CSIRO PUBLISHING

Australian Journal of Botany, 2012, **60**, 61–67
http://dx.doi.org/10.1071/BT11181

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

Jun-Tao Zhu[A,B,C,D,E], *Xiang-Yi Li*[A,B,C,F], *Xi-Ming Zhang*[A,B,C], *Qiang Yu*[D,E] *and Li-Sha Lin*[A,B,C]

[A]Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011, China.
[B]State Key Laboratory of Desert and Oasis Ecology, Urumqi 830011, China.
[C]Cele National Station of Observation & Research for Desert-grass Land Ecosystem in Xinjiang, Cele 848300, China.
[D]Plant Functional Biology and Climate Change Cluster, University of Technology, Sydney, PO Box 123, Broadway, NSW 2007, Australia.
[E]Key Laboratory of Water Cycle and Related Land Surface Processes, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101,China.
[F]Corresponding author. Email: lixy@ms.xjb.ac.cn

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 *K. caspica* and *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; *K. caspica* and *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.

Received 7 July 2011, accepted 22 December 2011

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 *A. sparsifolia*, *K. caspica* and *P. harmala* (Bruelheide *et al*. 2003). These desert plants mainly depend on groundwater for sustenance (Zhu *et al*. 2009). They are typical components of GDV, and must have access to groundwater to maintain their growth and function (Eamus *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 *et al*. 2000; Erley *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 *et al*. 2004; Feng *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 *et al*. 2004) and low-SLA (Warren *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 *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 (maximum in May and July) and an annual potential evaporation of ~2600 mm (Xia *et al*. 1993). Maximum temperatures reach 42°C in summer, and minimum temperatures are as low as –24°C 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 $\text{m}^{-2}\,\text{s}^{-1}$ 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 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 $\text{m}^{-2}\,\text{s}^{-1}$ PPFD was the maximum photosynthetic rate ($P_{\max}$) in the present study. Afterwards, light- and CO_2-saturated photosynthetic rate ($P_{\max}'$) was detected after 500 s under 2000 μmol $\text{m}^{-2}\,\text{s}^{-1}$ 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 ($P_n = \text{k}C_i + i$) within 50–200 μmol mol^{-1} C_i. Maximum carboxylation rate ($V_{c\max}$) and dark respiration rate (R_d) were calculated according to Farquhar and Sharkey (1982), as follows:

$$V_{c\max} = k[C_i + K_c(1 + O/K_o)]^2/[\Gamma^* + K_c(1 + O/K_o)] \quad \text{and} \qquad (1)$$

$$R_d = V_{c\max}(C_i - \Gamma^*)/[C_i + K_c(1 + O/K_c)] - (kC_i + i), \qquad (2)$$

where K_c and K_o are the Michaelis–Menten constants of Rubisco for carboxylation and oxidation, respectively; Γ^* is the CO_2 compensation point; O is the intercellular oxygen concentration, close to 210 mmol mol^{-1}. K_c, K_o and Γ^* are temperature dependent. Maximum electron transport rate ($J_{\max}$) was calculated according to Loustau *et al.* (1999), as follows:

$$J_{\max} = [4(P_{\max}' + R_d)(C_i + 2\Gamma^*)]/(C_i - \Gamma^*) \qquad (3)$$

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 $H_2SO_4/K_2Cr_2O_7$ oxidisation–$FeSO_4$ 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:

$$P_C = V_{c\max}/(6.25 V_{cr} N_A), \quad (4)$$

$$P_B = J_{\max}/(8.06 J_{mc} N_A) \quad \text{and} \quad (5)$$

$$P_L = C_C/(N_M C_B), \quad (6)$$

where C_C is leaf Chl concentration, N_M is mass-based leaf N content. V_{cr}, J_{mc} and C_B are constants (Niinemets 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_P) 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_L/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 *P. harmala* had significantly higher P_C, P_{C+B}, N_C, N_{C+B}, $P_{\max}$, AQY, $V_{c\max}$, N_C/N_P, N_B/N_P, PNUE, $P_{\max}/N_P$, 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_L/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_L and N_L, thus increasing its P_T and N_P to levels exceeding those in *K. caspica* and *P. harmala* (Table 1).

