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Physiological performances of maternally-dependent genotypes in the homoploid hybrid species *Hippophae goniocarpa*

Fei MA, Li-Tong CHEN, Bu-Qing YAO, and Chang-Ming ZHAO*

Key Laboratory of Arid and Grassland Ecology, Ministry of Education, School of Life Sciences, Lanzhou University, Lanzhou 730000, P.R. China

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ABSTRACT. Most homoploid hybrid species have different maternal donors and these maternal genotypes usually have biased distributions. It has been postulated that the geographical distributions of these genotypes may be due to random genetic drift and founder effects following range expansion after the initial recombination(s) that led to their speciation. However, the preferred habitats in their distributions also suggest that they may be adapted to different environments, but we have little knowledge regarding their physiological performances in the same habitats after their initial recombinant speciation when occurring sympatrically. *Hippophae goniocarpa* is a newly-evolved diploid shrub species that appears to have arisen via recombination events between *H. rhanmoides* ssp. *sinensis* × *H. neurocarp*. We compared the physiological performances of two genotypes with different maternal origins (*H. goniocarpa*-R and *H. goniocarpa*-N, mothered respectively by *H. rhanmoides* ssp. *sinensis* and *H. neurocarpa*) and the two parental species by measuring their: rates of photosynthesis (A_{max}), transpiration (E), quantum efficiencies (QE), carboxylation efficiency (CE), Light Compensation Point (LCP), instantaneous (A_{max}/E) and long-term ($\delta^{13}C$) indices of water use efficiency (WUE), effective quantum yield of PSII (Φ_{PSII}), non-photochemical quenching (NPQ), nitrogen contents per unit mass and area (N_{mass} and N_{area}, respectively), mean single leaf area (MSLA), leaf mass per unit area (LMA) and carbon concentration (C). The two *H. goniocarpa* genotypes distinctly differed in A_{max}, A_{max}/E, QE, CE, NPQ, LCP, long-term WUE ($\delta^{13}C$), N_{area}, MSLA, LMA and C. In addition, *H. goniocarpa*-R outperformed both parental species in A_{max}, long-term WUE ($\delta^{13}C$), NPQ, MSLA and LCP. However, A_{max} and long-term WUE ($\delta^{13}C$) values of *H. goniocarpa*-N were intermediate between those of the two parental species, and the variations in these traits showed no correlation with those of the maternal species. The instantaneous WUE (A_{max}/E) and N_{area} of both *H. goniocarpa* genotypes were distinctly higher than those of the two parental species, further suggesting that this recombinant species may be concordantly transgressive in these respects. These consistent performance may provide partly inherent power to combine all individuals of two genotypes as a distinct species unit. In contrast, the MSLA and N_{mass} of the two genotypes were intermediate between those of their parental species and their C concentrations and QE were distinctly lower. Our results reveal differences in the physiological performances of two genotypes of the same hybrid species with different maternal donors. These findings should help extend our understanding of the habitat preferences of the maternal genotypes within a few hybrid species.

Keywords: Genotypes; *Hippophae goniocarpa*; Homoploid hybrid; Physiological performance.

INTRODUCTION

Natural hybridization commonly occurs in various plants, and appears to play a crucial role in plant variation, speciation and evolution (Grant, 1981). As well as the common occurrence of alloploidization through hybridization followed by speciation, evidence of homoploid recombination speciation has also been detected in a few plant species (Rieseberg, 1997). Such recombination speciation is completed by reproductive isolation from the two parental species due to ecological divergence or chromosomal rearrangements following the initial homoploid hybridization (Arnold, 1997; Buerkle et al., 2000). It is possible that both parental species may serve as maternal donors in such a speciation (Arnold, 1997) and this possibility has been confirmed for most diploid hybrid species examined to date – including *Pinus densata*, *Argyranthemum sundingii*, *Helianthus anomalus* and *H. deserticola* (Brochman et al., 2000; Wang et al., 2001; Schwarzbach and Rieseberg, 2002; Gross et al., 2003). An interesting finding of the cited studies is

*Corresponding author. E-mail: zhaochm@lzu.edu.cn; Fax: +86-931-8912823; Tel: +86-931-8914305.

that different maternal genotypes of the same species usually have different distributions and occupy different habitats. It has been suggested that the differences in the distribution patterns of maternal genotypes may be due to random genetic drift, range expansion and founder effects following the initial recombination speciation events (Arnold, 1997). However, it remains unknown whether these differences in distribution mirror habitat preferences of maternal-dependent genotypes associated with differences in their physiological performance.

