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Responses of two endemic species of *Hippophae* at the Qinghai-Tibet Plateau to elevated CO_2 concentration

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Abstract

The responses of photosynthesis and growth to increasing CO_2 concentration ([CO_2]) were investigated in *Hippophae gyantsensis* and *H. rhamnoides* subsp. *yunnanensis*, which are endemic at the Qinghai-Tibet Plateau and phylogenetically related, but distributed parapatrically in divergent regions. Seedlings of the two species were grown at ambient [AC; 360 μmol(CO_2) mol^{-1}] and elevated [EC; 720 μmol(CO_2) mol^{-1}] [CO_2] in growth chambers. The responses to EC were significantly different between the two species. EC induced an increase in photosynthesis, stomatal conductance, intrinsic water-use efficiency, apparent quantum efficiency, total dry mass, and a decrease in photorespiration rate, maximum carboxylation rate of Rubisco, and maximum electron transport rate in *H. gyantsensis* compared to those in *H. rhamnoides* subsp. *yunnanensis*. Moreover, a significant increase in leaf nitrogen content and a decrease in root/shoot ratio was also observed in *H. gyantsensis*. *H. gyantsensis* showed a significantly higher specific leaf area than that of *H. rhamnoides* through treatments. Relative to *H. rhamnoides* subsp. *yunnanensis*, *H. gyantsensis* showed a greater potential to increase photosynthesis and growth to cope with the increasing [CO_2] and it might expand its distribution range in the future.

Additional key words: biomass allocation; leaf gas exchange; leaf properties.

Introduction

Atmospheric [CO_2] has risen from 280 μmol mol^{-1} before the industrial revolution to around 400 μmol mol^{-1} currently as a consequence of fossil-fuel combustion, deforestation, and land use change, and is projected to reach 700 μmol(CO_2) mol^{-1} by the end of this century (Le Quéré *et al.* 2013). This climatic change is considered to have particular impact on alpine ecosystems due to their important role in the global carbon cycle (Chapin *et al.* 2000, Oechel *et al.* 2000). The Qinghai-Tibet Plateau (QTP) is the largest and highest plateau in the world, with an average altitude of more than 4,000 m a. s. l. (Zheng 1996). The southeastern part of this region and the adjacent areas comprise one of the 25 global biodiversity 'hotspots' and one of only two in the northern hemisphere (Myers *et al.* 2000). Therefore, to predict how the QTP ecosystem structure and function is going to change in the future, it is essential to understand well ecophysiological responses of endemic plants to EC.

Physiological responses of plants to EC have been documented in numerous articles (Curtis and Wang 1998, Ainsworth and Long 2005, Leakey *et al.* 2009, Reddy *et al.* 2010, Urban *et al.* 2012). Photosynthesis, stomatal conductance, respiration, water-use efficiency, and growth, as well as biomass allocation patterns, leaf nitrogen

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Abbreviations: AC – ambient [CO_2] ; AQE – apparent quantum efficiency; [CO_2] – CO_2 concentration; C_{area} – area-based carbon content; C_i – intercellular [CO_2]; C/N – carbon/nitrogen ratio; EC – elevated [CO_2]; g_s – stomatal conductance; LMF – leaf mass fraction; MSLA – mean single leaf area; N_{area} – area-based nitrogen content; J_{max} – maximum electron transport rate; P_N – net photosynthetic rate; P_{Nmax} – light-saturated net photosynthetic rate; QTP – Qinghai-Tibet Plateau; R_D – dark respiration rate; R_L – photorespiration rate; RMF – root mass fraction; R/S – root/shoot ratio; SLA – specific leaf area; SMF – stem mass fraction; DM – total dry mass; V_{cmax} – maximum carboxylation rate of Rubisco; WUE_i – intrinsic water-use efficiency.

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content, and leaf area are shown to play key roles in plant response to EC. However, the effects of EC on these physiological traits vary greatly with species and such differences may have important consequences on future competitive relationships between species (Curtis *et al.* 1996, Smith *et al.* 2000, Körner *et al.* 2005, Dawes *et al.* 2011, Bezemer and Jones 2012, Chaturvedi *et al*. 2013). If a plant grows fast and possesses traits that contribute to fast growth, it is expected to be favored by the increasing [CO_2] (Smith *et al.* 2000, Manea and Leishman 2011).