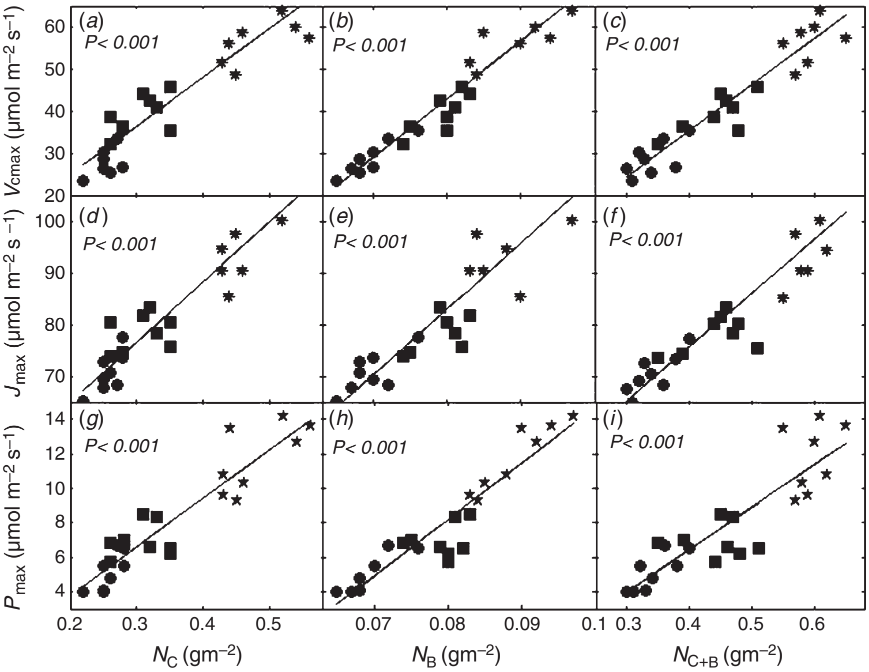

Fig. 1. (*a–c*) Maximum carboxylation rate ($V_{c\max}$), (*d–f*) maximum electron transport rate ($J_{\max}$) and (*g–i*) light-saturated photosynthetic rate ($P_{\max}$) as a function of N content in carboxylation (N_C), bioenergetics (N_B) and both carboxylation and bioenergetics (N_{C+B}) of *Karelinia 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.

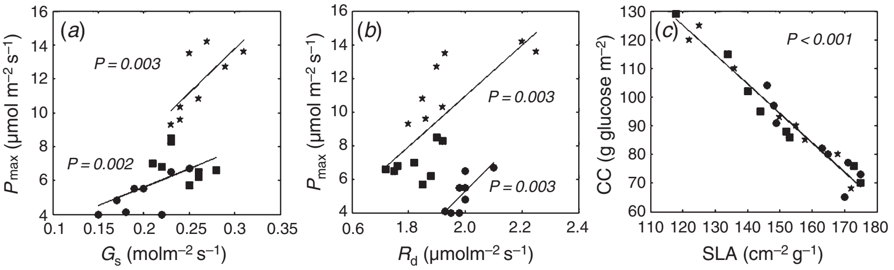

Fig. 2. Light-saturated photosynthetic rate (P_{max}) as (*a*) a function of stomatal conductance (G_s), (*b*) dark respiration rate (R_d) and (*c*) construction cost (CC) as a function of specific leaf area (SLA) of *Karelinia caspica* (stars), *Peganum harmala* (squares) and *Alhagi sparsifolia* (circles) 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.

