Postprint: Analysis of Diurnal Variation in Photosynthetic Characteristics of Three Sea Buckthorn Species in the Natural Hybrid Zone of Hippophae goniocarpa, Qilian, Qinghai

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Abstract

Hybrid zones are natural laboratories for studying speciation and evolution. To investigate the physio-ecological adaptability of three sea buckthorn species in the natural hybrid zone of *Hippophae goniocarpa*, we measured the diurnal variations in photosynthetic characteristics and related environmental factors for female and male plants of the three species in the region during mid-July with ample sunlight, aiming to provide a theoretical basis for the maintenance mechanism of the hybrid zone. The results showed that the diurnal variation patterns of photosynthesis were basically consistent between female and male plants of the same species. The differences in diurnal variation patterns of photosynthetic characteristics among different sea buckthorn species were mainly manifested as follows: the Pn diurnal variation of *Hippophae rhamnoides* ssp. *sinensis* showed a distinct bimodal curve, with peaks occurring at 10:00 and 14:00 when PAR and Ta were relatively high, reaching a maximum of 19.53±5.35 $mol \cdot m^{-2} \cdot s^{-1}$; the Pn diurnal variations of both *Hippophae goniocarpa* and *Hippophae neurocarpa* ssp. *neurocarpa* exhibited near-bimodal curves, with higher values at 8:00 and 16:00 when PAR and Ta were relatively low, with maximum values of 13.43±3.43 and 15.27±2.43 $mol \cdot m^{-2} \cdot s^{-1}$, respectively. The diurnal variation patterns of WUE were consistent with Pn for all three sea buckthorn species, but *Hippophae rhamnoides* ssp. *sinensis* had the highest WUE, reaching 6.72±0.95 $mol \cdot mmol^{-1}$, while the maximum diurnal WUE values for *Hippophae goniocarpa* and *Hippophae neurocarpa* ssp. *neurocarpa* were 4.03±1.08 and 4.93±0.86 $mol \cdot mmol^{-1}$, respectively. The diurnal variation patterns of Tr, Gs, Ci, and Ls were similar among the three sea buckthorn species, with Gs consistently decreasing after 10:00 and varying degrees of stomatal closure occurring around 12:00, which is one of the main reasons for their midday photosynthetic depression.

The differences in diurnal variation of photosynthetic characteristics among the three sea buckthorn species in the hybrid zone were mainly manifested between *Hippophae rhamnoides* ssp. *sinensis* and the other two species, while the variation patterns of the hybrid species *Hippophae goniocarpa* and its parental species *Hippophae neurocarpa* ssp. *neurocarpa* were basically consistent, and their Pn and WUE may have been influenced by environmental factors such as Ta, PAR, and RH.

Full Text

Diurnal Changes in Photosynthetic Characteristics of Three Seabuckthorn Species in the Qinghai Qilian Hybrid Zone

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Abstract: Hybrid zones serve as natural laboratories for studying speciation and evolution. To investigate the ecophysiological adaptability of three seabuckthorn species in the *Hippophae goniocarpa* natural hybrid zone, we measured diurnal changes in photosynthetic characteristics and related environmental factors for both female and male plants during mid-July under ample light conditions, aiming to provide a theoretical basis for the maintenance mechanisms of this hybrid zone. The results showed that diurnal patterns of photosynthesis were essentially consistent between female and male individuals within each species. However, significant differences emerged among species. *Hippophae rhamnoides* ssp. *sinensis* exhibited a pronounced bimodal curve in net photosynthetic rate (Pn), with peaks occurring at 10:00 and 14:00 when photosynthetically active radiation (PAR) and air temperature (Ta) were relatively high, reaching a maximum of 19.53 ± 5.35 $mol \cdot m^{-2} \cdot s^{-1}$. In contrast, both *Hippophae goniocarpa* and *Hippophae neurocarpa* ssp. *neurocarpa* showed near-bimodal curves, with higher values at 8:00 and 16:00 when PAR and Ta were lower, achieving maximum values of 13.43 ± 3.43 and 15.27 ± 2.43 $mol \cdot m^{-2} \cdot s^{-1}$, respectively. Water use efficiency (WUE) followed the same diurnal pattern as Pn across all three species, but *H. rhamnoides* ssp. *sinensis* demonstrated the highest WUE at 6.72 ± 0.95 $mol \cdot mmol^{-1}$, while *H. goniocarpa* and *H. neurocarpa* ssp. *neurocarpa* peaked at 4.03 ± 1.08 and 4.93 ± 0.86 $mol \cdot mmol^{-1}$, respectively. Diurnal patterns of transpiration rate (Tr), stomatal conductance (Gs), intercellular CO concentration (Ci), and stomatal limitation value (Ls) were similar among species, with Gs declining uniformly after 10:00 and varying degrees of stomatal closure occurring around 12:00—a primary contributor to midday photosynthetic depression. The principal differences in diurnal photosynthetic characteristics occurred between *H. rhamnoides* ssp. *sinensis* and the other two species, while the hybrid *H. goniocarpa* showed patterns largely consistent with its parental species *H. neurocarpa* ssp. *neurocarpa*. Its Pn and WUE