The genus *Hippophae* is widely distributed in the southwest, northwest, and northern regions of China (Chen *et al*. 2003). Due to its nitrogen-fixing characteristics and its importance in forest restoration, medicine, and food, this genus has been attracting more attention in the recent years (Lian 2000, Chen *et al*. 2003, Cheng *et al*. 2009, Jia *et al*. 2012). In this genus, *H. gyantsensis* and *H. rhanmoides* ssp. *yunnanensis* are both endemic to the QTP but are distributed parapatrically in divergent regions: *H. gyantsensis* mainly occurs in a high altitude region between 3,500 to 5,200 m, whereas *H. rhanmoides* ssp. *yunnanensis* is distributed at lower altitudes from 2,200 m to 3,700 m (Lian 2000, Chen *et al*. 2003, Cheng *et al*. 2009). Interestingly, our previous study on outlining the distribution of the maternally inherited chloroplast haplotypes of these two species indicated that they are phylogenetically related. Two alternative hypotheses regarding the relationship between these two species were proposed: homoploid hybrid origin of *H. gyantsensis* with *H. rhamnoides* ssp. *yunnanensis* as one of its putative parent and allopatric speciation of the two species. It has been suggested that the occurrence of *H. gyantsensis* at such a high altitude is the results of fixation of extreme traits enabling its establishment in a novel habitat, which has been confirmed in other species with a similar origin (Ma *et al*. 2010, Ma *et al*. 2013). However, a few studies were focused on the responses of these distinctly distributed species to climate changes, such as elevated [CO_2] and warming, which may determine their future presence and competitiveness.

Thus, in the present study, we subjected these two species to two [CO_2] regimes (AC and EC) in growth chambers. Our objectives were: (*1*) to assess the photosynthesis and growth responses of the two species to EC, (*2*) to determine whether *H. gyantsensis* shows a greater potential for photosynthesis and growth than *H. rhamnoides* ssp. *yunnanensis* at EC. EC mitigates the adverse effects of drought and low CO_2 partial pressure on the growth and reproduction of plants in high altitude habitats (Körner 1999, Li *et al*. 2007).

Materials and methods

Plants and growth conditions: Seeds of *H. gyantsensis* (HG) and *H. rhanmoides* ssp. *yunnanensis* (HRY) were collected from the species central distributions in 2009. The seeds were germinated and replanted in plastic pots (15 cm high × 10 cm in diameter). All pots were filled with a homogeneous mixture of vermiculite and peat containing 45% of organic matter, 1.89% of total N, and 0.53% of total P. Seedlings were incubated in a greenhouse for three months prior to the experiment under 25/18°C (day/night) temperature, 12/12 h (day/night) photoperiods, and PAR of 550–600 μmol m^{-2} s^{-1}. At the beginning of the experiment, 18 individual seedlings of each species, approximately 10 cm tall, were transferred to a growth chamber (*E7/2*, *Conviron*, Winnipeg, Canada) and grown under the following conditions: 25/18°C day/night temperature, 200–250 μmol m^{-2} s^{-1} PAR in daytime (08:00 – 20:00), and 50–60% of relative humidity. After two weeks of acclimation, the experiment was initiated by subjecting the seedlings to two CO_2 treatments: ambient [360 μmol(CO_2) mol^{-1}, AC] and elevated [CO_2] [720 μmol(CO_2) mol^{-1}, EC]. Nine seedlings per species per treatment were used. During the experiment from May to August in 2012, all seedlings were daily irrigated and all pots were periodically rotated inside each chamber and moved from one chamber to the other to avoid water stress and position effects. All measurements on seedlings were performed at the end of the experiment.

Leaf gas exchange: Net photosynthetic rate (P_N) and stomatal conductance (g_s) were measured using a portable photosynthesis system (*LI-6400, LI-COR Inc.*, Lincoln, NE, USA). Three fully expanded leaves of each species per treatment were selected, placed in the leaf chamber of the IRGA and illuminated for at least 30 min by an artificial light source *LI-6400-02B Redblue* (red/blue ratio, 9:1). PPFD between 0 and 1,000 μmol m^{-2} s^{-1} was used for light curve measurements. The external [CO_2] was set in accordance with the growth [CO_2]. Intrinsic water-use efficiency (WUE_i) was calculated as P_N/g_s.