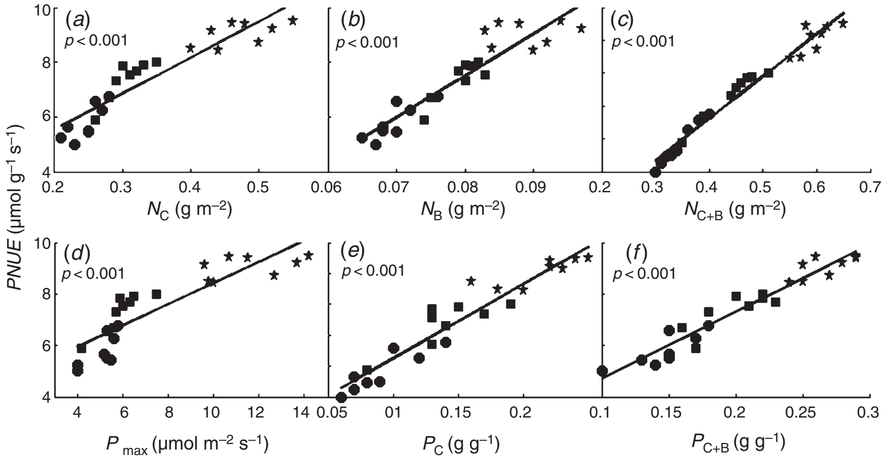

Fig. 3. Photosynthetic nitrogen-use efficiency (PNUE) as a function of (*a*) N content in carboxylation (N_C), (*b*) bioenergetics (N_B) and (*c*) both carboxylation and bioenergetics (N_{C+B}), and (*d*) light-saturated photosynthetic rate (P_{max}), (*e*) the fractions of total leaf N allocated to carboxylation (P_C) and (*f*) both carboxylation and bioenergetics (P_{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.

With the increase of N_C, N_B and N_{C+B}, V_{cmax}, J_{max} and P_{max} increased linearly (Fig. 1). The significant correlations between V_{cmax}–N_B and J_{max}–N_C resulted from the significant association between V_{cmax} and J_{max} (data not shown). With the increase of G_s and R_d, P_{max} also increased significantly (Fig. 2*a*, *b*). *K. caspica* and *P. harmala* had a significantly higher P_{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_{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. 2*c*). 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. 2*c*).

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.

Karelinia 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

Table 1. Means ± s.d. of the measured variables on the three species growing at the southern fringe of the Taklamakan Desert

F-values are from the one-way ANOVA ($n = 8$). Within a row, means followed by the same letter are not significantly different from each other at $P = 0.05$, as analysed by a *post hoc* test after Duncan. See text for definitions of variables. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$

Variable	*Karelinia caspica*	*Peganum harmala*	*Alhagi sparsifolia*	*F*-value
AQY (mol mol^{-1})	0.038 ± 0.003a	0.034 ± 0.004a	0.029 ± 0.002b	3.625*
$P_{\max}$ (μmol m^{-2} s^{-1})	11.7 ± 2.3a	9.5 ± 3.0a	6.9 ± 1.3b	12.724**
$J_{\max}$ (μmol m^{-2} s^{-1})	105.2 ± 10.1a	94.8 ± 7.5b	87.8 ± 6.3b	5.615*
V_{cmax} (μmol m^{-2} s^{-1})	62.5 ± 3.7a	38.7 ± 4.6b	30.8 ± 2.5c	10.082**
P_{C} (g g^{-1})	0.23 ± 0.04a	0.11 ± 0.03b	0.07 ± 0.02c	5.579***
P_{B} (g g^{-1})	0.04 ± 0.003	0.03 ± 0.003	0.03 ± 0.002	3.832
$P_{\mathrm{C+B}}$ (g g^{-1})	0.27 ± 0.05a	0.15 ± 0.03b	0.10 ± 0.02c	6.215***
P_{L} (g g^{-1})	0.10 ± 0.02c	0.17 ± 0.02b	0.28 ± 0.04a	8.232**
P_{T} (g g^{-1})	0.35 ± 0.03b	0.32 ± 0.05b	0.40 ± 0.05a	5.253**
N_{C} (g m^{-2})	0.48 ± 0.04a	0.31 ± 0.02b	0.23 ± 0.03c	12.325***
N_{B} (g m^{-2})	0.08 ± 0.005	0.08 ± 0.003	0.07 ± 0.005	2.323
$N_{\mathrm{C+B}}$ (g m^{-2})	0.50 ± 0.03a	0.39 ± 0.02b	0.31 ± 0.03c	14.536***
N_{L} (g m^{-2})	0.43 ± 0.02b	0.56 ± 0.03b	0.97 ± 0.02a	8.752***
N_{P} (g m^{-2})	0.89 ± 0.06b	0.96 ± 0.05b	1.27 ± 0.07a	5.672**
$N_{\mathrm{C}}/N_{\mathrm{P}}$	0.54 ± 0.04a	0.32 ± 0.05b	0.18 ± 0.07c	10.517***
$N_{\mathrm{B}}/N_{\mathrm{P}}$	0.09 ± 0.01a	0.08 ± 0.01a	0.06 ± 0.01b	4.265*
$N_{\mathrm{L}}/N_{\mathrm{P}}$	0.37 ± 0.02c	0.58 ± 0.04b	0.76 ± 0.05a	13.360***
N_{A} (g m^{-2})	2.07 ± 0.10c	2.81 ± 0.09b	3.33 ± 0.13a	9.226**
N_{M} (mg g^{-1})	31.75 ± 2.03c	40.80 ± 2.45b	45.79 ± 3.24a	9.128**
PNUE (μmol g^{-1} s^{-1})	9.50 ± 0.93a	8.89 ± 0.75a	5.82 ± 0.28b	6.054**
$P_{\max}/N_{\mathrm{P}}$ (μmol g^{-1} s^{-1})	13.15 ± 1.55a	9.86 ± 1.24b	5.43 ± 1.15c	4.835***
G_{s} (mol m^{-2} s^{-1})	0.27 ± 0.02	0.26 ± 0.02	0.24 ± 0.03	3.324
C_{i} (μmol mol^{-1})	210.5 ± 7.2	230.6 ± 5.5	237.8 ± 7.0	4.458
Chl (μmol m^{-2})	0.24 ± 0.04b	0.22 ± 0.03b	0.46 ± 0.05a	5.725**
LMF (g g^{-1})	0.65 ± 0.03a	0.58 ± 0.04a	0.35 ± 0.03b	16.535***
LAR (cm^{2} g^{-1})	97.5 ± 5.8a	88.7 ± 7.5a	58.5 ± 5.5b	10.336**
SLA (cm^{2} g^{-1})	153.4 ± 18.3a	145.2 ± 22.7b	137.5 ± 17.8c	2.415**

