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# Decoupling of above and belowground C and N pools within predominant plant species *Stipa grandis* along a precipitation gradient in Chinese steppe zone

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## Abstract

The coupling of the carbon and nutrient cycles drives the food web structure and biogeochemistry of ecosystems. However, across precipitation gradients, there may be a shift in C and N pools from above- to belowground because of shifting plant stoichiometry and allocation. Here, we present a study which is the first to explicitly compare above- and belowground pool sizes of N and C within predominant plant species along precipitation gradient. We dissected these pools into biomass allocation and nutrient concentrations. 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. Along a precipitation gradient in Chinese steppe zone, the effect sizes of the biomass shifts were remarkably consistent among the predominant species, *Stipa grandis*. 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 the shift in leaf [C] with aridity was much weaker than the biomass shift, leading to a decrease in the proportion of C belowground at dry sites. Precipitation gradients do decouple the C and N pool of *S. grandis* along a precipitation gradient in Chinese steppe zone.

## 1 Introduction

Plant carbon and nitrogen economies are closely coupled (Shaver and Chapin, 1991; Aerts and Chapin, 2000), and this coupling has important feedbacks to terrestrial carbon budget and climate (IPCC, 2007; Chapin et al., 2009). To capture and utilize light, nutrients, carbon and water, plants allocate resources both aboveground to leaves and stems and belowground to roots. Nitrogen is obtained belowground via roots and partly transported aboveground to support photosynthesis principally through the enzyme Rubisco and other parts of the photosynthetic system, while carbon is obtained aboveground via photosynthesis and partly transported belowground to support both water

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and mineral nutrient acquisition. 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 below-ground, 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 versus mesic sites, it is well documented that the allocation of biomass shifts to a higher proportion of roots versus 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 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

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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).

We investigate the above- and belowground pool sizes for C and N in the predominant plant species across one precipitation gradients in the semiarid to arid region of northern China. We then break down 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 one predominant species, *Stipa grandis*, which represent much of the biomass along the gradient. Our hypothesis is that, *from mesic towards dry sites, above and belowground C and N pools will diverge as a consequence of increasing biomass allocation belowground combined with greater leaf N concentration*. To our knowledge, this is the first large-scale field study to explicitly dissect carbon and nutrient pools both between and within organs of whole plants.

## 2 Methods

### 2.1 Study area and species

This study was conducted along a precipitation gradient in Chinese steppe zone, in the Inner Mongolia Autonomous Region (hereinafter, Inner Mongolia), N-China. The study area 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. 200 mm to 400 mm in the same range as the west part of North-East China. Transect (NECT) does (Zhang et al., 1997). 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. The warmest sites have the lowest relative inner-annual variability in temperature and the coldest sites have the highest variability, while

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the driest sites have the highest seasonality in precipitation and the wettest sites have the lowest variability (Ni and Zhang, 2000).

*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 predominates on the loamier soils, and often forms nearly pure stands in the semi-arid region of N China.

## 2.2 Field sampling and laboratory analysis

The field investigation was conducted from 6 to 20 August, 2006. Along each transect this was during the peak biomass period and well before the onset of senescence. In 10 total 35 sites were chosen along the precipitation gradient, 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 the west part of NECT (Zhang et al., 15 1997), respectively.

Three 1 m × 1 m quadrats were measured at each site. Within each quadrat, all living biomass was harvested, separated into species and oven-dried at 70 °C for  $\geq 48$  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 20 *S. grandis* were collected for lab analyses within each quadrat. Roots were collected by taking three 10-cm diameter soil cores from 0–40 cm depths. Roots of *S. grandis* were hand-sorted and washed clean for lab analyses, and roots of other species were mixed in situ into one composite sample.

Leaf and root biomass were measured after  $\geq 48$  h oven-drying at 70 °C. Leaf 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)

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concentration was determined using the method of  $K_2Cr_2O_7$ - $H_2SO_4$  solution digestion with oil-bath heating (Dong et al., 1996).

## 2.3 Data analysis

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

5 We analyzed relationship between each trait and precipitation using linear regression. Data for leaf P concentration, leaf K concentration, root P concentration, root K concentration, 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

10 Both aboveground and underground vegetation biomass were increased significantly with higher precipitation along the precipitation gradient (Table 1). The relative contribution of *S. grandis* to the plant community biomass ranged from 1 to 8 % (mean 298 %), but there was no distinctive relationship between percentage of vegetation due to *S. grandis* and mean annual precipitation ( $r^2 = 0.044$ ,  $P = 0.233$ ; Table 1, Fig. 1a).