P_N response to intercellular CO_2 concentration (C_i) was tested at 1,000 μmol m^{-2} s^{-1} PPFD with ambient [CO_2] ranging from 50 to 2,000 μmol(CO_2) mol^{-1}. Three replicates were made per species per treatment. All photosynthetic parameters were measured between 10:00 and 16:00 h, at a temperature of 25 ± 2°C and a vapor pressure deficit of 2.5 ± 0.3 kPa. Before the data were recorded, the measured leaves were kept in the leaf chamber for 3–4 min to reach a steady state of photosynthesis. Leaf area was measured with a portable leaf planimeter (*LI-3000A, LI-COR Inc*, Lincoln, NE, USA).

Sampling: At the beginning and at the end of the experiment, three and six plants of each species per treatment were harvested and divided into three parts (leaves, stems, and roots). The dry mass of each part was determined after drying to constant mass in a forced-air oven at 60°C. Total dry mass (DM), root to shoot ratio (R/S, root DM/shoot DM), leaf mass fraction (LMF, leaf DM/total DM), stem mass fraction (SMF, stem DM/total DM), and root mass fraction (RMF, root DM/total DM) were measured. Specific leaf area (SLA, leaf area/leaf DM) and mean single leaf area (MSLA, leaf area/leaf number) were also calculated.

Elemental analysis: Leaves with DM of *ca.* 0.2 g were collected from each seedling, on which photosynthetic measurements were made, and finely ground with a *Tissuelyzer* (*Retsch*, Haan, Germany). Mass-based nitrogen and carbon contents (N_{mass} and C_{mass}, respectively) were determined using a *CHN analyser* (*Vario EL*, *Elementar*, Hanau, Germany) at the Analytical Testing Center, Lanzhou University, China. The area-based nitrogen and carbon contents (N_{area} and C_{area}, respectively) were calculated by dividing N_{mass} and C_{mas} by the SLA.

Data analysis: The P_N/PPFD curves were modeled by a nonrectangular hyperbola, where P_{Nmax} is the upper asymptote and the initial slope is AQE; R_D is estimated from axis intercepts (Parsons and Ogstone 1997). The photorespiration rate (R_L), maximum carboxylation rate of Rubisco (V_{cmax}), and maximum electron transport rate (J_{max}) were estimated from P_N/C_i curves according to Farquhar and von Caemmerer (1982) and Parsons and Ogstone (1997) with the *Photosyn Assistant Program* of (*Version 1.1*, *Dundee Scientific*, Dundee, Scotland). Additionally, it is obvious that R_L, as presented here, is in fact CO_2 efflux into CO_2-free air; although this method of measuring R_L fails on several counts (Sharkey 1988), it is used routinely to quantify photorespiration rate, because none of the currently available methods to quantify photorespiration are without limitations (Busch 2012).

Data for the measured variables were analyzed by a two-factorial analysis of variance (*ANOVA*) to test the effects of different species, different CO_2 treatments, and the interactions between them. Regression analyses were used to examine relationships between P_N and g_s within species. All statistical analyses were carried out by the *SPSS* statistical software package (*version 13.0*, Chicago, USA).

Results

Leaf gas exchange: EC clearly enhanced the responses of P_N, g_s, and WUE_i to increasing PPFD in both species and the extent of P_N, g_s, and WUE_i enhancement was greater in HG than that in HRY (Fig. 1). EC significantly increased P_{Nmax} and AQE and significantly decreased R_L, V_{cmax}, and J_{max} in both species, while the increase in R_D was only significant in HRY (Fig. 2). P_{Nmax} and AQE increased by 184% and 92%, respectively, in HG and those of HRY increased by 70% and 59%, respectively, at EC (Fig. 2*A*,*B*). R_L, V_{cmax}, and J_{max} decreased by 14%, 39%, and 44% in HG and those of HRY decreased by 8%, 26%, and 25%, respectively, at EC (Fig. 2*D,E,F*). In addition, our results showed that P_N was positively correlated with g_s through treatments within species when pooled the P_N and g_s at PPFD above the light saturation point (Fig. 3).

