Leaf nitrogen allocation and partitioning in three groundwater-dependent herbaceous species in a hyper-arid desert region of north-western China

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Abstract. Groundwater-dependent vegetation (GDV) is useful as an indicator of watertable depth and water availability in north-western China. Nitrogen (N) is an essential limiting resource for growth of GDV. To elucidate how leaf N allocation and partitioning influence photosynthesis and photosynthetic N-use efficiency (PNUE), three typical GDV species were selected, and their photosynthesis, leaf N allocation and partitioning were investigated in the Taklamakan Desert. The results showed that Karelinia caspica (Pall.) Less. and Peganum harmala L. had lower leaf N content, and allocated a lower fraction of leaf N to photosynthesis. However, they were more efficient in photosynthetic N partitioning among photosynthetic components. They partitioned a higher fraction of the photosynthetic N to carboxylation and showed higher PNUE, whereas Alhagi sparsifolia Shap. partitioned a higher fraction of the photosynthetic N to light-harvesting components. For \textit{K. caspica} and \textit{P. harmala}, the higher fraction of leaf N was allocated to carboxylation and bioenergetics, which led to a higher maximum net photosynthetic rate, and therefore to a higher PNUE, water-use efficiency (WUE), respiration efficiency (RE) and so on. In the desert, N and water are limiting resources; \textit{K. caspica} and \textit{P. harmala} can benefit from the increased PNUE and WUE. These physiological advantages and their higher leaf-area ratio (LAR) may contribute to their higher resource-capture ability.

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Introduction

Indigenous vegetation at the southern margin of the Taklamakan Desert in Xinjiang, north-western China, located in the central part of Eurasian Continent, is dominated by a few perennial phraetophytes, such as \textit{A. sparsifolia}, \textit{K. caspica} and \textit{P. harmala} (Bruelheide \textit{et al.} 2003). These desert plants mainly depend on groundwater for sustenance (Zhu \textit{et al.} 2009). They are typical components of GDV, and must have access to groundwater to maintain their growth and function (Eamus \textit{et al.} 2006). Although water is essential for plant growth, N availability has also been determined as a critical factor limiting plant growth in arid regions (Noy-Meir 1973; Gutierrez and Whitford 1987).

Leaves accumulate most of N in the plant, and about half the total leaf N is used for photosynthetic activities (Poorter and Evans 1998). Many studies have indicated that leaf N content correlates strongly with photosynthetic capacity (Kazda \textit{et al.} 2000; Erley \textit{et al.} 2007), with most of the leaf N being allocated to the photosynthetic apparatus (Evans 1989). Leaf N also influences PNUE significantly; PNUE increases with the increase in leaf N content and decreases after reaching the highest value at an intermediate leaf N content (Hikosaka and Terashima 1995).

The fraction of the total leaf N allocated to the photosynthetic apparatus is a factor that influences PNUE (Onoda \textit{et al.} 2004; Feng \textit{et al.} 2007). Deciduous species and species with a high specific leaf area (SLA) often allocate a higher fraction of leaf N to the photosynthetic apparatus and have a higher PNUE than do evergreen (Takashima \textit{et al.} 2004) and low-SLA (Warren \textit{et al.} 2006) species, respectively. Partitioning of the photosynthetic N among different photosynthetic apparatus (carboxylation, bioenergetics and light-harvesting components) may also differ among species (Hikosaka \textit{et al.} 1998), contributing to the differences in PNUE. Studying leaf N and N-allocation and -partitioning patterns in GDV species is important to understand how GDV adapt to environments where N limits growth.

A trade-off between leaf N allocation to photosynthesis and cell walls is another factor influencing PNUE that has been
documented (Onoda et al. 2004). Leaf N can be allocated to N-based defensive compounds such as alkaloids and cyanogenic glycosides or to cell walls, contributing to chemical and physical defence against natural enemies (Burns et al. 2002). Cell walls are an important N sink (Lambers and Poorter 1992), with 5–10% of primary-wall mass being protein (Loomis 1997). Cyanogenic glycosides can account for up to 15% of total leaf N in some Eucalyptus trees, and the accumulation of cyanogenic glycosides is associated with a reduction in net assimilation rate (NAR) at a constant leaf N (Goodger et al. 2006).

