

251   positive effect on root phosphorus concentration (RPC) in *S. grandis* (slope 0.125

252   percent RPC per 100 mm/yr, r^2 = 0.128 and *P* = 0.038), a marginal negative effect in *A.*

253   *ordosica* (slope -0.224 percent RPC per 100 mm/yr, r^2 = 0.205, *P* = 0.10) and no effect in

254   *S. bungeana* (Supplementary figure S1b, r^2 = 0.084, *P* = 0.189). With increasing MAP, root

255   potassium concentration (RKC) appeared to decrease in *S. bungeana* (slope 0.082

256   percent RKC per 100 mm/yr, r^2 = 0.151, *P* = 0.074) but showed no clear trend in *S.*

257   *grandis* or *A. ordosica* (Supplementary Figure S1a). Stem phosphorus concentration

258   (SPC) of *A. ordosica* showed no trend (r^2 = 0.039, *P* = 0.50), while stem potassium

259   concentration (SKC) significantly decreased with increasing MAP in OT (Supplementary

260   Figure S1, slope -2.904 percent SKC per 100 mm/yr, r2 = 0.248 and *P* = 0.070).

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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).

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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

303   two trends would cancel each other out, resulting in similar proportions of N

304   aboveground versus belowground pool size across aridity gradients.

305   We found that like other aridity gradients across the world (Maherali & DeLucia

306   2001, Austin & Sala 2002, Santiago et al. 2005, He et al. 2008), there was a shift from

307   more aboveground towards more belowground biomass allocation with decreasing

308   precipitation in *S. bungeana* (Figure 3b). Also consistent with our expectation, there was

309   a significant increase in leaf N concentration from the drier towards the more mesic sites

310   in *S. grandis* and *A. ordosica*, and a weaker increase in leaf N concentration in *S.*

311   *bungeana* (r^2=0.167, p=0.059) (Figure 4a). Integrating both patterns, we found that for

312   one species, *S. bungeana,* there was a significant positive trend in proportion of N

313   aboveground with precipitation (Figure 4d). The other two species did not show

314   relationships that differed significantly from flat. This was neither due to differing

315   biomass allocation, the slopes of which relationships were very similar (Figure 3b); nor

316   to root N concentration, which also showed similar pattern for the three plant species

317   (Figure 4b). Instead, *S. bungeana* did not increase leaf N concentration in response to

318   aridity to nearly the extent that the other two species did (Figure 4a). This meant that

319   unlike in the two other species where N and biomass shifts came close to equal effect

320   sizes, in *S. bungeana* the biomass effect dominated and the proportion of N aboveground

321   increased with precipitation.

322   Species differ in their intraspecific variation—both for biomass allocation and the

323   extent to which they adjust their N concentration. While intraspecific variation in leaf

324   traits (including N concentration and leaf mass per area) has been relatively widely

325   studied (e.g. Shipley & Almeida-Cortez 2003, McGill et al. 2006, Ackerly & Cornwell

326   2007, Cornwell & Ackerly 2009, Albert et al. 2010, Messier et al. 2010), there is still no

327   consensus on why species differ in the magnitude of their intraspecific variation. We

328   suggest that intraspecific variation in a few key traits, especially N and C allocation, is

329   crucial for understanding how much of N and biomass cycling occurs belowground

330   versus above ground as living biomass and then on the surface of the soil as leaf and

331   stem litter.

332   In our study of three predominant species in Inner Mongolia, in two cases (clearly in

333   *S. grandis*, borderline in *A. ordosica*) intraspecific variation in biomass allocation

334   balanced shifts in the concentration of leaf N. In the third species, *S. bungeana,* biomass

335   allocation changed, but the shift in N concentration did not fully compensate. Where *S.*

336   *bungeana* was predominant, a greater proportion of N was held aboveground in mesic

337   versus dry place. In contrast, where *S. grandis* was predominant, the pool sizes of N

338   above- versus belowground were similar in mesic versus dry place, but the pool size of C

339   was not. There was much more C aboveground in mesic versus dry place, but that C was

340   accompanied with a lower concentration of N.