Plant biomass: EC significantly increased plant biomass of both species, with an increase of DM by 66% in HG and by 28% in HRY (Table 1). The significant increase in DM caused by EC was also associated with changes in biomass allocation. For HG, EC significantly increased SMF by 10% and decreased RMF by 25%, which caused a 32% decrease in R/S, while in HRY, EC showed only an insignificant effect on LMF, SMF, RMF, and R/S (Table 1).

Leaf properties: EC significantly decreased SLA of both species, with a decrease by 25% in HG and by 32% in HRY, while MSLA significantly decreased with EC only in HG (Table 1). However, HG showed a significantly higher SLA than HRY during treatments (Table 1). N_{area} of both species responded differently to EC; N_{area} of HG increased significantly by 36% at EC, while that of HRY was nearly constant (Fig. 4*A*). C_{area} and C/N increased with EC in both species with a 54% and 12% enhancement in HG and a 45% and 59% increase in HRY, respectively (Fig. 4*B,C*).

Discussion

This study supported the point that increasing [CO_2] promotes plant photosynthesis which is accompanied by reduction in photorespiration (Sanz-Elorza *et al.* 2003, Singh *et al.* 2006). EC significantly increased P_{Nmax} and decreased R_L in both HG and HRY (Fig. 2*A*,*D*). AQE, the estimate of the maximum efficiency of light harvesting during CO_2 assimilation (Bernacchi *et al.* 2003), showed a similar trend with P_{Nmax} (Fig. 2*B*). However, the photosynthetic responses to EC varied with species (Körner and Diemer 1994, Dixon *et al.* 1995, Olivo *et al.* 2002, Bezemer and Jones 2012). Our data show that HG exhibited a greater rise in P_{Nmax} and AQE than HRY, suggesting a higher capacity in CO_2 assimilation and light utilization in the former species under EC.

The g_s often regulates photosynthesis as well as water loss from the plant and is very sensitive to changes in atmospheric [CO_2] (Avola *et al.* 2008). As [CO_2] increases, g_s is expected to be reduced (Curtis and Wang 1998, Ainsworth and Long 2005, Ainsworth and Rogers 2007, Leakey *et al.* 2009), but there are some