A recombinant species initially arises from random hybridization between two parental species (Rieseberg, 1997). The initial hybrids often vary in performance relative to their parental species, for instance the first hybrid generation may be heterotic, while hybrid transgression may be reduced in subsequent generations (Arnold, 1997; Arntz et al., 1998; Burke and Arnold, 2001; Campbell and Waser, 2001; Johnseon et al., 2001; Campbell et al., 2005). However, whether or not hybrid transgression has played a critical role during their speciation and mature hybrid species have continued to be transgressive are questions that have long been debated (Schemske, 2000). The possibility that recombinant species have transgressive performance has been tested recently (Rieseberg et al., 2003). However, little research has focused on possible differences in hybrid performance related to the maternal origins of representatives of natural homoploid hybrid species. The reproductive isolation of these hybrid species presumably evolved as a consequence of divergent natural selection via adaptation to different niches to those of the parental species (Schluter, 2000). Therefore, sound knowledge of the physiological performances of different maternal genotypes in hybrid species could substantially enhance our understanding of homoploid speciation mechanisms and the habitat preferences of the hybrids.

Hippophae goniocarpa was first described from a few specimens originating from Qinghai and Sichuan, China (Lian et al., 1995). Individuals of this shrub species vary in height from 0.5 m to 3 m in the field. Most morphological characters of *H. goniocarpa* are intermediate between those of *H. rhanmoides* ssp. *sinensis* and *H. neurocarpa*. All *H. goniocarpa* individuals examined to date are diploids with $2n = 24$ (Lian et al., 1998). These three species, and others in this genus, are dioecious, wind-pollinated, and their gender is genetically determined (Bartish et al., 2000). The hybrid origin of *H. goniocarpa* from *H. rhanmoides* ssp. *sinensis* × *H. neurocarpa* has been unequivocally demonstrated by RAPD and ITS data (Bartish et al., 2000; Sun et al., 2003). Bartish et al. (2002) further demonstrated that cpDNA is maternally inherited in *Hippophae* and a recent population analysis of these three sympatric species suggested that both *H. rhanmoides* ssp. *sinensis* and *H. neurocarpa* had served as maternal donors to the genetic composition of *H. goniocarpa* (Wang et al., 2008). The three species occur in the same habitats in the northeast Qinghai-Tibetan Plateau in China. However, *H. goniocarpa* shows distinct reproductive isolation from *H. rhanmoides* ssp. *sinensis* and *H. neurocarpa* (Lian et al., 2000; Wang et al., 2008), and the seed germination and growth rates of this hybrid species are higher than those of both parental species. In addition, chromosome pairing and segregation at meiosis are normal in this species and it produces highly viable progeny, suggesting that these individuals represent an independent lineage, rather than the early hybrid generations (for example, F_1 and F_2, in which chromosome pairing and segregation are irregular) recurrently produced between two parental species (Lian et al., 2000). All these lines of evidence suggest that this species has escaped from unfit recombinants (for example, hybrid sterility and breakdown) from the initial hybrid generations and completed reproductive isolation. However, its limited distribution suggests that this species has not inhabited a different niche from either parental species through range expansion as in other diploid recombination species. Therefore, *H. goniocarpa* provides a good model system to compare the physiological performances of different maternal genotypes relative to its two parental species.

Photosynthesis rates (A_{max}), transpiration (E), instantaneous (A_{max}/E) and long-term ($\delta^{13}C$) indices of water use efficiency (WUE), effective quantum yield of PSII (Φ_{PSII}) and non-photochemical quenching (NPQ), Light Compensation Point (LCP), nitrogen contents per unit mass and area (N_{mass} and N_{area}, respectively), mean single leaf area (MSLA), leaf mass per unit area (LMA) and carbon concentration (C) are leaf traits that play key roles in the physiological performance of plants (Genty et al., 1989; Bilger and Björkman, 1990; Ackerly, 2004). LMA strongly reflects the dry-mass cost of producing new leaves, and correlates negatively with leaf N concentrations (Wright et al., 2005). Leaf N concentration is also strongly positively correlated with photosynthetic capacity (Reich, 2004) because N is essential for the synthesis of Rubisco, the key photosynthetic enzyme (Taiz and Zeiger, 1998). In this study, we evaluated these physiological parameters in two different maternal genotypes of *H. goniocarpo* (mothered respectively by *H. neurocarpa* and *H. rhamnoides*) and both parental species. Specifically, we aimed to address the following questions: (1) Do the recombinant hybrid species perform differently from their parents in these physiological respects? (2) Are there distinct differences between the two genotypes with different maternal origins?