### 15 3.1 Plant biomass and its allocation along NECT

Both leaf and root biomass of *S. grandis* had significant positive relationship with MAP (Table 1). The proportion of aboveground biomass ranged from 11.7 % to 87.0 %, and increased linearly with MAP in *S. grandis* ( $r^2 = 0.274$ ,  $P = 0.001$ ; Table 1, Fig. 1b); the slope of proportion of aboveground biomass as a function of MAP was a mean of 217 %  
20 additional allocation aboveground for every  $100 \text{ mm yr}^{-1}$  of additional rainfall.

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### 3.2 Plant element concentrations along NECT

Precipitation had a negative and significant relationship with leaf nitrogen concentration (LNC) and leaf phosphorus concentration (LPC), with significant positive effect on root phosphorus concentration (RPC) (Table 1).

MAP decreased LNC in *S. grandis* (slope  $-1.24 \text{ mg g}^{-1}$  per  $100 \text{ mm yr}^{-1}$ ,  $r^2 = 0.718$ ,  $P < 0.001$ ), and had no significant effect on RNC (Fig. 2a). *S. grandis* have similar leaf carbon concentration (LCC) and root carbon concentration (RCC), and MAP had no significant effect on LCC or RCC (Fig. 2b).

With increasing MAP, LPC appeared to decrease significantly in *S. grandis* (slope  $-0.048 \text{ mg g}^{-1}$  per  $100 \text{ mm yr}^{-1}$ ,  $r^2 = 0.341$ ,  $P < 0.001$ ), while RPC appeared to increase significantly (slope  $0.019 \text{ mg g}^{-1}$  per  $100 \text{ mm yr}^{-1}$ ,  $r^2 = 0.128$  and  $P = 0.038$ ) (Appendix Fig. A1a). MAP had no significant effect on LKC or RKC (Appendix Fig. A1b).

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

There was no significant relationship between MAP and proportion of N aboveground content in *S. grandis* (Fig. 2c), but a significant positive relationship between MAP and proportion of C (slope  $0.236$  percent per  $100 \text{ mm yr}^{-1}$ ,  $r^2 = 0.270$ ,  $P = 0.002$ ; Fig. 2d).

MAP increased proportion of K aboveground content significantly (slope  $0.167$  percent per  $100 \text{ mm yr}^{-1}$ ,  $r^2 = 0.232$ ,  $P = 0.004$ ; Appendix Fig. A1d), while had no significantly effect on proportion of P aboveground content in *S. grandis* (Appendix Fig. A1c).

## 20 4 Discussion

The aboveground versus belowground pool sizes 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 many fungi and animals associated with the plants – mutualists, pathogens, herbivores, decomposers – the whole plant C and N

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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.

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 places (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 versus mesic environments. 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 sizes across aridity gradients.

We found that like other aridity gradients across the world, there was a shift from more aboveground towards more belowground biomass allocation with decreasing precipitation (Fig. 1b). Also consistent with our expectation, there was an increase in leaf N concentration in the drier versus the more mesic sites (Fig. 2a). Integrating both patterns, we found that for *S. grandis*, there was no significant relationship in proportion of N aboveground with precipitation (Fig. 2c). This meant that in *S. grandis*, the N and biomass shifts came close to equal effect sizes. We also found that for *S. grandis*, leaf and root C concentration remained stable with the raising MAP (Fig. 2b) though the biomass effect dominated and the proportion of C aboveground increased with MAP (Fig. 2d). These results confirm our hypothesis that from mesic towards dry sites, above and belowground C and N pools diverged. The pool sizes of N above- versus

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belowground were similar in mesic versus dry places, but the pool size of C was not. There was much more C aboveground in mesic versus dry places, but that C was accompanied with a lower concentration of N.

It is well known that species differ in their intraspecific variation – both for biomass allocation and leaf traits, including N concentration and leaf mass per area (e.g. Shipley and Almeida-Cortez, 2003; McGill et al., 2006; Ackerly and Cornwell, 2007; Cornwell and Ackerly, 2009; Albert et al., 2010; Messier et al., 2010). There may be three potential patterns in N pool size which are determined by the relative effect sizes of the trends in biomass allocation and N concentration. 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 aboveground as living biomass and then on the surface of the soil as leaf and stem litter.