341   We propose one potentially important consequence of the decreasing aboveground

342   allocation to biomass that is richer in N as aridity gets more severe. Logically, at the level

343   of the plant individual, a given proportion of consumption of aboveground biomass by

344   herbivores in a more arid site will remove a relatively large proportion of the plant's

345   total N pool, which has to be compensated for to the extent possible by N uptake from

346   the soil. Under strong grazing regimes, uptake may not keep up with N removal and this

347   might lead to exhaustion of the aboveground N pool and eventually lead to shoot death,

348   with consequences for the soil stabilizing function of the vegetation in these

349   erosion-prone areas. Thus, increasing divergence of above- versus belowground N and C

350   pool with increasing aridity could accelerate land degradation; as many semi-arid and

351   arid lands are grazed by livestock, often heavily, the dominant vegetation could drive a

352   positive feedback on land degradation by livestock at low precipitation regimes. This

353   situation will not be unique to Inner Mongolia, as extensive regions in a similar climate

354   zone in at least West, Central and East Asia and North America (Figure 2, insert) host

355   similar vegetation types and similarly heavy use by livestock. This possibility may

356   deserve in depth study that would have to extend to vegetation regrowth patterns and N

357   and C pathway and pool via livestock at different animal densities. It would also be

358   important to test whether and how the possible feedback suggested above might be

359   influenced by possible changes in preference of livestock for different food plants as

360   related to changing leaf nutritional value for the different species, with consequences for

361   their abundance hierarchies at different points along the precipitation gradient.

362

363   **Conclusion**

364   The C and N cycle are usually tightly coupled, because the proportion of N that is

365   needed in specific tissue types is relatively constrained—N is usually low in structural

366   tissue and high in absorbing (roots) and photosynthetic (leaves) tissue (Sterner and

367   Elser 2002). Therefore, decoupling of the C and N pool across different climates is a

368   paradox. Changing water availability potentially decouples the C and the N pool because

369   of greater allocation to high N leaves in dry sites. Here we have fully decomposed above-

370   and below ground C and N allocation and stoichiometry. We have found examples of

371   consistent N pool sizes above- and belowground and a shift to a greater proportion of

372   belowground N in drier sites depending on the species. We suggest that precipitation

373   gradients do potentially decouple the C and N pool, but the exact nature of the

374   decoupling depends on the dominant species' capacity for intraspecific variation. Even in

375   cases where the above- versus belowground N and C pool themselves do not change

376   proportionally, smaller biomass allocation to shoots with higher N concentrations in

377   drier areas might facilitate a positive feedback to land degradation by livestock.

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513   Table 1. Effects of species and mean annual precipitation on each plant trait in the

514   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.
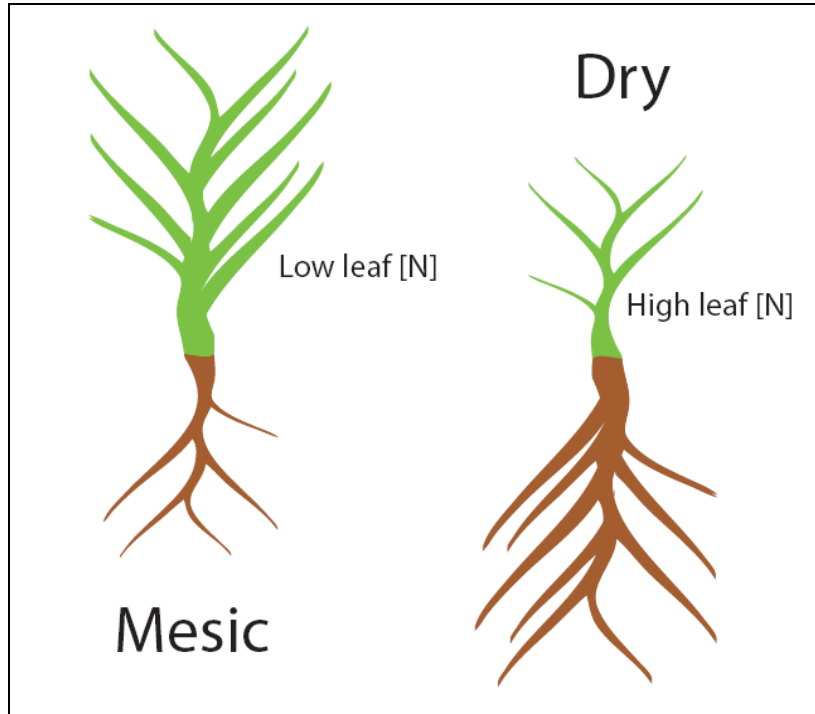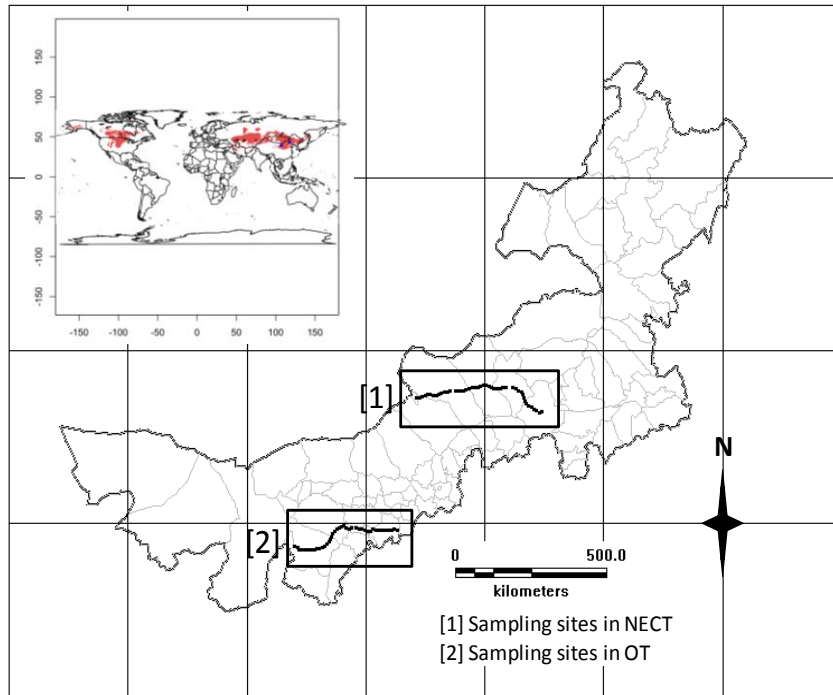
Figure 1