MATERIALS AND METHODS

Study site and samples of individuals

We conducted our experiments in the northeast Qinghai-Tibetan Plateau (38°05' N, 100°19' E; altitude, 2,751 m) where the three species occur sympatrically. A preliminary analysis of *H. neurocarpa* and *H. rhanmoides* ssp. *sinensis* (27 individuals of each species) showed that the chloroplast DNA *trn*L-F region differs at 15 sites in these two species. Therefore, we analyzed the sequences of the maternally-inherited cpDNA in this region to determine the maternal origins of 12 *H. goniocarpa* individuals, three of which were found to be mothered by *H. neurocarpa* (*H. goniocarpa*-N) and the other nine by *H. rhanmoides* ssp. *sinensis* (*H. goniocarpa*-R) (Wang et al., 2008). We also analyzed the nuclear internal transcribed spacer region (ITS) to confirm the hybrid origin of all 12 of the *H. goniocarpa* individuals. The two parental species differ from each other at nine sites in the analyzed region of this marker, and none of the sampled individuals of either *H. neurocarpa* or *H. rhanmoides* ssp. *sinensis* showed additivity at any of these sites (Wang et al., 2008). However, all 12 sampled individuals of *H. goniocarpa* showed hybrid additivity. We chose four genotypes (*H. goniocarpa*-R, *H. goniocarpa*-N, *H. neurocarpa* and *H. rhanmoides* ssp. *sinensis*) to conduct the following experiments and each genotype was represented by three individuals. The selected individuals had similar heights around 2.8 m (and thus ages) and are situated in the same valley.

Gas exchange measurements

Photosynthetic parameters were measured using an LI-COR 6400 infrared gas-analyzer (IRGA; LI-COR Lincoln, NE, USA) in sunny days, from 09:00 to 11:00 between 12 and 16, August 2005. Five fully and expanded leaves were selected from the top of the second-year branches for measurements. Each of the sampled leaves was individually placed in the leaf chamber of the IRGA and illuminated by an LI-6400-02B LED light source (LI-COR) attached to the sensor head. A range of photosynthetic photon flux densities (PPFD) between 0 and 2000 μmol $m^{-2}s^{-1}$ were used for light curve measurements, starting at 2000 μmol $m^{-2}s^{-1}$ and ending at 0 μmol $m^{-2}s^{-1}$. During the gas-exchange measurements the ambient CO_2 concentration in the chamber was maintained at 360 μmol mol^{-1}, using the LI-6400-01 CO_2 mixture (LI-COR), and leaf temperature was maintained at 28 ± 0.5°C. The relationship between net assimilation rate and the intercellular CO_2 concentrations (*A-ci* curve) was examined by measuring CO_2 uptake over a range of external CO_2 concentrations (*Ca*) from approximately 50 μmol mol^{-1} to 2000 μmol mol^{-1}. Measurements were taken under saturating light of 1500 μmol $m^{-2}s^{-1}$, cuvette temperatures were maintained at ambient levels, and before the measurements each sampled leaf was illuminated for a few minutes. After measuring leaf area with a LI-COR-3000A planimeter (LI-COR Lincoln, NE, USA), values per unit leaf area were calculated for each of the photosynthetic parameters.

Chlorophyll fluorescence measurements

Chlorophyll fluorescence was measured using a LI-6400-40 (LI-COR Lincoln, NE, USA) fluorescence attachment after allowing the leaves to adapt to the dark for approximately 30 min. The minimal fluorescence yield (F_o) and maximal fluorescence yield (F_m) were measured. At each PPFD level, the fluorescence yield at steady state (F_s) and maximum fluorescence yield in light-adapted state (Fm′) were respectively determined. During these measurements leaf temperature was maintained at 28± 0.5°C. The maximum photochemical efficiency of PSII (F_v/F_m), effective quantum yield of PSII (Φ_{PSII}) and non-photochemical quenching (NPQ) were calculated as described by Genty et al. (1989) and Bilger and Björkman (1990).