We propose one potentially important consequence of the decreasing aboveground allocation to biomass that is richer in N as aridity gets more severe. Logically, every kilogram of foliage eaten by herbivores removes a relatively large proportion of the plants' total N pool, which has to be compensated for to the extent possible by N uptake from the soil. But in arid areas, every kilogram of foliage lost means larger proportion of plants' total N pool, N uptake more likely to 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 pools 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 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 pathways and pools via livestock at different animal densities.

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## 5 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) tissues (Sterner and Elser, 2002).

5 Therefore, decoupling of the C and N pools 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

10 proportion of belowground C pool size in more arid sites. We suggest that precipitation gradients do potentially decouple the C and N pool. Even in cases where the above- versus belowground N and C pools themselves do not change proportionally, smaller biomass allocation to shoots with higher N concentrations in more arid areas more likely to facilitate a positive feedback to land degradation by livestock.

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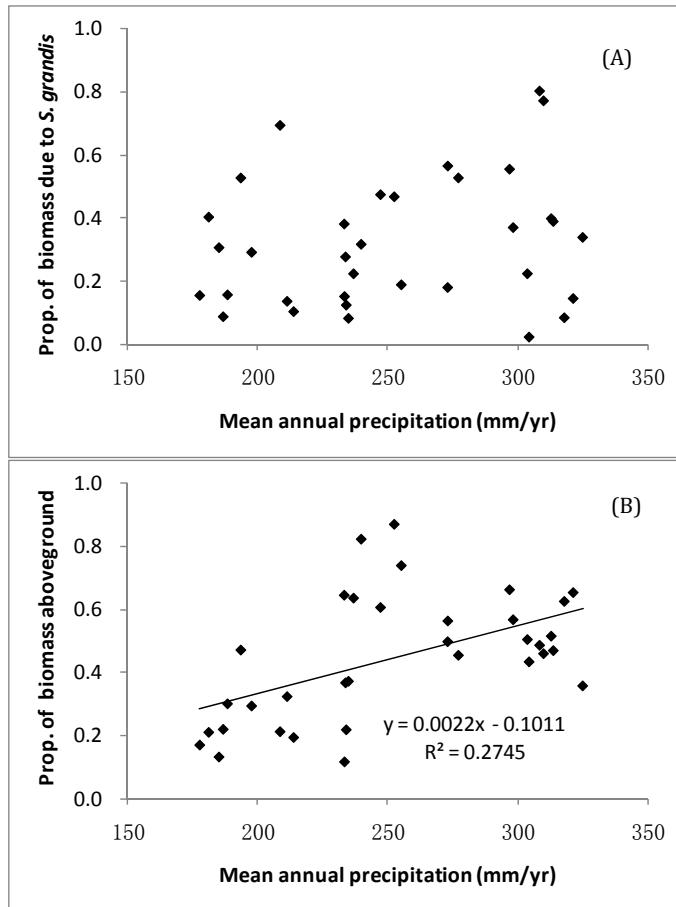
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Interactive Discussion

**Table 1.** Correlation coefficients between mean annual precipitation and each plant trait of *Stipa grandis* in the transect. Bold values indicate  $P < 0.05$ .

