Variation in Net Photosynthetic Rate of Grapevine and Its Influencing Factors in Northwest Arid Region: Postprint

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Abstract

As one of the main economic crops in the arid regions of northwestern China, understanding its photosynthetic production process is crucial for cultivation. To investigate the photosynthetic physiological characteristics of grapes under natural field conditions and the main factors affecting grape photosynthesis, this study measured the diurnal variation of leaf photosynthesis and its physiological and ecological factors in grape (variety: Thompson Seedless) from June to September 2019, employed path analysis to examine the direct and indirect effects of various factors on leaf net photosynthetic rate, and identified the main influencing factors. Additionally, the response of grape leaf net photosynthetic rate to various physiological and ecological factors was further analyzed using a time-divided mode throughout the day. The results indicate: (1) The diurnal variation of grape leaf net photosynthetic rate generally exhibited a unimodal curve pattern characterized by an initial increase followed by a decrease; (2) Grape leaf net photosynthetic rate showed extremely significant positive correlations with photosynthetically active radiation, saturated vapor pressure deficit, air temperature, stomatal conductance, and transpiration rate, and extremely significant negative correlations with relative humidity and intercellular CO2 concentration; (3) The main determining factors affecting the variation of grape leaf net photosynthetic rate were transpiration rate in June, August, and September, while in July it was stomatal conductance; (4) The response of grape leaf net photosynthetic rate to air temperature, photosynthetically active radiation, and saturated vapor pressure deficit from June to September all displayed a "hysteresis loop" relationship, exhibited good linear relationships with transpiration rate and stomatal conductance ($R^2>0.85$), and showed an exponential functional relationship with intercellular CO2 concentration ($R^2=0.53$). The study demonstrates that grapes possess strong adaptability to the environment of northwestern arid regions, and management can be optimized and yield

improved by controlling transpiration rate and stomatal conductance, but the direct and indirect effects of other factors must also be considered.

Full Text

Preamble

Variation of Net Photosynthetic Rate of Grape and Its Influencing Factors in the Arid Region of Northwest China

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Abstract

Grapes are one of the main economic crops in the arid region of Northwest China, and understanding their photosynthetic production process is crucial for cultivation management. To investigate the photosynthetic physiological characteristics of grapes and the key factors influencing grape photosynthesis under natural field conditions, this study measured the diurnal variations of leaf photosynthesis and associated physiological-ecological factors of grape (variety: Seedless White) from June to September 2019. Path analysis was employed to examine the direct and indirect effects of various factors on leaf net photosynthetic rate (Pn) and to identify the primary influencing factors. Additionally, the responses of grape leaf Pn to different physiological-ecological factors were analyzed across different time periods throughout the day. The results showed that: (1) The diurnal variation of grape leaf Pn generally exhibited a single-peak curve pattern, increasing first and then decreasing; (2) Grape leaf Pn was extremely significantly positively correlated with photosynthetically active radiation (PAR), vapor pressure deficit (VPD), air temperature (Ta), stomatal conductance (Gs), and transpiration rate (T), while it was extremely significantly negatively correlated with relative humidity (RH) and intercellular CO concentration (Ci); (3) The main determinant factors affecting grape leaf Pn varied by month: transpiration rate was the primary factor in June, August, and September, while stomatal conductance was dominant in July; (4) From June to September, the responses of grape leaf Pn to air temperature, PAR, and VPD all showed a "hysteresis loop" relationship, whereas Pn exhibited strong linear relationships with transpiration rate and stomatal conductance ($R^2 > 0.85$), and an exponential relationship with intercellular CO concentration ($R^2 = 0.53$). These findings demonstrate that grapes possess strong adaptive capacity to the arid environment of Northwest China, and that yield optimization and management can be achieved by controlling transpiration rate and stomatal conductance, though the direct and indirect effects of other factors must also be considered.

Keywords: grape, net photosynthetic rate, physiological-ecological factors, path analysis, hysteresis loop

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Introduction

Photosynthesis is the process by which plants utilize light energy to convert absorbed CO_2 and water into organic compounds while releasing oxygen, representing the fundamental pathway for plant material accumulation and growth production (Xu, 1999; Long et al., 2010). Plant photosynthesis is jointly influenced by internal and external factors, including ecological environmental factors such as photosynthetically active radiation, vapor pressure deficit, air temperature, and atmospheric relative humidity, as well as physiological-biochemical factors like net photosynthetic rate, stomatal conductance, transpiration rate, and intercellular CO_2 concentration (Ma et al., 2018; Liu et al., 2020). Net photosynthetic rate serves as a direct indicator of plant photosynthetic capacity (Liu et al., 2020), and studying its relationship with various physiological-ecological factors holds significant importance for plant cultivation management (Lange et al., 1975).