Leaf carbon isotope composition and elemental content

Fifteen leaves of each individual tree were selected to determine their single leaf area (MSLA) using the LI-COR 3000A planimeter. They were randomly classified into three groups, then oven-dried for 48 h at 80°C, weighed to determine their LMA (leaf mass per unit area), and finally grounded using a mortar into fine powders. The powders obtained from each group were split into two portions. The isotope composition of one portion of each of the samples was measured according to Tieszen (1979) using a MAT-252 (Finnigan, USA) mass spectrometer. The overall precision in δ-values was better than 0.1‰ as determined by analysis of repeated samples. The other portions were used to determine leaf nitrogen (N_{mass}) and carbon (C) contents using a CHN analyzer (Vario EL, Elementar corporation, Germany). Leaf N content per unit area (N_{area}) was then calculated by multiplying N_{mass} by LMA.

Statistical analysis

One-way ANOVA and Post hoc-LSD tests were used to compare the physiological parameters between different genotypes. Prior to comparison, all the data were tested for normality. We followed Schwarzbach et al. (2001) to describe whether the measured variables are transgressive (negative or positive) (the hybrid species differed significantly from parental species) or intermediate (*H. neurocarpa*-like or *H. rhanmoides*-like). Data analyses were performed and figures were generated using SPSS software ver. 11.0. Data are presented as means ± SD.

RESULTS

Photosynthetic parameters

The light response curves obtained from the four genotypes were similar (Figure 1a), but their light saturation levels distinctly differed, being approximately 400-800 μmol $m^{-2}s^{-1}$ for *H. rhanmoides* ssp. *sinensis* and *H. goniocarpa*-N, 800-1000 μmol $m^{-2}s^{-1}$ for *H. neurocarpa* and 1200 μmol $m^{-2}s^{-1}$ for *H. goniocarpo*-R. The instantaneous WUE (A_{max}/E) values for *H. goniocarpo*-R and *H. goniocarpo*-N also significantly differed, but were significantly higher in both cases than those of both of the two parental species (Table 1). In contrast, the quantum efficiencies (QE) of the two hybrid genotypes were significantly different, but were lower than those

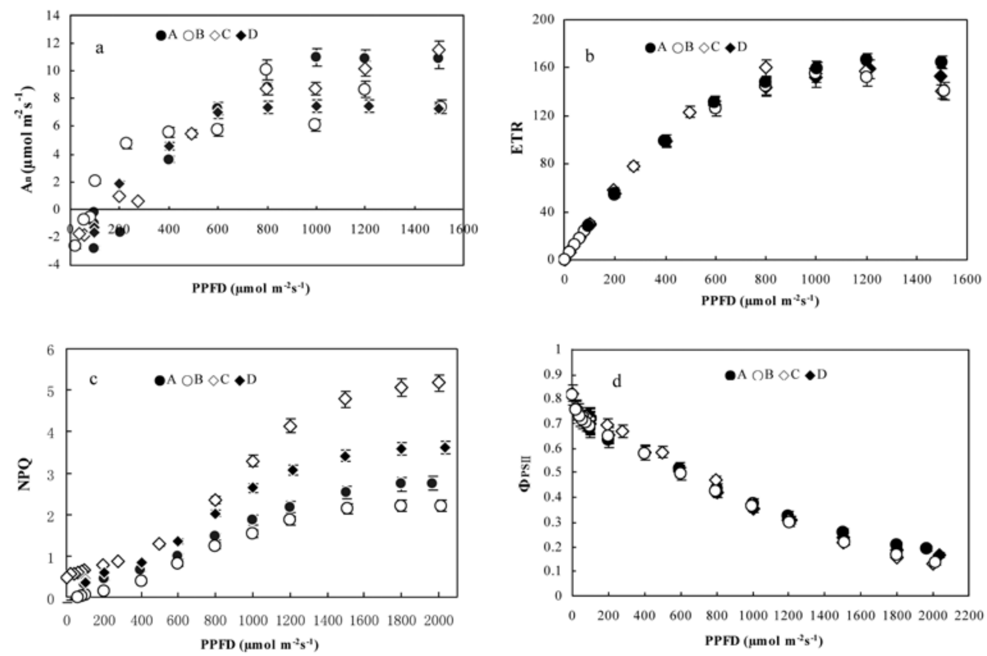

Figure 1. Variance of photosynthetic and chlorophyll fluorescence parameters with increasing light intensities measured in four genotypes: A (*H. neurocarpa*), B (*H. goniocarpa*-N), C (*H. goniocarpa*-R), D (*H. rhanmoides* ssp. *sinensis*). Means ± SD. a, Net carbon accumulation (A_n); b, Electron transport rate (ETR); c, Non-photochemical quenching (NPQ); d, Effective PSII quantum yield ($\Phi_{PS\,II}$).

of the two parental species. The carboxylation efficiency (CE) of *goniocarpa*-R was distinctly different from that of *H. goniocarpa*-N, and the former genotype had a higher CE than the two parental species while the latter was intermediate between the parental species in this respect. In addition, the light compensation point (LCP) was higher in *H. goniocarpa*-R than in the two parental species, while that of *H. goniocarpa*-N was lower (Table 1).