[1] Sampling sites in NECT
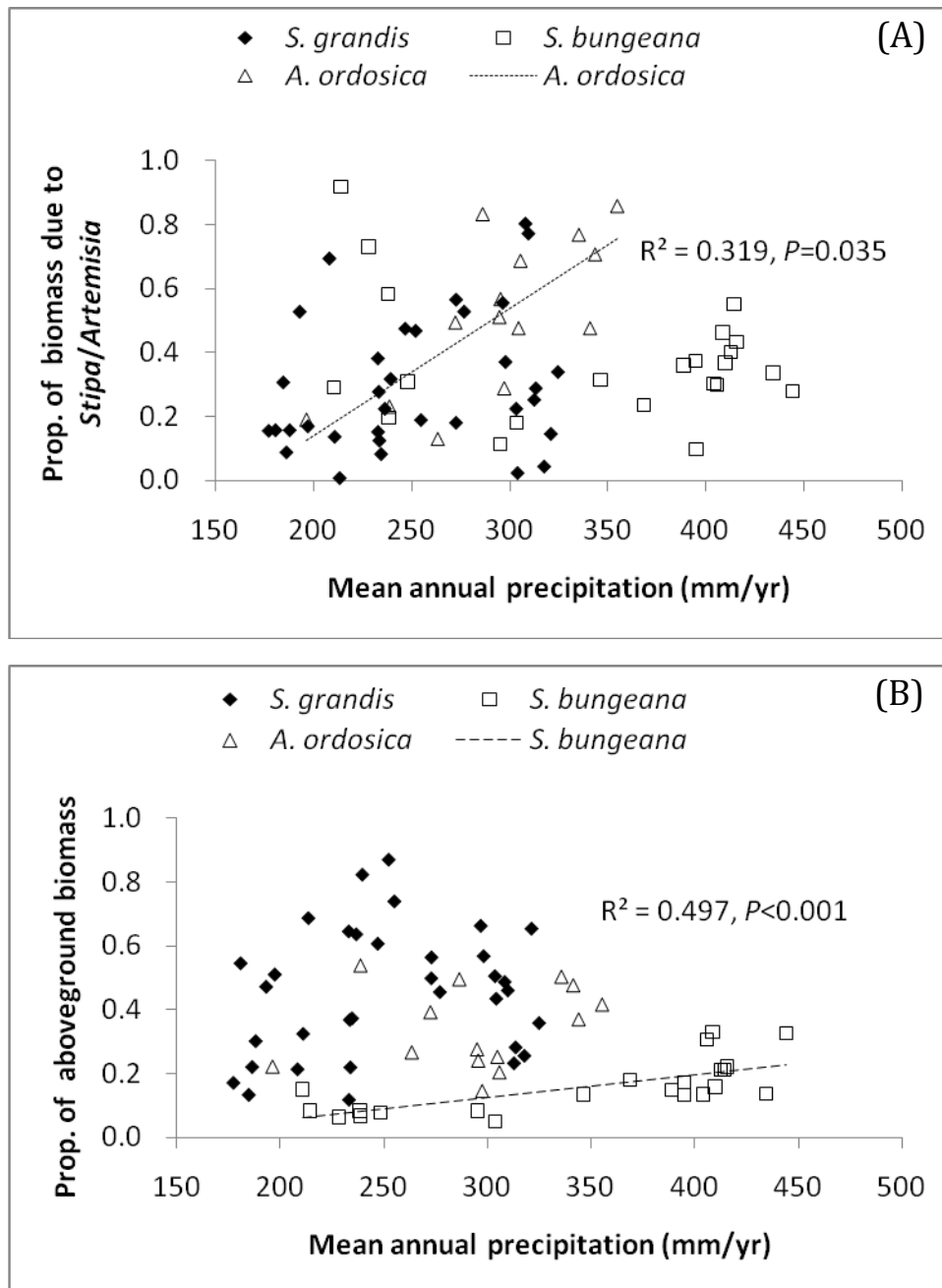