The Seedless White grape, also known as "Wuhebai," is characterized by its cold, heat, and drought tolerance, making it widely cultivated in regions with large diurnal temperature variations (Tao, 2020). Consequently, it has become one of the primary economic crops in the arid regions of Northwest China. With strong government support, Seedless White grapes have been cultivated in Dunhuang for over 60 years, and the industry has expanded considerably. Currently, the Yangguan area of Dunhuang has 1,333 hectares of Seedless White grapes, accounting for 99% of the irrigated farmland area. Grape harvests have thus become a vital means for local farmers to increase income and improve livelihoods. However, water resource scarcity remains the most prominent local issue. Therefore, a deep understanding of the photosynthetic mechanisms of grapes in this region is crucial for water conservation and effective management of grape cultivation in arid areas. Numerous scholars have studied grape photosynthetic characteristics under controlled conditions such as water stress (Chen et al., 2011; Wang et al., 2014; Hu et al., 2016; Liu, 2020; Sun et al., 2019), temperature stress (Liu, 2007; Luo et al., 2010), and varying nutrient supply (Sun et al., 2017). However, few studies have thoroughly investigated the monthly leaf photosynthetic processes of grapes during the main growing season in Northwest China' s arid regions.

This study examined grapes grown under natural field conditions in the arid region of Northwest China, using a portable photosynthesis-fluorescence measurement system (GFS-3000) to measure leaf photosynthesis and physiological-ecological factors from June to September, the main growing season. The study aimed to address three questions: (1) reveal the diurnal and monthly variation patterns of grape leaf photosynthesis; (2) clarify the relationships between grape leaf Pn and various physiological-ecological factors using path analysis; and (3) analyze the time-lag effects between grape leaf Pn and physiological-ecological factors. The results provide a theoretical basis for scientific cultivation, effective management, and yield improvement of grapes in arid regions.

1.1 Study Area Overview

The experimental site is located in Nanhu Township, southwest Dunhuang City, Gansu Province, at geographic coordinates of 94°07 E, 39°53 N. The region features a typical continental climate within a warm temperate arid zone, characterized by low rainfall, high evaporation, large diurnal temperature variations, and long sunshine duration. The annual average temperature is 9.6 °C, with maximum temperatures reaching 38.3 °C and minimum temperatures dropping to -22.1 °C. Annual precipitation is only 30.7 mm, while potential evaporation reaches 2,486 mm. Annual sunshine duration ranges from 3,115 to 3,247 hours, with total annual radiation of 5,903.4–6,309.5 MW · m ^{2} and a frost-free period of approximately 150 days.

1.2 Experimental Design

In 2019, the study selected the main cultivated grape variety "Seedless White" as the experimental material. The grapevines were 11 years old, grown in a slanted single-cordon trellis system with a height of 2.5 m, plant spacing of 1 m, and row spacing of 3 m. The vineyard soil had a pH of approximately 8, classified as gray-calcic desert soil with a sandy loam texture. Conventional management practices included monthly irrigation, pruning one week before flowering, application of nitrogen fertilizer at approximately 370 kg · hm ^{2} in early May, diammonium phosphate at about 400 kg · hm ^{2} in early June, and compound fertilizer at 370 kg · hm ^{2} in July.

1.3 Measurement Indices and Methods

The observation period covered the typical growing season from June to September, encompassing four growth stages: flowering (June 8–July 3), berry development (July 4–August 10), berry maturation (August 11–September 15), and shoot maturation and leaf senescence (September 16–October 11). Given the region' s long sunshine duration, observations were conducted from 06:00 to 22:00 Beijing time. Under natural field conditions, three grapevines with similar growth vigor were selected and marked. On clear, cloudless days (June 14, June 23, July 16, July 25, August 17, August 28, September 17, and September 23), photosynthesis observations were performed on one leaf from the middle canopy of each of the three grapevines, maintaining the natural leaf angle during measurement. Sample leaves were selected from the middle canopy as healthy, mature, flat, and sun-exposed leaves. Using a portable photosynthesis-fluorescence measurement system (GFS-3000), real-time data were recorded every 10 minutes. Measured parameters included photosynthetically active radiation (PAR), vapor pressure deficit (VPD), air temperature (Ta), relative humidity (RH), net photosynthetic rate (Pn), stomatal conductance (Gs), transpiration rate (T), and intercellular CO concentration (Ci).