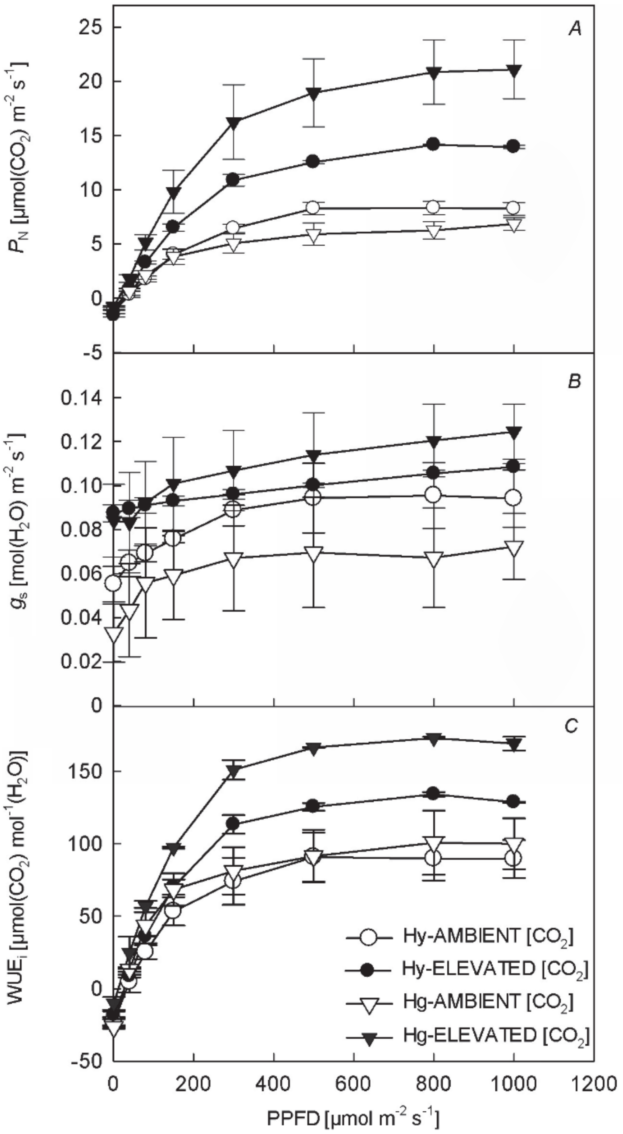

Fig. 1. Responses of net photosynthetic rate (P_N, *A*), stomatal conductance (g_s, *B*), and intrinsic water-use efficiency (WUE$_i$, *C*) to photosynthetic photon flux density (PPFD) of *Hippophae gyantsensis* (Hg) and *H. rhamnoides* subsp. *yunnanensis* (Hy) grown at elevated [CO$_2$] [720 μmol(CO$_2$) mol^{-1}] and ambient [CO$_2$] [360 μmol(CO$_2$) mol^{-1}]. Each value represents the mean and SE of three measurements.

notable exceptions indicating increased or constant g_s under EC, depending on the duration of CO$_2$ exposure and species investigated (Curtis and Wang 1998, Roberntz *et al*. 1998, Medlyn *et al*. 2001). In the present study, g_s increased with EC in both species (Fig. 1*B*), but the responses varied with species. HG obviously increased g_s more than HRY at EC, which suggested that HG could maintain a higher stomata openness to benefit photosynthetic gas exchange. Our result also showed a significant positive correlation between g_s and P_N and we concluded that g_s highly accounted for the variance in P_N within species (Fig. 3). However, the increase in g_s was lower than that in P_N in response to EC, which directly led to an enhancement of WUE$_i$ (P_N/g_s) in both species. The more enhanced WUE$_i$ in HG compared to that in HRY suggested this species used water more efficiently under EC (Fig. 1*C*).

EC significantly increased DM of both species (Table 1), similarly as reported in many studies (Curtis and Wang 1998, Smith *et al.* 2000, Ainsworth and Long 2005, Bhatt *et al*. 2007, Song *et al*. 2009). But the growth responses between the two species were different, with HG accumulating more biomass (DM) under EC than HRY, in accordance with its higher photosynthesis and water-use efficiency. The interspecific variation in growth response to EC is likely to have important consequences on competitive relationships between species (Baxter *et al.* 1994, Dixon *et al.* 1995, Curtis *et al.* 1996, Ward and Strain 1997, Dawes *et al*. 2011, Ziska *et al*. 2003, Song *et al.* 2009, Manea and Leishman 2011). Plants with fast growth are considered to be favored under high [CO$_2$] (Smith *et al.* 2000, Manea and Leishman 2011). Thus, the greater growth response of HG to EC is expected to increase its competitive ability under high [CO$_2$] compared to that of HRY.

Biomass allocation changed with EC depending on species, with HG allocating more biomass to aboveground parts reflected by the significant decrease in RMF and R/S and significant increase in SMF, but those of HRY showed no significant changes (Table 1). Similar results were found in many studies (Curtis and Wang 1998, Norby *et al.* 1999, Long *et al.* 2004, Ainsworth and Long 2005, Aranda *et al.* 2006, De Graaff *et al.* 2006, Song *et al.* 2009), although reductions in R/S were also found (Curtis and Wang 1998, Norby *et al.* 1999). The allocation of biomass to stems, increasing both stem length and stem diameter, would help plant species efficiently capture light and withstand strong wind on the QTP. It is possible that a limited root zone might influence the root growth, and subsequently the R/S, but our observations suggest that the pot-size effect on root growth was minimal for both species.