of the photosynthetic N to light-harvesting components and had higher P_{L} and $N_{\mathrm{L}}/N_{\mathrm{P}}$. *K. caspica* and *P. harmala* were more efficient in photosynthetic N partitioning, as indicated by their higher $P_{\max}/N_{\mathrm{P}}$. Their higher P_{C} contributed greatly to their higher $P_{\max}$, leading to higher N_{C} and $N_{\mathrm{C+B}}$, which correlated significantly with V_{cmax}, $J_{\max}$ and $P_{\max}$. For the three species, $P_{\max}$ correlated significantly with P_{C}, V_{cmax} and $J_{\max}$, 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 $P_{\max}$ 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_{cmax} and $J_{\max}$), again confirming the importance of their higher P_{C}.

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

Karelinia 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 $P_{\max}$. Feng (2008) considered that the higher P_{C} was the ultimate reason for the higher PNUE and WUE. It was demonstrated in the present study that the higher P_{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 $P_{\max}$, 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_{C}. For some species, $P_{\max}$ 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_{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 indicated that *K. caspica* and *P. harmala* had higher PNUE, which is important for seedling establishment and growth. Species with high PNUE usually have a high growth rate (Schieving and Poorter 1999). At the southern fringe of the Taklamakan Desert, N and water are limiting resources for GDV species. *K. caspica* 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+B}, which further led to higher P_{max} by increasing V_{cmax} and J_{max}, and therefore to higher PNUE, WUE, AQY and RE. *K. caspica* and *P. harmala* had a significantly higher P_{max} at the same value of R_d according to the results of ANCOVA, thus increasing V_{cmax} and J_{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.

Acknowledgements

The authors are grateful to Professor Yan Li, Dr Guofang Liu and Qiang Zhang, for their valuable comments on an earlier version of the manuscript. This study was funded by National Basic Research Program of China (2009CB421303), the key Project in the National Science and Technology Pillar Program (2009BAC54B03), the key program for Science and Technology Development of Xinjiang (200933125) and National Youth Natural Science Foundation of China (41101056), Postdoctoral Science Foundation of China (20110490571).