1.4 Data Analysis

Path analysis extends correlation and regression analysis by decomposing the relationships between independent and dependent variables into direct and indirect effects (Shi et al., 2019; Wen et al., 2019). IBM SPSS Statistics 25 was used to perform linear regression for path analysis, where the standardized coefficients of the linear regression equation represent direct path coefficients, and indirect path coefficients are calculated as the product of the correlation coefficient between two independent variables and the direct path coefficient of the indirect variable (Du and Chen, 2010; Du, 2012). Decision coefficients can be calculated to determine the comprehensive effect of each independent variable on the dependent variable, ultimately identifying the main determining and limiting variables affecting the dependent variable (Jin et al., 2011). The decision coefficient $R^2(i)$ is calculated using Equation (1), where P is the direct path coefficient of independent variable i, and r y is the correlation coefficient between independent variable i and dependent variable y. Observation data were organized using Microsoft Excel 2010, and all figures were generated in MATLAB R2018a.

$$R^2(i) = 2P_i r_i y - P_i^2$$

2 Results and Analysis

2.1 Diurnal Variation of Ecological Factors Around Grape Leaves in Different Months

Figure 1 shows the diurnal variation characteristics of ecological environmental factors around grape leaves on clear, cloudless days from June to September. PAR exhibited a diurnal pattern of increasing first and then decreasing, with daily maximum values exceeding 1,300 μmol · m ² · s ¹ in all months, reaching approximately 1,800 μmol · m ² · s ¹ in July and August. VPD, which reflects the combined effects of Ta and RH (Yang et al., 2015), showed considerable fluctuation, with monthly daily averages of 3.22, 3.51, 3.07, and 2.64 kPa from June to September, respectively. VPD had lower values around sunrise and sunset, with values after sunset being significantly higher than those before sunrise, primarily because afternoon temperatures in arid regions are higher than morning temperatures, while afternoon humidity is generally lower than morning humidity. The diurnal variation curve of Ta also showed an increase followed by a decrease, with large temperature differences between morning and evening. The daily average temperatures for June through September were 24.75, 26.94, 27.26, and 18.87 °C, respectively. RH displayed a concave valley-shaped pattern with high values in the morning and evening and low values at noon, with peaks occurring around sunrise and sunset. The daily average RH values were 52.05%, 47.72%, 55.34%, and 38.65% for each month. As PAR and Ta increased throughout the day, RH gradually decreased; during midday when PAR and Ta were high, RH remained low and stable, then began to recover as PAR and Ta decreased.

2.2 Diurnal Variation of Grape Leaf Physiological Factors in Different Months

Figure 2 indicates that the diurnal variation of grape leaf Pn in each month followed a single-peak curve, characterized by an increase in the morning and decrease in the afternoon. The daily peak Pn values in June and August occurred around 14:00, at 13.99 and 20.41 μmol · m ^{2} · s ^{1}, respectively. In July, the peak appeared at 13:00 (15.83 μmol · m ^{2} · s ^{1}), while in September it occurred around 12:00 (13.57 μmol · m ^{2} · s ^{1}). The ranking of daily peak values was August > July > June > September. As shown in Figure 3, August had significantly higher daily peak and mean values of grape leaf Pn compared to other months. The ranking of daily mean Pn values was August (9.23 μmol · m ^{2} · s ^{1}) > July (7.41 μmol · m ^{2} · s ^{1}) > June (6.62 μmol · m ^{2} · s ^{1}) > September (5.17 μmol · m ^{2} · s ^{1}). The trends and rankings of daily peak and mean Pn values were consistent across months. The diurnal variation of grape leaf Gs from June to September showed a pattern of increasing first and then decreasing, with daily peaks of 178.64, 182.39, 185.64, and 114.41 mmol · m ^{2} · s ^{1}, respectively. The ranking of daily mean Gs values was August (93.24 mmol · m ^{2} · s ^{1}) > July (77.04 mmol · m ^{2} · s ^{1}) > June (71.26 mmol · m ^{2} · s ^{1}) > September (45.45 mmol · m ^{2} · s ^{1}). The slope of the Gs curve in the morning was greater than in the afternoon, indicating a faster increase in the morning and slower decrease in the afternoon. The diurnal variation curve of T showed a similar trend to Gs, with rapid increase and slow decrease. The ranking of daily mean T values was July (2.63 mmol · m ^{2} · s ^{1}) > June (2.38 mmol · m ^{2} · s ^{1}) > August (2.21 mmol · m ^{2} · s ^{1}) > September (1.53 mmol · m ^{2} · s ^{1}). In contrast, the diurnal variation of Ci showed the opposite pattern to Gs and T, with higher values in the morning and evening and lower, relatively stable values at noon, forming a "U-shaped" curve. The ranking of daily mean Ci values was September (304.14 μmol · mol ^{1}) > August (272.78 μmol · mol ^{1}) > July (264.53 μmol · mol ^{1}) > June (248.53 μmol · mol ^{1}).