Chlorophyll fluorescence

The electron transport rate (ETR) and effective PSII quantum yield ($\Phi_{PS\,II}$) increased with PPFDs, and there were no significant differences in these variables among the four genotypes (Figure 1b, d). However, their non-photochemical quenching (NPQ) responses to increases in PPFDs varied strongly, reaching higher levels in *H. goniocarpa*-R and lower levels in *H. goniocarpo*-N than in either of the parental types (Figure 1c). In addition, there was no indication that these differences were due to significant stressors prior to the measurements because F_v/F_m remained constant, between 0.82 and 0.84.

Carbon isotope ratio and elemental analyses

The long-term ($\delta^{13}C$) indices of water use efficiency (WUE) varied among the four types. ANOVA tests suggested that *H. goniocarpa*-R significantly differed from *H. goniocarpa*-N in this respect, and the WUE value was higher for the former genotype than for both of the parental species while that of the latter was between intermediate those of the two parental species.

Table 1. Values of photosynthetic parameters derived from light curve and A-ci curve determinations: maximum photosynthetic rate (A_{max}), transpiration (E), quantum efficiency (QE), carboxylation efficiency (CE), instantaneous (A_{max}/E), light compensation point (LCP). Different letters in each column indicate statistically significant differences ($P < 0.05$) according to one way variance analysis (ANOVA). Arithmetic means ± SD.

	H. neurocarpa	*H. goniocarpa*		*H. rhanmoides* ssp. *sinensis*
		H. goniocarpa-N	*H. goniocarpa*-R	
A_{max} (μmol CO_2 $m^{-2}s^{-1}$)	12.5 ± 0.15^a	11.1 ± 0.22^b	12.8 ± 0.12^c	8.45 ± 0.43^d
E (mmol H_2O $m^{-2}s^{-1}$)	3.50 ± 0.13^a	2.41 ± 0.21^b	2.40 ± 0.18^b	3.71 ± 0.15^c
A_{max}/E	3.57 ± 0.14^a	4.61 ± 0.22^b	5.34 ± 0.15^c	2.28 ± 0.29^d
QE	0.05 ± 0.006^a	0.0297 ± 0.0051^b	0.0165 ± 0.0032^c	0.0322 ± 0.0047^d
CE	0.132 ± 0.021^a	0.237 ± 0.015^b	0.088 ± 0.011^c	0.071 ± 0.034^c
LCP	129 ± 5.2^a	67 ± 6.9^b	210 ± 9.4^c	140 ± 8.2^d

There was no significant difference in leaf N concentrations between *H. goniocarpa*-R and *H. goniocarpa*-N, and both had values between those of the two parental species. However, leaf C concentrations of these two genotypes were distinctly different and lower, in both cases, than those of the two parental species (Figure 2). Furthermore, the two *goniocarpa* types differed from each other in N_{area}, and both had higher N_{area} values than the two parental species. The LMAs of the two hybrid genotypes also differed, but the *H. goniocarpa*-N LMA was similar to that of *H. rhanmoides* ssp. *sinensis* while the LMA of *H. goniocarpa*-R was intermediate between those of the two parental species. MSLAs of both hybrid genotypes differed from each other and were intermediate between those of the two parental species (Table 2). Compared with two parental species, a few measured variables in *H. goniocarpa* and two genotypes are transgressive or intermediate (Table 3).