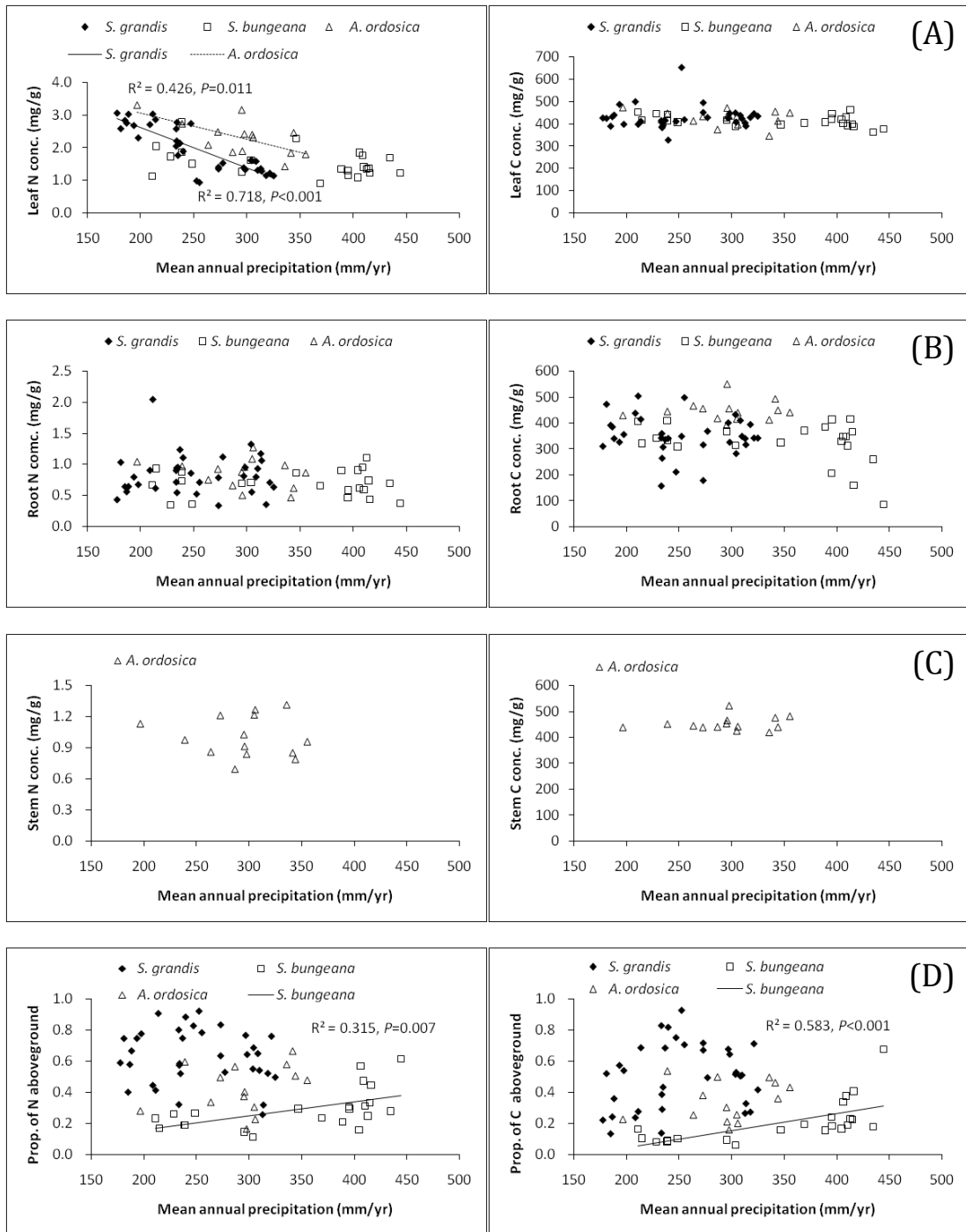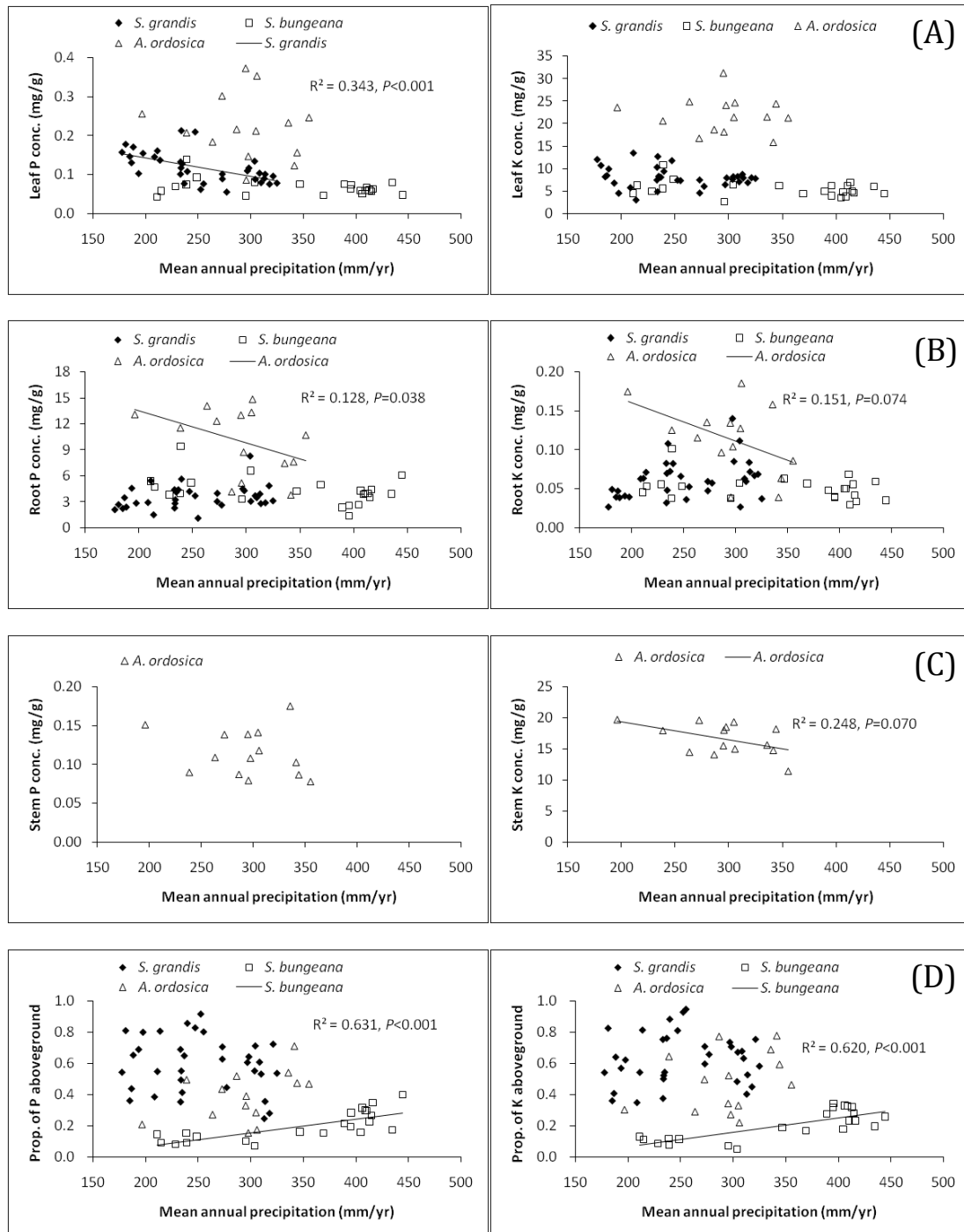[2] Sampling sites in OT

Figure 2

Figure 3

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.