may be influenced by environmental factors including Ta, PAR, and relative humidity (RH).

Keywords: hybrid zone; *Hippophae*; diurnal change of photosynthesis; water use efficiency

Introduction

Hybridization represents an evolutionary force in plant populations (Barton, 2010). Natural hybrid zones—regions where previously diverged species re-establish contact and interbreed to produce hybrid offspring (Arnold, 1997)—have long served as focal points for research on genetic structure, reproductive isolation mechanisms, and speciation (Hewitt, 1988). The maintenance of hybrid zones depends on the combined effects of endogenous selection (selection on hybrid genotypes) (Barton, 1985) and exogenous selection (environmental influences) (Moore, 1977; Arnold, 1996). Consequently, the fitness of hybrid individuals in natural hybrid zones reflects genotype-by-environment interactions (Kimball & Campbell, 2009). Johnston et al. (2003) proposed that fitness manifests across various life history stages, including seed germination, seedling growth, vegetative development, and reproductive phases. Studies have demonstrated that plant physiological traits—such as photosynthetic characteristics, seedling growth, and chlorophyll content—can reflect the fitness of hybrids relative to parental species (Campbell et al., 2005; Kimball & Campbell, 2009; Donovan et al., 2010). Photosynthetic traits are constrained not only by external conditions like temperature, air, and light but also by inherent genetic characteristics (Jiang et al., 2007; Zhong et al., 2014; Zou et al., 2015). Investigating diurnal patterns of photosynthetic characteristics in hybrids and parental species under natural conditions is therefore crucial for understanding photosynthetic physiological fitness.

Recent analyses of ITS, cpDNA *trnS-G*, and *trnL-F* sequences have confirmed that *Hippophae goniocarpa* originated through homoploid hybridization between sympatrically distributed *Hippophae rhamnoides* ssp. *sinensis* and *Hippophae neurocarpa* ssp. *neurocarpa* (Sun et al., 2003; Zhang, 2005; Du, 2008; Jiang et al., 2014). Previous research has examined the fitness of *H. goniocarpa* and its parental species from perspectives including seed germination, protective enzyme activity, clonal structure, and clonal diversity (Tang, 2009; Jiang, 2013). However, how do the photosynthetic characteristics of these three seabuckthorn species differ within the natural hybrid zone? This study measured diurnal changes in photosynthetic traits and related environmental factors for three seabuckthorn species in the *H. goniocarpa* natural hybrid zone in Qilian County, Qinghai Province. Our objective was to provide evidence for the ecophysiological adaptability of these species from a photosynthetic physiology perspective and to offer theoretical insights into the maintenance mechanisms of the seabuckthorn hybrid zone.

1.1 Study Area Description

The study area was located in Qilian County, Haibei Tibetan Autonomous Prefecture, Qinghai Province (100°24 E, 38°9 N, elevation 3,020 m). The region features a cold, semi-arid, and semi-humid montane forest-steppe climate, with a mean annual temperature of 0.7 °C. January mean temperature is -13.1 °C, while July mean temperature ranges from 10 to 14 °C. Annual precipitation averages 435.5 mm, concentrated primarily from May to September, often occurring as heavy rainstorms that account for 88.6% of total annual precipitation.