DISCUSSION

Physiological performances of *H. goniocarpa*

Hybridization has played an important role in enhancing adaptive fitness through complementary recombination, and heterosis has often been observed in F_1 hybrids (Arnold, 1997; Campbell et al., 2005). However, such superiority may be transient and subsequently disappear in natural recombinant species (Schemske, 2000). Our physiological measurements suggest that both maternal genotypes of *H. goniocarpa* have significantly higher water use efficiency (WUE, A_{max}/E), and nitrogen contents (N_{area}); i.e. both of them are positively transgressive than their two parental species (Table 3). In addition, *H. neurocarpa* tended to have higher water use efficiency than *H. rhanmoides* ssp. *sinensis,* which is consistent with the habitat distribution of these two species (the former occurring in a drier region at higher altitudes than the latter; Lian et al., 2000). This finding is consistent with the reported heterosis of *Ipomopsis* F_1 hybrids in instantaneous water use efficiency (Campbell et al., 2005). However, to our knowledge, there have been no previous detailed comparisons of the instantaneous WUE between natural hybrid species and their parental species. It remains unknown whether this performance is stable when the hybrid species extends to the other habitats. However, the positively transgressive WUE of *H. goniocarpa*

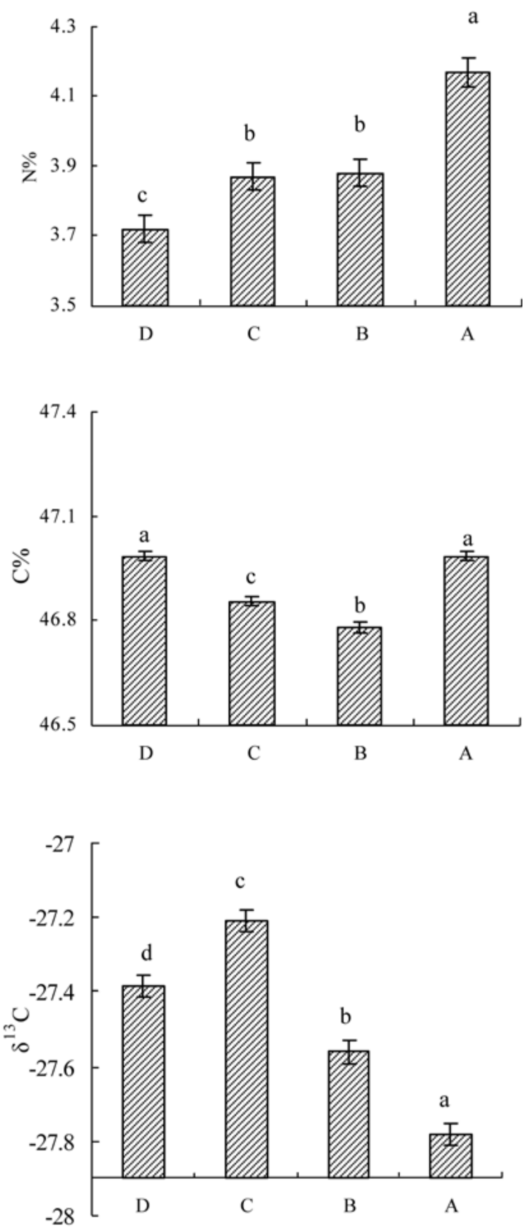

Figure 2. Concentration of nitrogen and carbon (N%, C%) and integrated water use efficiency ($\delta^{13}C$) measurements for the four genotypes A (*H. neurocarpa*), B (*H. goniocarpa*-N), C (*H. goniocarpa*-R), D (*H. rhanmoides* ssp. *sinensis*) at the study site. Means ± SD. Different letters (a, b, c, d) within the same column denote significant differences (p < 0.05).

Table 2. Nitrogen content per unit area (N_{area}), leaf mass per unit area (LMA) and mean single leaf area (MSLA) (means ± SD) in *H. neurocarpa, H. goniocarpo*-N, *H. goniocarpo*-R, *H. rhamnoides.* Different letters in each column indicate statistically significant differences ($P < 0.05$) according to one way variance analysis (ANOVA).

	H. neurocarpa	*H. goniocarpa*		*H. rhanmoides* ssp. *sinensis*
		H. goniocarpa-N	*H. goniocarpa*-R	
N_{area} (g/m^2)	3.06 ± 0.27^a	3.93 ± 0.31^b	3.63 ± 0.10^c	2.82 ± 0.08^d
LMA (g/m^2)	73.44 ± 6.48^a	101.41 ± 8.12^b	77.11 ± 2.25^a	95.59 ± 2.54^b
MSLA (cm^2)	1.17 ± 0.15^a	1.94 ± 0.11^b	2.37 ± 0.04^c	2.96 ± 0.15^d

Table 3. Positive (Pos) and intermediate physiological measurements of two hybrid genotypes (*H. goniocarpo*-N and *H. goniocarpo*-R, mothered respectively by *H. neurocarpa* and *H. rhamnoides*) related to two parental species.