Nitrogen is an essential limiting resource for GDV growth, especially in the desert regions. To evaluate leaf photosynthetic response to environmental change, N allocation and PNUE in GDV, and elucidate how N content and N allocation in leaves influence leaf photosynthesis and PNUE, three typical GDV species, namely A. sparsifolia, K. caspica and P. harmala, were selected for the present study, and their leaf photosynthesis and N allocation were investigated at the southern fringe of the Taklamakan Desert. Particular attention was paid to the physiological and ecological significance of N allocation and partitioning.

Materials and methods

Study sites

The present study was carried out in the foreland of the river oasis of Qira (Cele; 37°03′32″N, 80°35′54″E, 1350 m asl), located at the southern fringe of the Taklamakan Desert, Xinjiang—Uighur Autonomous Region, north-western China. The climate of this region is extremely arid, with an annual precipitation of 40 mm in winter (a climate diagram is presented in Thomas et al. 2000). The water source for plants is groundwater, which is recharged by melting snow from the Kunlun Mountains. In our study, the groundwater depth was 8.5 m. The soil pH was 7.88, and the concentrations of soil organic matter, active N, active phosphorus and active potassium were 2.34 g kg\(^{-1}\), 24.07 mg kg\(^{-1}\), 2.05 mg kg\(^{-1}\) and 150.27 mg kg\(^{-1}\), respectively.

Plant material

Alhagi sparsifolia, K. caspica and P. harmala, the three species chosen for the study, are predominant perennial plants that are typical components of GDV, and were in the same stage of growing. A. sparsifolia is a C\(_3\) herbaceous, deep-rooted, thorny herb plant up to 1–1.5 m tall, P. harmala is a C\(_3\) grass of ~0.5–1 m height and K. caspica is a spiny, perennial herb and a C\(_3\) grass of ~1.0-m height, with few and big leaves. The study plants are described in more detail by Thomas et al. (2000).

Measurements

On sunny days, between 1000 hours and 1300 hours local time, in July 2009 and 2010, eight mature leaves that were exposed to sun were chosen for observation per each plant (24 replicate plants were used in total). From July to August, the measurements were repeated six to eight times on the same individual per species (i.e. observations were taken on 6–8 different days). To avoid additional variation, we conducted the photosynthetic measurements always on the same leaves, if possible. Photosynthetic response to intercellular CO\(_2\) concentration (C\(_i\)) and photosynthetic photon flux density (PPFD) were determined on the youngest fully expanded leaves (the third or fourth south-facing leaf counted from top) with a Li-6400 Portable Photosynthesis System (Li-Cor, Lincoln, NE, USA). Under 380 μmol mol\(^{-1}\) CO\(_2\), photosynthetic rate (P\(_n\)) was measured at 2000, 1500, 1000, 800, 600, 400, 300, 250, 200, 150, 100, 50, 20 and 0 μmol m\(^{-2}\) s\(^{-1}\) PPFD. Apparent quantum yield (AQY) and saturated PPFD were derived from the P\(_n\)–PPFD curve. Under saturated PPFD, P\(_n\) was measured at 380, 300, 260, 220, 180, 140, 110, 80, 50 and 0 μmol m\(^{-1}\) mol\(^{-1}\) CO\(_2\) in the reference chamber. Relative humidity of the air in leaf chamber was controlled at 25% and leaf temperature at 25°C. Stomatal conductance (G\(_s\)), P\(_n\) and C\(_i\) were recorded when the sample leaf was balanced for 200 s under each PPFD and CO\(_2\) step. Photosynthesis measured at 380 μmol mol\(^{-1}\) CO\(_2\) and 2000 μmol m\(^{-2}\) s\(^{-1}\) PPFD was the maximum photosynthetic rate (P\(_\text{max}\)) in the present study. Afterwards, light- and CO\(_2\)-saturated photosynthetic rate (P\(_\text{max,n}\)) was detected after 500 s under 2000 μmol m\(^{-2}\) s\(^{-1}\) PPFD and 1500 μmol mol\(^{-1}\) CO\(_2\). Prior to the measurement, sample leaf was illuminated with saturated PPFD provided by the light-emitting diodes for 10–30 min to achieve fully photosynthetic induction. No photoinhibition occurred during the measurements.