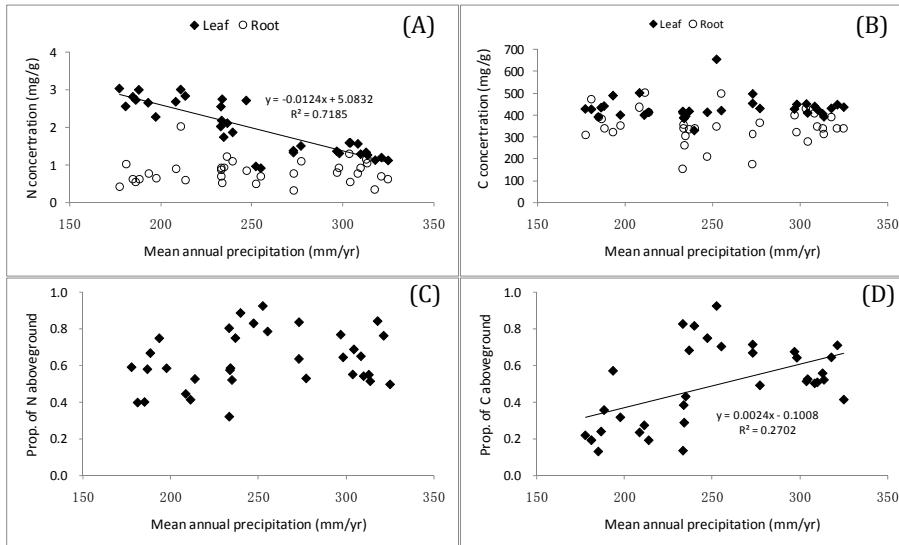
Plant traits		<i>N</i>	Pearson Correlation	Sig. (2-tailed)
Biomass	Leaf biomass of <i>S. grandis</i>	34	0.511582	<b>0.002</b>
	Root biomass of <i>S. grandis</i>	34	0.477416	<b>0.004</b>
	Percentage of biomass aboveground in <i>S. grandis</i>	34	0.523915	<b>0.001</b>
	aboveground vegetation biomass	34	0.602717	<b>0.000</b>
	underground vegetation biomass	34	0.540203	<b>0.001</b>
	Percentage of vegetation biomass due to <i>S. grandis</i>	34	0.209913	0.233
Nitrogen	Leaf N Concentration	34	-0.84765	<b>0.000</b>
	Root N concentration	34	0.022406	0.900
	Proportion of N aboveground	34	0.237402	0.176
Carbon	Leaf C Concentration	34	0.050962	0.775
	Root C concentration	34	-0.11324	0.524
	Proportion of C aboveground	34	0.519837	<b>0.002</b>
Phosphorus	Leaf P Concentration	34	-0.58359	<b>0.000</b>
	Root P concentration	34	0.357837	<b>0.038</b>
	Proportion of P aboveground	34	0.249769	0.154
Potassium	Leaf K Concentration	34	-0.20213	0.252
	Root K concentration	34	0.2723929	0.119
	Proportion of K aboveground	34	0.4822742	<b>0.004</b>



**Fig. 1.** Relationship between percentage of vegetation biomass due to *Stipa grandis* and mean annual precipitation (**A**), percentage of biomass aboveground in *S. grandis* and mean annual precipitation (**B**), along the transect.

## Decoupling of above and belowground C and N pools

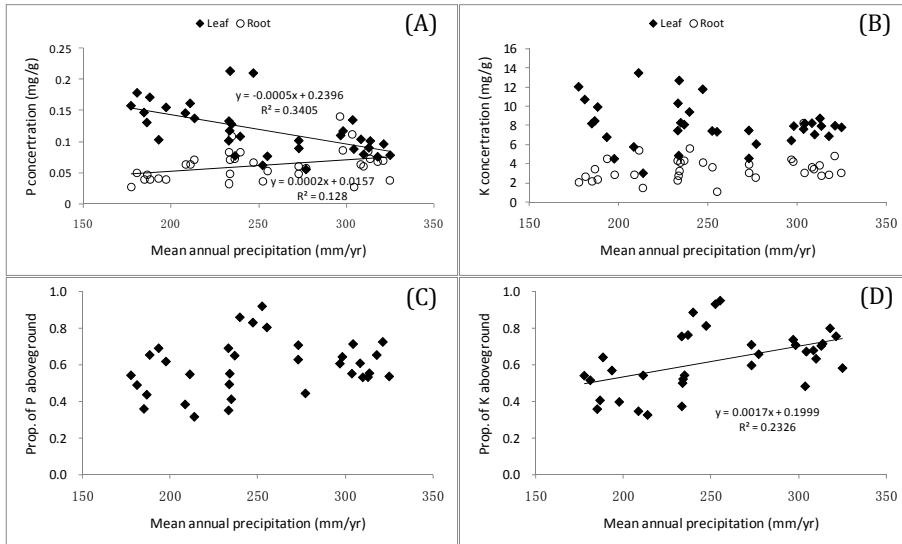
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**Fig. 2.** The relationship between mean annual precipitation and plant traits: **(A)** leaf nitrogen (LNC) and root nitrogen (RNC), **(B)** leaf carbon concentration (LCC) and root carbon concentration (RCC), **(C)** proportion of N aboveground, and **(D)** proportion of C aboveground.

## Decoupling of above and belowground C and N pools

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**Fig. A1.** The relationship between precipitation and plant traits, **(A)** LPC and RPC, **(B)** LKC and RKC, **(C)** proportion of P aboveground, and **(D)** proportion of K aboveground. LPC leaf phosphorus concentration; LKC leaf potassium concentration; RPC root phosphorus concentration; RKC, root potassium concentration.

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