Seabuckthorn shrublands represent the dominant vegetation in this region. *Hippophae rhamnoides* ssp. *sinensis* and *H. neurocarpa* ssp. *neurocarpa* are co-dominant species that intermix within floodplain seabuckthorn communities, forming a natural hybrid zone where *H. goniocarpa* has emerged.

1.2 Materials and Methods

We selected *H. rhamnoides* ssp. *sinensis*, *H. neurocarpa* ssp. *neurocarpa*, and their hybrid *H. goniocarpa* from the natural hybrid zone in Qilian County (Rixu Village floodplain) as study materials. Three healthy female and three male plants of consistent age and vigorous growth were randomly chosen for each species. During mid-July 2017, under clear, calm, and well-lit conditions, we measured photosynthetic parameters of mature, robust leaves from outer canopy layers in different orientations using a portable photosynthesis system (TPS-2, PP Systems, UK). Natural light was used for all measurements, with three replicates per measurement. Data were collected every two hours from 8:00 to 18:00 over three consecutive days. To minimize errors from instrument shading and light source variation, the leaf cuvette was positioned perpendicular to natural light during measurements.

Measured photosynthetic parameters included: net photosynthetic rate (Pn), transpiration rate (Tr), stomatal conductance (Gs), and intercellular CO concentration (Ci). Instantaneous water use efficiency (WUE) was calculated as WUE = Pn/Tr, and stomatal limitation value (Ls) as Ls = 1 - Ci/Ca. Simultaneously measured environmental factors included photosynthetically active radiation (PAR), air relative humidity (RH), ambient CO concentration (Ca), and air temperature (Ta).

Statistical analysis involved correlation analysis among environmental factors with significance testing, and one-way ANOVA ($P = 0.05$) to compare differences among data groups. All data are presented as mean ± standard deviation.

2.1 Diurnal Variation of Environmental Factors

Diurnal changes in major environmental factors are shown in [Figure 1: see original paper]. From 8:00 to 18:00, both PAR and Ta exhibited trends of initial increase followed by decrease [FIGURE:1:a]. The study area experienced high light intensity, with PAR peaking at 2,136.5 ± 116.83 $mol \cdot m^{-2} \cdot s^{-1}$ at noon

(12:00). Ta showed a time-lag effect relative to PAR, reaching its maximum of 30.87 ± 0.5 °C at 14:00. Correlation analysis revealed a significant positive correlation between PAR and Ta ($P < 0.05$) .

Diurnal curves for Ca and RH both displayed a "V" shape [FIGURE:1:b]. Ca reached its minimum of 420.5 ± 12.5 mol · mol ^{1} at 12:00, with only modest recovery thereafter; plant photosynthetic uptake of CO represents a major factor in this decline. Due to frequent rainfall in mid-July, RH remained high throughout the day, reaching its lowest point of 41.42 ± 1.47% at 14:00. Both Ca and RH showed extremely significant negative correlations with Ta .

2.2.1 Diurnal Variation of Net Photosynthetic Rate

The diurnal variation of net photosynthetic rate (Pn) in the three seabuckthorn species followed bimodal or near-bimodal curves with distinct peak patterns [Figure 2: see original paper]. *Hippophae rhamnoides* ssp. *sinensis* showed peaks at 10:00 and 14:00, reaching a maximum of 19.53 ± 5.35 mol · m ^{2} · s ^{1}. *Hippophae goniocarpa* and *H. neurocarpa* ssp. *neurocarpa* exhibited similar trends, with higher values at 8:00 and 16:00. Maximum Pn values were 13.43 ± 3.43 mol · m ^{2} · s ^{1} for *H. goniocarpa* and 15.27 ± 2.43 mol · m ^{2} · s ^{1} for *H. neurocarpa* ssp. *neurocarpa*. Diurnal patterns were essentially similar between female and male plants within each species.