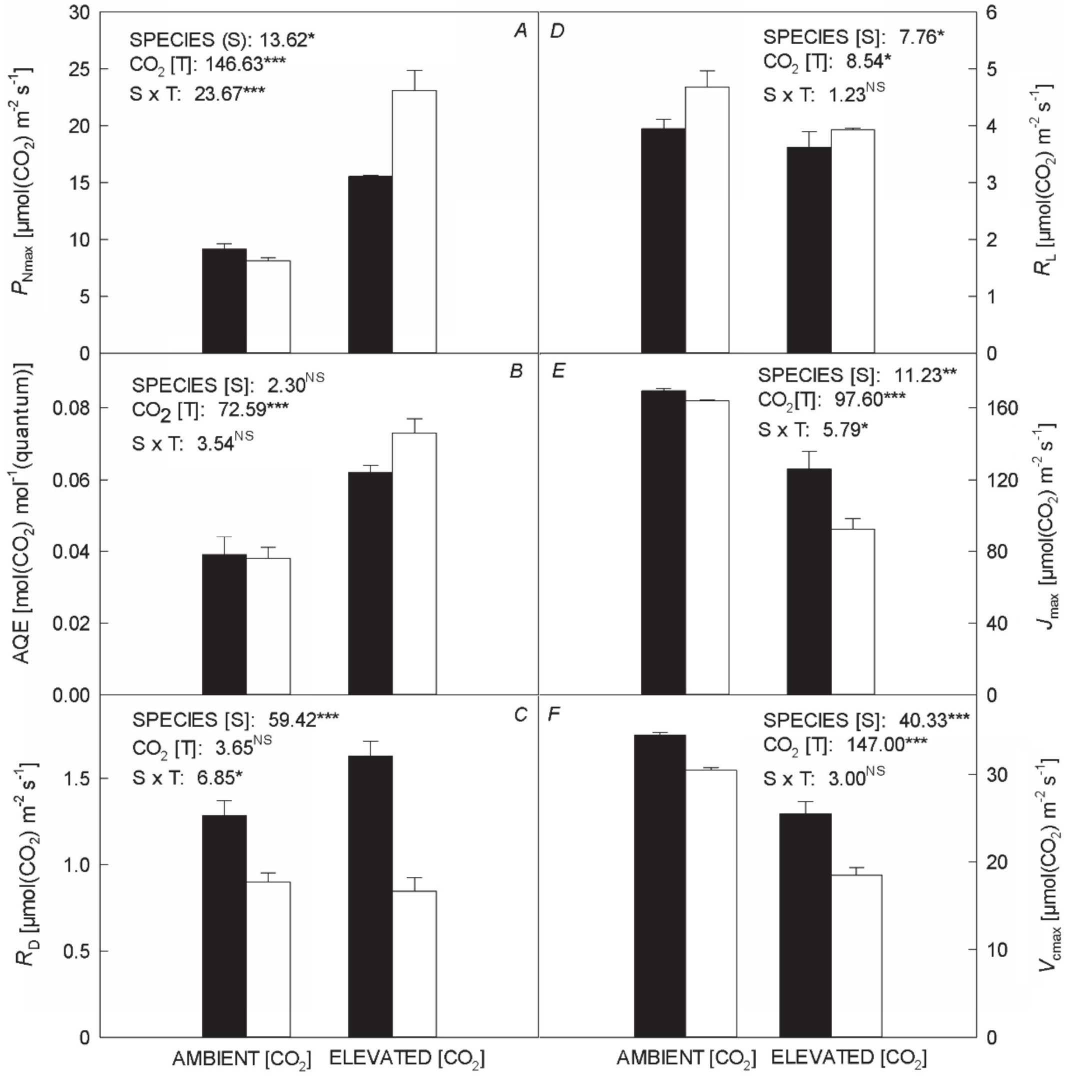

Fig. 2. Light-saturated net photosynthetic rate (P_{Nmax}, *A*), apparent quantum yield (AQE, *B*), dark respiration rate (R_D, *C*), photorespiration rate (R_L, *D*), light-saturated rate of electron transport (J_{max}, *E*), and maximum rate of carboxylation (V_{cmax}, *F*) in leaves of *Hippophae gyantsensis* (*white bars*) and *H. rhamnoides* subsp. *yunnanensis* (*black bars*) grown at elevated [CO_2] [720 µmol(CO_2) mol^{-1}] and ambient [CO_2] [360 µmol(CO_2) mol^{-1}]. Each value represents the mean and SE of three measurements. *F*-values and significance levels are shown: *** – $P<0.001$; ** – $P<0.01$; * – $P<0.05$; NS – not significant, $P\geq0.05$.