The aboveground parts of each sample plant were harvested after the measurement of photosynthesis. Leaf area was determined with a SHY-150 leaf-area meter (Harbin Optical Instrument Factory, Harbin, China). Plant parts were oven-dried for 48 h at 60°C. Leaf mass fraction (LMF) and LAR were calculated as the ratios of leaf mass and leaf area, respectively, to the total aboveground mass. The P\(_n\)–C\(_i\) curve was fitted with a linear equation (P\(_n\)=kC\(_i\)+i) within 50–200 μmol mol\(^{-1}\) C\(_i\). Maximum carboxylation rate (V\(_{\text{max}}\)) and dark respiration rate (R\(_d\)) were calculated according to Farquhar and Sharkey (1982), as follows:

\[
V_{\text{max}} = k[C_i + K_c(1 + O/K_o)]/[\Gamma + K_c(1 + O/K_o)] \text{ and}
\]

\[
R_d = V_{\text{max}}(C_i - \Gamma^*)/[C_i + K_c(1 + O/K_o)] - (kC_i + i),
\]

where K\(_c\) and K\(_o\) are the Michaelis–Menten constants of Rubisco for carboxylation and oxidation, respectively; \(\Gamma^*\) is the CO\(_2\) compensation point; O is the intercellular oxygen concentration, close to 210 mmol mol\(^{-1}\). K\(_c\), K\(_o\) and \(\Gamma^*\) are temperature dependent. Maximum electron transport rate (J\(_{\text{max}}\)) was calculated according to Loustau et al. (1999), as follows:

\[
J_{\text{max}} = [4(P_{\text{max,n}} + R_d)(C_i + 2\Gamma^*)]/(C_i - \Gamma^*)
\]

Leaf discs with a definite area were taken from each sample leaf and oven-dried at 60°C for 48 h. SLA was calculated as the ratio of leaf area to leaf mass. Leaf N and carbon contents were determined with a Kjeldahl apparatus (BUCHI Auto Kjeldahl Unit K-370, BUCHI Labortechnik AG, Switzerland) and by H\(_2\)SO\(_4\)/K\(_2\)Cr\(_2\)O\(_7\) oxidation–FeSO\(_4\) titration method, respectively. The measurements were performed by the Biogeochemistry Laboratory of Xinjiang Institute of Ecology.
and Geography, Chinese Academy of Sciences. Leaf construction cost (CC) was calculated according to McDowell (2002). Leaf chlorophyll content (Chl) was measured by chemical methods (acetone extraction) (Lichtenthaler and Wellburn 1983). The same leaf of each sample plant was used if possible for measurements of photosynthesis, SLA, Chl, the content of carbon and N (N_A). In this way, differences among the leaves of the same plant could be avoided when the relationships among variables were analysed.

The fractions of the total leaf N allocated to carboxylation (P_C, g g⁻¹), bioenergetics (P_B, g g⁻¹) and light-harvesting components (P_L, g g⁻¹) of the photosynthetic apparatus were calculated as follows:

\[ P_C = \frac{V_{c,max}}{(6.25V_{c,N_A})}, \]
\[ P_B = \frac{J_{max}}{(8.06J_{mc,N_A})} \]
\[ P_L = \frac{C_C}{(N_M C_B)}, \]

where \( C_C \) is leaf Chl concentration, \( N_M \) is mass-based leaf N content. \( V_{c}, J_{mc} \) and \( C_B \) are constants (Niiemets and Tenhunen 1997). The fractions of leaf N allocated to both carboxylation and bioenergetics (\( P_{C+B}, g g^{-1} \)) and to all components of the photosynthetic apparatus (\( P_T, g g^{-1} \)) were calculated as the sum of \( P_C \) and \( P_B \) and the sum of \( P_C \), \( P_B \) and \( P_L \), respectively. N contents in carboxylation (\( N_C \)), bioenergetics (\( N_B \)), carboxylation and bioenergetics (\( N_{C+B} \)), light-harvesting components (\( N_L \)) and all components of the photosynthetic apparatus (\( N_T \)) were calculated as the products of \( N_A \) and \( P_C \), \( P_B \), \( P_{C+B} \), \( P_L \) and \( P_T \), respectively. The fractions of the photosynthetic N partitioned to carboxylation, bioenergetics and light-harvesting components were indicated by \( N_C/N_P \), \( N_B/N_P \) and \( N_T/N_P \), respectively. Photosynthetic-use efficiency of the photosynthetic N was indicated by \( P_{max}/N_P \).