Traits	Hybrid genotype	
	H. goniocarpa-N	*H. goniocarpa*-R
A_{max} (μmol CO_2 $m^{-2}s^{-1}$)	intermediate	pos. transgressive
E (mmol H_2O $m^{-2}s^{-1}$)	neg. transgressive	neg. transgressive
A_{max}/E	**pos. transgressive**	**pos. transgressive**
QE	neg. transgressive	neg. transgressive
CE	pos. transgressive	rhanmoides-like
LCP	neg. transgressive	pos. transgressive
N_{area} (g/m^2)	**pos. transgressive**	**pos. transgressive**
LMA (g/m^2)	pos. transgressive	neurocarpa-like
MSLA (cm^2)	intermediate	intermediate
$\delta^{13}C$	pos. transgressive	intermediate
N%	intermediate	intermediate
C%	neg. transgressive	neg. transgressive

may suggest that this physiological performance may be involved in speciation and ecological isolation of such recombination species. If so, this finding conflicts with the previous hypothesis that WUE heterosis may not be genetically based and may be solely due to dominance, overdominance, or positive epistastis, in which specific interactions between genes from the two species increase the trait value in the F_1 hybrids (Campbell et al., 2005). However, all confirmed homoploid hybrid species have been found in more extreme habitats than those of any congener, i.e., deserts and high mountains (Arnold, 1997; Rieseberg, 1997). Their enhanced WUE presumably helps these hybrid species to cope with the arid habitats and establish initial populations. Our results further suggest that the enhanced instantaneous water use efficiency of the two hybrid genotypes is closely correlated with increases in their leaf nitrogen contents per unit area (N_{area}). This is probably because the photosynthetic enzymes and pigments represent a major investment in leaf nitrogen (Field and Mooney, 1986). However, the nitrogen concentrations per unit mass (N_{mass}) did not exhibit such a trend, since this parameter was higher in *H. neurocarpa* than in *H. rhanmoides* ssp. *sinensis* and intermediate in the two *H. goniocarpa* types. This may be due to the differences in leaf thickness between the four genotypes.

While we here focused on differences in physiological traits between *H. goniocarpa* and the parental species, it should be noted that this species differs from the parental species in the other traits. For example, the germination rate of this species is higher than that of the parental species (Lian et al., 1998). In addition, we found that seedlings of this species grow faster than those of both parental species. The reproductive isolation of homoploid hybrid species may arise through rapid chromosomal repartitioning, ecological divergence and/or spatial separation (Buerkle et al., 2000). Amongst these processes, ecological divergence may be especially important, at least according to simulations indicating that such speciation is unlikely to occur in the absence of niche separation (McCarthy et al., 1995). *Hippophae goniocarpa* occurs sympatrically with the two parental species without spatial separation, but the ecological divergence in this hybrid species in flowering parameters (Lian et al., 1998) and reproductive isolations may arise from a combination of all these different performances, which may also together provide inherent power to combine all individuals of two genotypes as a distinct species unit.

Differences in physiological performances between the two maternal genotypes

Despite their concordant and positive transgression in some physiological traits, our results suggest that there are distinct differences in physiological performances between the two maternal genotypes of *H. goniocarpa*. Apart from the total N concentration and transpiration (E), all of the other traits showed distinct differences between the two genotypes; A_{max}, A_{max}/E, CE, QE, NPQ, LCP, long-term WUE ($\delta^{13}C$), N_{area}, MSLA, LMA and C. QE, CE, N_{area}, LMA and long-term WUE ($\delta^{13}C$) were higher in *H. goniocarpa*-N than in *H. goniocarpa*-R while the contrary trends were found for A_{max}, A_{max}/E, NPQ, LCP, MSLA and C. We initially expected these differences to show correlations with the maternal species, i.e. traits with high values in the maternal species to have high values in the hybrid genotypes of *H. goniocarpa* they respectively mothered. However, we did not detect such overall correlations among all examined traits ($P > 0.05$). For example, A_{max} and A_{max}/E were higher in *H. neurocarpa* than in *H. rhanmoides* ssp. *sinensis*, but lower in *H. goniocarpa*-N, mothered by the former species than in *H. goniocarpa*-R, mothered by the latter species. The differences in the other traits, i.e., QE, CE, NPQ, long-term WUE ($\delta^{13}C$), N_{area}, MSLA, LMA and C concentrations in the two *H. goniocarpa* genotypes agree well with the differences between their maternal species. If the maternal species showed a higher value in one of these traits, the mothered *H. goniocarpa* genotype accordingly had a higher difference than the genotype mothered by the other species. These differences suggest that maternal origins have not had direct effects on the hybrid progeny.