References

Aerts R (1996) Nutrient resorption from senescing leaves of perennials: are there general patterns? *Journal of Ecology* **84**, 597–608. doi:10.2307/2261481

Bruelheide H, Jandt U, Gries D, Thomas FM, Foetzki A, Buerkert A, Wang G, Zhang XM, Runge M (2003) Vegetation changes in a river oasis on the southern rim of the Taklamakan Desert in China between 1956 and 2000. *Phytocoenologia* **33**, 801–818. doi:10.1127/0340-269X/2003/0033-0801

Burns AE, Gleadow RM, Woodrow IE (2002) Light alters the allocation of nitrogen to cyanogenic glycosides in *Eucalyptus cladocalyx. Oecologia* **133**, 288–294. doi:10.1007/s00442-002-1055-9

Eamus D, Froend R, Loomes R, Hose G, Murray B (2006) A functional methodology for determining the groundwater regime needed to maintain the health of groundwater-dependent vegetation. *Australian Journal of Botany* **54**, 97–114. doi:10.1071/BT05031

Erley GSA, Wijaya KA, Ulas A (2007) Leaf senescence and N uptake parameters as selection traits for nitrogen efficiency of oilseed rape cultivars. *Physiologia Plantarum* **130**, 519–531. doi:10.1111/j.1399-3054.2007.00921.x

Evans JR (1989) Photosynthesis and nitrogen relationships in leaves of C_3 plants. *Oecologia* **78**, 9–19. doi:10.1007/BF00377192

Ewe SML, Sternberg LSL (2003) Seasonal exchange characteristics of *Schinus terebinthifolius* in a native and disturbed upland community in Everglade National Park, Florida. *Forest Ecology and Management* **179**, 27–36.

Farquhar GD, Sharkey TD (1982) Stomatal conductance and photosynthesis. *Annual Review of Plant Biology* **11**, 191–210.

Feng YL (2008) Nitrogen allocation and partitioning in invasive and native *Eupatorium* species. *Physiologia Plantarum* **132**, 350–358. doi:10.1111/j.1399-3054.2007.01019.x

Feng YL, Wang JF, Sang WG (2007) Biomass allocation, morphology and photosynthesis of invasive and noninvasive exotic species grown at four irradiance levels. *Acta Oecologica* **31**, 40–47. doi:10.1016/j.actao.2006.03.009

Goodger JQD, Gleadow RM, Woodrow IE (2006) Growth cost and ontogenetic expression patterns of defence in cyanogenic *Eucalyptus* spp. *Trees. Structure and Function* **20**, 757–765. doi:10.1007/s00468-006-0090-2

Gutierrez JR, Whitford WG (1987) Chihuahuan desert annuals: importance of water and nitrogen. *Ecology* **68**, 2032–2045. doi:10.2307/1939894

Hikosaka K, Terashima I (1995) A model of the acclimation of photosynthesis in the leaves of C_3 plants to sun and shade with respect to nitrogen use. *Plant, Cell & Environment* **18**, 605–618. doi:10.1111/j.1365-3040.1995.tb00562.x

Hikosaka K, Hanba YT, Hirose T, Terashima I (1998) Photosynthetic nitrogen-use efficiency in leaves of woody and herbaceous species. *Functional Ecology* **12**, 896–905. doi:10.1046/j.1365-2435.1998.00272.x

Kazda M, Salzer J, Reiter I (2000) Photosynthetic capacity in relation to nitrogen in the canopy of a *Quercus robur, Fraxinus angustifolia* and *Tilia cordata* flood plain forest. *Tree Physiology* **20**, 2029–2037.

Killingbeck KT, Whitford WG (1996) High foliar nitrogen in desert shrubs: an important ecosystem trait or defective desert doctrine. *Ecology* **77**, 1728–1737. doi:10.2307/2265778

Lambers H, Poorter H (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Advances in Ecological Research* **23**, 187–261. doi:10.1016/S0065-2504(08)60148-8

Lichtenthaler HK, Wellburn AR (1983) Determination of total carotenoids and chlorophyll *a* and *b* of leaf extracts in different solvents. *Biochemical Society Transactions* **603**, 591–592.

Li YL, Mao W, Zhao XY, Zhang TH (2010) Leaf nitrogen and phosphorus stoichiometry in typical desert and desertified regions, north China. *Environmental Sciences* **31**, 1716–1725.