**Statistical analyses**

The differences among species were analysed with a one-way ANOVA, and a post hoc test (Duncan test) was conducted if the differences were significant. A one-way ANCOVA was used to detect the differences in correlation between each pair of variables among the three GDV species and the results are presented in Figs 1–3. Species was used as a fixed factor and variables indicated by y-axis and x-axis in each panel were used as dependent variables and a covariates, respectively. All analyses were carried out using SPSS13.0 (SPSS Inc., Chicago, IL, USA).

**Results**

*Karelinia caspica* and *Peganum harmala* had significantly higher \( P_C, P_{C+B}, N_C, N_{C+B}, P_{max}, A_QY, V_{c,max}, N_C/N_P, N_B/N_P, P_{max}/N_P, LMF, LAR \) and SLA than did *A. sparsifolia* (Table 1). *K. caspica* had also a higher \( J_{max} \), but the difference between *P. harmala* and *A. sparsifolia* was not significant (Table 1). *A. sparsifolia* had higher \( P_L, P_T, N_L, N_P, N_A, \) Chl and \( N_T/N_P \), with the differences between *A. sparsifolia* and *K. caspica* and *P. harmala* being significant. The higher \( P_C \) of *K. caspica* and *P. harmala* contributed to their higher \( N_C, N_{C+B} \) and \( P_{C+B} \). *A. sparsifolia* had significantly higher Chl and \( N_A \), leading to higher \( P_T \) and \( N_T \), thus increasing its \( P_T \) and \( N_T \) to levels exceeding those in *K. caspica* and *P. harmala* (Table 1).

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**Fig. 1.** (a–c) Maximum carboxylation rate (\( V_{c,max} \)), (d–f) maximum electron transport rate (\( J_{max} \)) and (g–i) light-saturated photosynthetic rate (\( P_{max} \)) as a function of N content in carboxylation (\( N_C \)), bioenergetics (\( N_B \)) and both carboxylation and bioenergetics (\( N_{C+B} \)) of *Karelinia caspica* (stars), *Peganum harmala* (squares) and *Alhagi sparsifolia* (circles) growing at the southern fringe of the Taklamakan Desert. Lines fitted for all three species are given.
ANCOVA. Otherwise, only one line
the Taklamakan Desert. Lines
as a function of speci-
V
\text{carboxylation} \text{ and bioenergetics (}\text{P}\text{).}
Fig. 1.
\text{Light-saturated photosynthetic rate (}P_{\text{max}}\text{) as (a) a function of stomatal conductance (}G_s\text{), (b) dark respiration rate (}R_d\text{) and (c) construction cost (CC) as a function of specific leaf area (SLA) of Karelinia caspica (stars), Peganum harmala (squares) and Alhagi sparsifolia (circles) growing at the southern fringe of the Taklamakan Desert. Lines fitted for the three species are given, respectively, if the difference among the three species was significant according to the results of ANCOVA. Otherwise, only one line fitted for all the three studied species is given.}

With the increase of \(N_C, N_B\) and \(N_{C+B}\), \(V_{\text{cmax}}, J_{\text{max}}\) and \(P_{\text{max}}\) increased linearly (Fig. 1). The significant correlations between \(V_{\text{cmax}}\), \(J_{\text{max}}\) and \(P_{\text{max}}\) resulted from the significant association between \(V_{\text{cmax}}\) and \(J_{\text{max}}\) (data not shown). With the increase of \(G_s\) and \(R_d\), \(P_{\text{max}}\) also increased significantly (Fig. 2a, b). \(K.\ caspica\) and \(P.\ harmala\) had a significantly higher \(P_{\text{max}}\) at the same value of \(G_s\) or \(R_d\) according to the results of ANCOVA, thus showing higher RE and WUE. With the increase of \(P_{\text{max}}, P_C, P_{C+B}, N_C, N_B\) and \(N_{C+B}\), PNUE increased significantly (Fig. 3). Leaf CC increased significantly with a decrease in SLA (Fig. 2c). The differences in CC (\(P < 0.325\)) and SLA (\(P = 0.216\)) among \(A.\ sparsifolia\) and \(K.\ caspica\) and \(P.\ harmala\) were not significant (Fig. 2c).