2.2.2 Diurnal Variation of Transpiration Rate and Stomatal Conductance

Transpiration rate (Tr) patterns resembled those of Pn across the three species [Figure 3: see original paper]. *Hippophae rhamnoides* ssp. *sinensis* showed Tr peaks at 10:00 and 16:00. *Hippophae goniocarpa* exhibited higher Tr values at 8:00 and 16:00. The second Tr peak differed between sexes in *H. neurocarpa* ssp. *neurocarpa*, occurring at 14:00 in male plants and 16:00 in female plants. Daily Tr ranges were 2.08 ± 0.16–3.21 ± 0.29 mmol · m ^{2} · s ^{1} for *H. rhamnoides* ssp. *sinensis*, 2.27 ± 0.13–3.29 ± 0.20 mmol · m ^{2} · s ^{1} for *H. goniocarpa*, and 1.8 ± 0.35–3.2 ± 0.12 mmol · m ^{2} · s ^{1} for *H. neurocarpa* ssp. *neurocarpa*.

Stomatal conductance (Gs) showed consistent trends across all three species, with high values from 8:00–10:00, followed by sharp declines and maintenance at low levels with minimal fluctuation after 12:00 [Figure 4: see original paper].

2.2.3 Diurnal Variation of Intercellular CO Concentration and Stomatal Limitation Value

Intercellular CO concentration (Ci) was highest at 8:00 for all three species, reaching its minimum at noon (12:00) within a range of 360–620 mol · mol ^{1}, with only slight recovery thereafter [Figure 5: see original paper].

Stomatal limitation value (Ls) showed similar trends across species [Figure 6: see original paper], peaking at 12:00. Additionally, *H. rhamnoides* ssp. *sinensis*

exhibited relatively high Ls at 8:00, but lower values than the other two species thereafter.

2.2.4 Diurnal Variation of Water Use Efficiency

Water use efficiency (WUE) displayed bimodal curves across all three species [Figure 7: see original paper], mirroring Pn patterns. *Hippophae rhamnoides* ssp. *sinensis* showed peaks at 10:00 and 14:00, while *H. goniocarpa* and *H. neurocarpa* ssp. *neurocarpa* had higher values at 8:00 and 16:00. *Hippophae rhamnoides* ssp. *sinensis* WUE differed extremely significantly from the other two species ($P < 0.01$), with a maximum of 6.72 ± 0.95 mol · mmol ^{1}, compared to 4.03 ± 1.08 mol · mmol ^{1} for *H. goniocarpa* and 4.93 ± 0.86 mol · mmol ^{1} for *H. neurocarpa* ssp. *neurocarpa*.

3.1 Photosynthetic Characteristics of the Three Seabuckthorn Species

Photosynthesis is a complex internal physiological process significantly influenced by environmental factors, with different plants exhibiting distinct photosynthetic traits (Wei et al., 2010; Ye et al., 2016). Photosynthetic rate reflects the intensity of photosynthesis and serves as a crucial metric. Previous studies have identified various diurnal curve patterns for net photosynthetic rate, including unimodal, bimodal, flat, and irregular types (Wang et al., 2000). Our findings indicate that diurnal photosynthetic patterns were similar between sexes within each species but differed among species.

All three species exhibited bimodal or near-bimodal Pn curves, indicating some degree of midday photosynthetic depression. However, *H. rhamnoides* ssp. *sinensis* differed markedly from *H. goniocarpa* and *H. neurocarpa* ssp. *neurocarpa* [Figure 2: see original paper]. *Hippophae rhamnoides* ssp. *sinensis* achieved high Pn (19.53 ± 5.35 mol · m ^{2} · s ^{1}) and WUE (6.72 ± 0.95 mol · mmol ^{1}) with relatively low Ls [Figure 6: see original paper] at high PAR levels ($1{,}270.83 \pm 263.93$ mol · m ^{2} · s ^{1} at 10:00 and $1{,}905.00 \pm 435.07$ mol · m ^{2} · s ^{1} at 14:00) [Figure 1: see original paper], suggesting superior light utilization under high PAR and Ta conditions. In contrast, *H. goniocarpa* and *H. neurocarpa* ssp. *neurocarpa* showed near-bimodal Pn and WUE curves [FIGURE:1, FIGURE:7], with relatively high Pn values even at low PAR (169.33 ± 45.7 mol · m ^{2} · s ^{1}) at 8:00. Elevated nighttime respiration had accumulated substantial CO , resulting in high Ca (665.5 ± 40.86 mol · mol ^{1}) at this time, while both species also exhibited high Gs and Ci, contributing to their relatively high morning Pn values. However, their Pn and WUE remained lower than those of *H. rhamnoides* ssp. *sinensis* throughout the day, indicating that their photosynthetic capacity and water use efficiency were somewhat constrained by PAR and Ta.