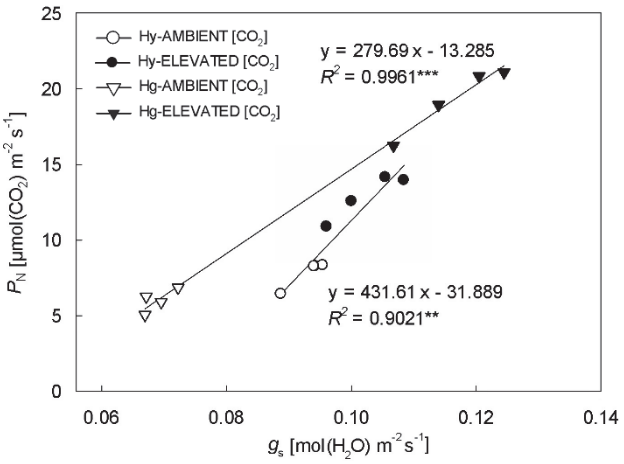

Fig. 3. Relationships between net photosynthetic rate (P_N) and stomatal conductance (g_s) at PPFD above the light saturation point for *Hippophae gyantsensis* (Hg) and *H. rhamnoides* subsp. *yunnanensis* (Hy) during treatments. The equation, coefficient of determination (R^2), and significance (*** – $P<0.001$; ** – $P<0.01$) are shown for each regression.

Table 1. Growth, biomass allocation, and leaf morphology in seedlings of *Hippophae gyantsensis* and *H. rhamnoides* subsp. *yunnanensis* grown at elevated [CO_2] [720 µmol(CO_2) mol^{-1}] and ambient [CO_2] [360 µmol(CO_2) mol^{-1}]. Each value represents the mean and SE of six measurements. DM – total dry mass; R/S – root/shoot ratio; LMF – leaf mass fraction; SMF– stem mass fraction; RMF – root mass fraction; SLA – specific leaf area; MSLA – mean single leaf area. *F*-values and significance levels are shown: *** – $P < 0.001$; ** – $P<0.01$; * – $P<0.05$; NS – not significant, $P \geq 0.05$.

Variables	*H. gyantsensis*		*H. rhamnoides*		*F*, *P*-value		
	Ambient [CO_2]	Elevated [CO_2]	Ambient [CO_2]	Elevated [CO_2]	CO_2	Species	Species × CO_2
Growth							
DM [g]	1.18 ± 0.13	1.96 ± 0.21	1.59 ± 0.13	2.03 ± 0.12	16.60***	2.55 ^{NS}	1.20 ^{NS}
Allocation							
R/S	0.19 ± 0.01	0.13 ± 0.01	0.13 ± 0.01	0.12 ± 0.01	7.74**	7.96***	2.81 ^{NS}
LMF [g g^{-1}]	0.44 ± 0.01	0.45 ± 0.01	0.49 ± 0.01	0.47 ± 0.01	0.51 ^{NS}	11.06**	1.14 ^{NS}
SMF [g g^{-1}]	0.40 ± 0.01	0.44 ± 0.01	0.39 ± 0.02	0.42 ± 0.01	8.68**	0.41 ^{NS}	0.17 ^{NS}
RMF [g g^{-1}]	0.16 ± 0.01	0.12 ± 0.01	0.12 ± 0.01	0.11 ± 0.01	7.53*	7.97**	2.62 ^{NS}
Leaf morphology							
SLA [m^2 g^{-1}]	19.32 ± 1.02	14.40 ± 0.70	16.61 ± 0.47	11.25 ± 0.32	16.74***	51.67**	0.91 ^{NS}
MSLA [cm^2]	0.99 ± 0.07	0.73 ± 0.03	1.25 ± 0.09	1.20 ± 0.05	6.01*	30.42***	2.36 ^{NS}