Loomis RS (1997) Commentary on the utility of nitrogen in leaves. *Proceedings of the National Academy of Sciences, USA* **94**, 13 378–13 379. doi:10.1073/pnas.94.25.13378

Loustau D, Beahim M, Gaudillère JP, Dreyer E (1999) Photosynthetic responses to phosphorous nutrition in two-year-old maritime pine seedlings. *Tree Physiology* **19**, 707–715.

McDowell SCL (2002) Photosynthetic characteristics of invasive and noninvasive species of *Rubus* (Rosaceae). *American Journal of Botany* **89**, 1431–1438.

Niinemets Ü, Tenhunen JD (1997) A model separating leaf structural and physiological effects on carbon gain along light gradients for the shade-tolerant species *Acer saccharum*. *Plant, Cell & Environment* **20**, 845–866. doi:10.1046/j.1365-3040.1997.d01-133.x

Niinemets Ü, Valladares F, Ceulemans R (2003) Leaf-level phenotypic variability and plasticity of invasive *Rhododendron ponticum* and non-invasive *Ilex aquifolium* co-occurring at two contrasting European sites. *Plant, Cell & Environment* **26**, 941–956. doi:10.1046/j.1365-3040.2003.01027.x

Noy-Meir I (1973) Desert ecosystems, environment and producers. *Annual Review of Ecology and Systematics* **4**, 25–51. doi:10.1146/annurev.es.04.110173.000325

Onoda Y, Hikosaka K, Hirose T (2004) Allocation of nitrogen to cell walls decreases photosynthetic nitrogen-use efficiency. *Functional Ecology* **18**, 419–425. doi:10.1111/j.0269-8463.2004.00847.x

Pattison RR, Goldstein G, Ares A (1998) Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rain-forest species. *Oecologia* **117**, 449–459. doi:10.1007/s004420050680

Poorter H, Evans JR (1998) Photosynthetic nitrogen-use efficiency of species that differ inherently in specific leaf area. *Oecologia* **116**, 26–37. doi:10.1007/s004420050560

Schieving F, Poorter H (1999) Carbon gain in a multispecies canopy: the role of specific leaf area and photosynthetic nitrogen-use efficiency in the tragedy of the commons. *New Phytologist* **143**, 201–211. doi:10.1046/j.1469-8137.1999.00431.x

Shipley B (2006) Net assimilation rate, specific leaf area and leaf mass ratio: which is most closely correlated with relative growth rate? A meta-analysis. *Functional Ecology* **20**, 565–574. doi:10.1111/j.1365-2435.2006.01135.x

Skujins J (1981) Nitrogen cycling in arid ecosystems. In ‘Terrestrial nitrogen cycles. Ecological Bulletin’. (Eds FE Clark, T Roswall T) pp. 477–491. (Stockholm)

Sobrado MA (1991) Cost-benefit relationships in deciduous and evergreen leaves of tropical dry forest species. *Functional Ecology* **5**, 608–616. doi:10.2307/2389479

Takashima T, Hikosaka K, Hirose T (2004) Photosynthesis or persistence: nitrogen allocation in leaves of evergreen and deciduous *Quercus* species. *Plant, Cell & Environment* **27**, 1047–1054. doi:10.1111/j.1365-3040.2004.01209.x

Thomas FM, Arndt SK, Bruelheide H (2000) Ecological basis for a sustainable management of the indigenous vegetation in a central-Asian desert: presentation and first results. *Journal of Applied Botany* **74**, 212–219.

Warren CR, Dreyer E, Tausz M, Adams MA (2006) Ecotype adaptation and acclimation of leaf traits to rainfall in 29 species of 16-year-old *Eucalyptus* at two common gardens. *Functional Ecology* **20**, 929–940. doi:10.1111/j.1365-2435.2006.01198.x

Xia XC, Li CS, Zhou XJ, Zhang HN, Huang PZ, Pan BR (1993) ‘Desertification and control of blown sand disasters in Xinjiang.’ (Science Press: Beijing)

Zhu Y, Ren L, Skaggs T, Lu H, Yu Z, Wu Y, Fang X (2009) Simulation of *Populus euphratica* root uptake of groundwater in an arid woodland of the Ejina Basin, China. *Hydrological Processes* **23**, 2460–2469. doi:10.1002/hyp.7353