Stomata constitute crucial channels for gas exchange between plants and the atmosphere, with Gs directly influencing Pn and Tr (Zhao et al., 2014). All three seabuckthorn species showed consistent Gs diurnal patterns [Figure 4: see original paper], with high values from 8:00–10:00 followed by sharp declines and

varying degrees of stomatal closure around 12:00. Ci patterns were also similar across species [Figure 5: see original paper], decreasing before 12:00 while Ls increased [Figure 6: see original paper]. However, Ls values remained relatively low, fluctuating around 0.1, indicating that midday Pn depression was influenced by both stomatal and non-stomatal factors.

Overall, *H. rhamnoides* ssp. *sinensis* exhibited the highest Pn and WUE, while *H. goniocarpa* and *H. neurocarpa* ssp. *neurocarpa* showed lower values. Research by Jin et al. (2011) on *H. rhamnoides* ssp. *sinensis* in the Loess Plateau found higher Pn and WUE under conditions of ample light, higher temperature, and humidity. This may reflect that the Pn and WUE of *H. goniocarpa* and *H. neurocarpa* ssp. *neurocarpa*, distributed in high-altitude cold environments, are constrained by environmental factors such as Ta, PAR, and RH.

3.2 Physiological Fitness of the Three Seabuckthorn Species

Differences in photosynthetic characteristics between parental and hybrid offspring relate to both genetic traits and environmental influences. Examining photosynthetic rate and water use efficiency is essential for revealing plant physiological fitness (Donovan & Ehleringer, 1994; Arntz & Delph, 2001). Campbell et al. (2005) compared photosynthetic rates and water use efficiency between parental and hybrid *Ipomopsis* populations to analyze physiological fitness, finding that hybrids exhibited heterosis in instantaneous water use efficiency and showed high survival rates in arid environments, colonizing novel habitats. Our results demonstrate that in the natural hybrid zone, the parental species *H. rhamnoides* ssp. *sinensis* achieved the highest Pn and WUE, peaking during high-temperature periods, whereas the hybrid *H. goniocarpa* did not exhibit heterosis in water use efficiency. Instead, its patterns closely resembled those of *H. neurocarpa* ssp. *neurocarpa*, with both showing higher Pn and WUE during cooler periods, reflecting better ecophysiological adaptation to high-altitude environments.

Hybrid zone theory posits that maintenance depends on the combined effects of endogenous and exogenous selection (Schweitzer, 2002). Studies indicate that *H. neurocarpa* ssp. *neurocarpa* and *H. goniocarpa* are distributed at elevations of 2,700–4,300 m and 2,700–3,100 m, respectively. The hybrid *H. goniocarpa* possesses photosynthetic physiological characteristics similar to its parental species *H. neurocarpa* ssp. *neurocarpa* for adapting to high-altitude environments, yet does not demonstrate superior physiological adaptability to colonize novel habitats through exogenous selection, which may provide theoretical insights into hybrid zone maintenance mechanisms. Furthermore, Schierenbeck et al. (1993) noted that high Pn and WUE typically indicate strong survival and broad distribution capabilities. Among the three species, *H. rhamnoides* ssp. *sinensis* is widely distributed across lower elevations (400–3,100 m), occupying a relatively broad niche, and its Pn and WUE are significantly higher than those of *H. neurocarpa* ssp. *neurocarpa* and *H. goniocarpa*.

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Note: Figure translations are in progress. See original paper for figures.