Instead, the physiological traits of these two genotypes appear to have arisen from hybrid recombination and ecological processes from those of both parental species.

The observed differences between the two maternal genotypes of *H. goniocarpa* may reflect their differences in ecological preference. For example, the higher A_{max} in *H. goniocarpa*-R implies that its growth may be faster due to more rapid biomass accumulation (Aarssen and Clauss, 1992; Arntz et al., 1998, 2000; Aarssen and Keogh, 2002). In addition, the higher non-photochemical quenching (NPQ) of chlorophyll fluorescence in this genotype may facilitate its occupation of high altitude habitats by allowing it to dissipate excess light in the form of non-radiative energy to avoid or mitigate photodamage to its leaves through the presence of high xanthophyll contents (Xu et al., 1998; Zhao and Wang, 2002; Zhao et al., 2007). The differences in both instantaneous (A_{max}/E) and long-term ($\delta^{13}C$) indices of water use efficiency between the maternal genotypes may reflect differences in water availability in their habitats, and thus their habitat preferences. If so, the findings indicate that these different maternal genotypes may occupy more distinctly different habitats during their range expansion in the future. Accordingly, available data regarding the molecular phylogeography of other diploid hybrid species suggest that different maternal genotypes usually inhabit different regions (Brochman et al., 2000; Wang et al., 2001; Schwarzbach and Rieseberg, 2002; Gross et al., 2003). The differences in physiological performances between the maternal genotypes found in the present study may partly explain the general differences in distribution of different maternal genotypes of natural hybrid species, in addition to founder effects during their range expansion.

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棱果沙棘不同母本起源基因型的生理特徵研究

馬 飛 陳立同 姚步青 趙長明

中國甘肅蘭州大學 生命科學學院乾旱與草地教育部重點實驗室

同倍性雜交物種通常具有來自不同物種的基因型，並且它們常具有地理分佈上的差異。但是，它們在同一生境條件下的生理差異從來沒有進行過比較研究。棱果沙棘 (*Hippophae goniocarpa*) 是雜交起源物種，其親本分別是中國沙棘 (*H. rhamnoides* ssp. *sinensis*) 和肋果沙棘 (*H. neurocarpa* ssp. *neurocarpa*)。本研究旨在比較棱果沙棘不同母本起源基因型 (*H. goniocarpa*-R，以中國沙棘爲母本和 *H. goniocarpa*-N，以肋果沙棘爲母本) 之間以及它們與兩個親本種的生理特徵差異。所研究的生理指標包括光合速率 (A_{max})，蒸騰速率 (E)，量子效率 (QE)，羧化效率 (CE)，光補償點 (LCP)，暫態水分利用效率 (A_{max}/E) 和長期水分利用效率 ($\delta^{13}C$)，光系統 II 的有效光量子效率 ($\Phi_{PS\ II}$)，非光化學淬滅 (NPQ)，單位重量的氮 (N_{mass}) 和碳含量 (C), 單位面積的氮含量 (N_{area}), 平均單葉面積 (MSLA) 和單位面積幹重 (LMA)。結果顯示兩個基因型之間在 A_{max}, A_{max}/E, QE, CE, NPQ, LCP, $\delta^{13}C$, N_{area}, MSLA, LMA 和 C 方面都存在差異。*H. goniocarpa*-R 基因型在 A_{max}, $\delta^{13}C$, NPQ, MSLA 和 LCP 都比兩個親本種高 ； 而 *H. goniocarpa*-N 基因型的 A_{max} 和 $\delta^{13}C$ 介於兩個親本之間，與母系來源沒有關係。兩個基因型的 A_{max}/E 和 N_{area} 都明顯高於兩個親本種，表明該雜交物種在這些生理特徵方面具有一致性、並表現出超親特性，可能是將不同基因型組合成一個物種進化單元的關鍵因素。此外，兩個基因型的 MSLA 和 N_{mass} 都介於兩個親本種之間，而 C 和 QE 明顯低於兩個親本種。我們的研究結果表明雜交起源的物種中，依賴母系來源的基因型存在生理區別 ； 這些發現將進一步有助於我們理解爲什麼在雜交起源的物種中，不同母系來源的基因型常佔據不同的生境。

關鍵詞 ： 基因型 ； 棱果沙棘 ； 同倍性雜交物種 ； 生理特徵。