**Discussion**

In the present study, the average leaf N content (39.45 ± 2.57 mg/g) in the three plant species studied was higher than the average leaf N content of 214 kinds (24.45 ± 8.1 mg/g) in a typical desert and desertification region of northern China (Li et al. 2010). The southern fringe of the Taklamakan Desert is an extremely arid zone, and the leaf N content of the plants is higher in this region. This conclusion further confirmed the hypothesis that leaf N content was relatively higher under the arid desert environment (Aerts 1996). The average leaf N content of the three species was basically the same as the average leaf N content (>30 mg/g) reported by Skujins (1981) in the arid desert region, thus supporting their results. But Killingbeck and Whitford (1996) reported that the average leaf N content of 78 species was between 22.0 mg/g and 30.0 mg/g in the arid desert region. The differences might be due to different regions, species or numbers of the samples.

\(K.\ caspica\) and \(P.\ harmala\) had lower leaf N content than did \(A.\ sparsifolia\), and the difference was significant. These two species allocated a lower fraction of leaf N to photosynthesis (lower in \(P_T\) and \(N_P\)) than did \(A.\ sparsifolia\). The lower \(P_T\) was in accord with their higher SLA, which regulated N allocation to photosynthesis through influencing N allocation to cell walls (Onoda et al. 2004). Partitioning of the photosynthetic N among carboxylation, bioenergetics and light-harvesting components was significantly different among the species (Hikosaka et al. 1998). \(K.\ caspica\) and \(P.\ harmala\) partitioned a higher fraction of the photosynthetic N to carboxylation components and had higher \(P_C\) and \(N_C/N_P\), whereas \(A.\ sparsifolia\) partitioned a higher fraction...
of the photosynthetic N to light-harvesting components and had higher \(P_L\) and \(N_\text{C}/N_{\text{NP}}\). \(K.\ caspica\) and \(P.\ harmala\) were more efficient in photosynthetic N partitioning, as indicated by their higher \(P_{\text{max}}/N_{\text{NP}}\). Their higher \(P_{\text{C}}\) contributed greatly to their higher \(P_{\text{max}}\), leading to higher \(N_\text{C}\) and \(N_{\text{C}/N_{\text{NP}}}\), which correlated significantly with \(V_{\text{cmax}}, J_{\text{max}}\) and \(P_{\text{max}}\). For the three species, \(P_{\text{max}}\) correlated significantly with \(P_{\text{C}}, V_{\text{cmax}}\) and \(J_{\text{max}}\), respectively (data not shown). It has been reported that photosynthetic N partitioning influences photosynthesis (Poorter and Evans 1998). The differences in \(G_s\) and \(C_i\) among the three species were not significant, indicating that the stomata had no decisive effect on the higher \(P_{\text{max}}\) of \(K.\ caspica\) and \(P.\ harmala\), although the latter is positively correlated with \(G_s\). In addition, the relatively lower \(C_i\) of \(K.\ caspica\) and \(P.\ harmala\) showed that they had a higher ability to use intercellular \(CO_2\), which was related to their higher biochemical capacity for photosynthesis \((V_{\text{cmax}}\) and \(J_{\text{max}}\)), again confirming the importance of their higher \(P_{\text{C}}\).

\(K.\ caspica\) and \(P.\ harmala\) had a higher PNUE. McDowell (2002) attributed the higher PNUE to the lower \(N_\text{A}\) content. With the decrease of \(N_\text{A}\), PNUE increases (Hikosaka and Terashima 1995). \(K.\ caspica\) and \(P.\ harmala\) were lower in \(N_\text{A}\) than was \(A.\ sparsifolia\), but the relationship between PNUE and \(N_\text{A}\) was not significant in the present study (data not shown). Niinemets et al. (2003) attributed the higher PNUE to the higher \(P_{\text{max}}\). Furthermore, the difference in PNUE between \(K.\ caspica\) and \(P.\ harmala\) and \(A.\ sparsifolia\) could be further attributed to the difference in photosynthetic N partitioning in the present study. The higher \(P_{\text{C}}\) led to higher \(N_\text{C}, N_{\text{C}/N_{\text{NP}}}\), and therefore higher \(P_{\text{max}}\) and PNUE in \(K.\ caspica\) and \(P.\ harmala\). The lower \(P_{\text{C}}\) of \(A.\ sparsifolia\) enhanced the negative effect of its relatively higher \(N_\text{A}\) on PNUE. Similarly, in \(Chenopodium\ album\), higher N allocation to Rubisco contributed to its higher PNUE (Hikosaka et al. 1998).