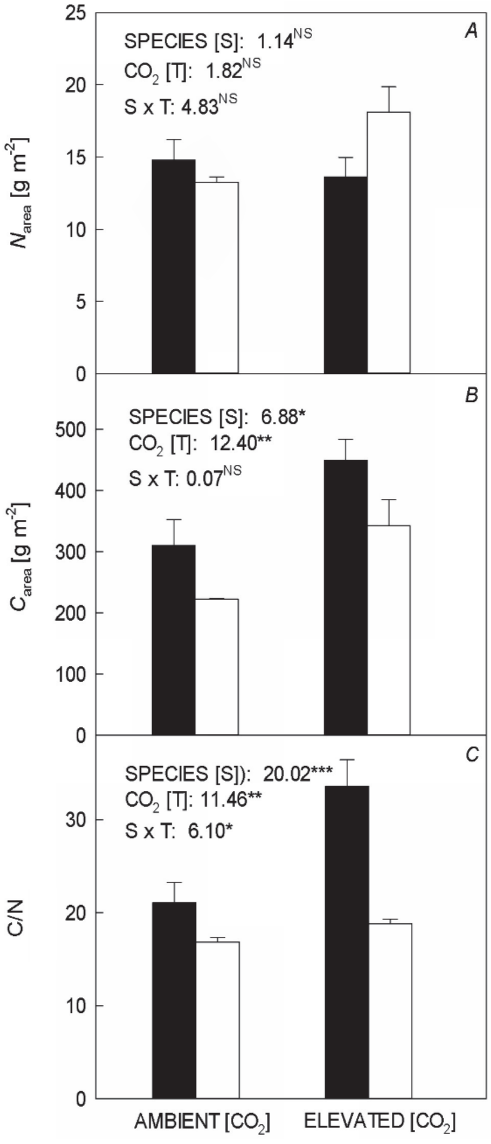

Fig. 4. Area-based nitrogen content (N_{area}, *A*), area-based carbon content (C_{area}, *B*) and carbon/nitrogen ratio (C/N, *C*) in leaves of *Hippophae gyantsensis* (*white bars*) and *H. rhamnoides* subsp. *yunnanensis* (*black bars*) grown at elevated [CO_2] [720 µmol(CO_2) mol^{-1}] and ambient [CO_2] [360 µmol(CO_2) mol^{-1}]. Each value represents the mean and SE of three measurements. *F*-values and significance levels are shown: *** – $P<0.001$; ** – $P<0.01$; * – $P<0.05$; NS – not significant, $P \geq 0.05$.

Photosynthetic acclimation is generally attributed to decrease in a Rubisco content and activity (Seneweera *et al.* 2002, Aranda *et al.* 2006). In the present study, we observed a reduction in Rubisco activity inferring from the significant decrease in V_{cmax} and J_{max} at EC compared with those at AC in both species (Fig. 2*E,F*). Moreover, Urban *et al.* (2012) revealed an inverse relationship between N_{area} and Rubisco specific activity. The significantly increased N_{area} in HG and constant N_{area} in HRY probably suggested a decline in Rubisco specific activity in HG and constant activity in HRY at EC. In addition, compared to the unchanged N_{area} of HRY, the significantly increased N_{area} in HG suggested probably a higher nitrogen-fixing capacity under EC in this species (Rogers *et al.* 2009).

EC reduced SLA of both species, which was also reported in many other studies (Poorter and Navas 2003, Song *et al.* 2009, Wang *et al.* 2012). A higher SLA in HG compared to that of HRY probably suggested a more extensive foliar display for light capture, which may ultimately result in more biomass accumulation (Niinemets 1999).

In conclusion, EC strongly affected photosynthesis and growth of both species, but the response to EC was species-specific. Compared to *H. rhamnoides* ssp. *yunnanensis*, *H. gyantsensis* showed a greater increase in P_{Nmax}, AQE, g_s, WUE_i, N_{area}, and DM and a greater decrease in R_L, V_{cmax}, J_{max}, and R/S at EC, associated with a higher SLA through treatments. Those results supported the hypothesis that EC differentially affected photosynthesis and growth of the two species and *H. gyantsensis* showed a greater potential in photosynthesis and growth, which may allow to expand its distribution in the future.

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