\(K.\ caspica\) and \(P.\ harmala\) had also a higher WUE than did \(A.\ sparsifolia\), breaking the trade-off between PNUE and WUE. This is consistent with the results from other species (Ewe and Sternberg 2003). McDowell (2002) attributed the higher WUE of some species to their higher \(P_{\text{max}}\). Feng (2008) considered that the higher \(P_{\text{C}}\) was the ultimate reason for the higher PNUE and WUE. It was demonstrated in the present study that the higher \(P_{\text{C}}\) was also the reason for the higher PNUE and WUE of \(K.\ caspica\) and \(P.\ harmala\). It has been found that PNUE, WUE (Sobrado 1991) and N allocation to photosynthesis (Takashima et al. 2004) are higher in deciduous species than in evergreen species, also indicating the importance of N allocation in determining PNUE and WUE.

For \(K.\ caspica\) and \(P.\ harmala\), the higher \(P_{\text{max}}, AQY, PNUE, WUE, RE\) and LAR may contribute to their higher resource-capture ability. The higher LAR was due to their higher LMF and SLA. The higher values of the physiological variables of \(K.\ caspica\) and \(P.\ harmala\) were derived from their higher \(P_{\text{C}}\). For some species, \(P_{\text{max}}\) is positively correlated with NAR...
(Feng et al. 2007). Pattison et al. (1998) reported that, in some species, growth rate is positively related to \( P_{\text{max}} \). The higher NAR and LAR can theoretically result in a higher growth rate of some species (Shipley 2006), being consistent with growth observations in the field. Thus, a higher growth rate is very important for the survival of GDV species at the southern fringe of the Taklamakan Desert. The higher AQY and RE may contribute to their higher \( P_{\text{max}} \), and leading to higher RE. These physiological advantages and the higher LAR of \( K. \) caspica and \( P. \) harmala may contribute to their higher resource-capture ability. Therefore, \( K. \) caspica and \( P. \) harmala can consist of the dominant communities together with \( A. \) sparsifolia at the southern fringe of the Taklamakan Desert. \( A. \) sparsifolia has lower \( A. \) sparsifolia can partition the nitrogen fixation and \( P. \) harmala can benefit from the increased PNUE and WUE.

In conclusion, the higher \( P_{C} \) of \( K. \) caspica and \( P. \) harmala led to higher \( N_{C} \) and \( N_{C-EB} \), which further led to higher \( P_{\text{max}} \) by increasing \( V_{\text{max}} \) and \( J_{\text{max}} \), and therefore to higher PNUE, WUE, AQY and RE. \( K. \) caspica and \( P. \) harmala had a significantly higher \( P_{\text{max}} \) at the same value of \( R_{Q} \) according to the results of ANCOVA, thus increasing \( V_{\text{max}} \) and \( J_{\text{max}} \), and leading to higher RE. These physiological advantages and the higher LAR of \( K. \) caspica and \( P. \) harmala may contribute to their higher resource-capture ability. Therefore, \( K. \) caspica and \( P. \) harmala can consist of the dominant communities together with \( A. \) sparsifolia at the southern fringe of the Taklamakan Desert. \( A. \) sparsifolia has lower \( P_{C} \) and PNUE but it is a leguminous plants. The leguminous plants can fix \( N_{2} \) from the air. So this species is still a part of the dominant communities of the desert. However, the ecophysiological features found in \( K. \) caspica, \( P. \) harmala and \( A. \) sparsifolia should not be extrapolated simply to other plant species, and other factors may also be important in explaining these phenomena. Further comparative studies on a wide range of GDV species in other desert regions are necessary to fully assess the general validity of the N-allocation and -partitioning patterns found in GDV species.

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