2.3 Path Analysis of Grape Leaf Net Photosynthetic Rate and Physiological-Ecological Factors

Correlation coefficients (r) reflect the strength of relationships between two variables. Typically, |r| values between 0.00–0.33 indicate low correlation, 0.33–0.67 indicate moderate correlation, and 0.67–1.00 indicate high correlation. Table 1 shows that from June to September, grape leaf Pn was extremely significantly correlated ($P < 0.01$) with all physiological-ecological factors (PAR, VPD, Ta, RH, Gs, T, and Ci), showing moderate to high correlation levels. Specifically, Pn was positively correlated with PAR, VPD, Ta, Gs, and T, and negatively correlated with RH and Ci. Overall, the correlation coefficients between Pn and both T and Gs exceeded 0.9, followed by Ta, then PAR, RH, VPD, and Ci.

The path analysis results in Table 1 reveal that the ranking of direct path coefficients of physiological-ecological factors on grape leaf Pn varied by month: in June, T > Gs > Ta > PAR > RH > VPD > Ci; in July, Gs > T > VPD > PAR > Ci > RH > Ta; in August, T > Gs > PAR > Ta > RH > Ci > VPD; and in September, T > Gs > Ta > PAR > Ci > RH > VPD. In all months, PAR, T, and Gs exerted direct positive effects on Pn, with T and Gs having greater direct effects than their indirect effects through other factors and greater than the direct effects of other factors, indicating their substantial promoting effect on Pn. Table 1 also shows that for some factors, direct effects were offset by indirect effects through other factors, resulting in substantial changes in correlation coefficients with Pn. For example, in June, July, and August, RH had positive direct effects on Pn, but these were masked by indirect negative effects through other factors, resulting in negative correlation coefficients between RH and Pn, demonstrating the complexity and comprehensiveness of factor interactions.

Furthermore, analyzing the decision coefficients (R^2) of various eco-physiological factors on grape leaf Pn in Table 1 helped identify the main determining and limiting factors for Pn in different months. The factor with the largest decision coefficient was the main determining factor, while factors with small, negative decision coefficients were the main limiting factors (Jin et al., 2011). Analysis of decision coefficient rankings revealed that the primary physiological-ecological factors affecting grape leaf Pn differed by month: the main determining factor was T in June, August, and September, but Gs in July. The main limiting factor was VPD in June, Ta in July, and Ci in August and September, with additional influence from other physiological-ecological factors.

Table 1 Correlation coefficients, path coefficients, and decision coefficients between net photosynthetic rate (Pn) and physiological-ecological factors

Montl	Physiological-ecological factor	Correlation coefficient	Direct path coefficient	Indirect path coefficient	Decision coefficient $R^2(i)$
June	PAR	0.864**	0.947**	-0.802**	0.624**
	VPD	0.976**	0.958**	-0.903**	0.746**
	Ta	0.917**	-0.538**	0.468**	0.973**
	RH	0.979**	-0.605**	0.820**	0.907**
	Gs	-0.735**	0.729**	0.982**	0.958**
	T	-0.781**	0.687**	0.819**	-0.766**
	Ci	0.607**	0.989**	-0.963**	-0.776**
July	PAR	0.864**	0.947**	-0.802**	0.624**
	VPD	0.976**	0.958**	-0.903**	0.746**
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Note: ** indicates extremely significant correlation ($P < 0.01$); * indicates significant correlation ($P < 0.05$).

Analyzing the monthly responses of grape leaf Pn to ecological factors revealed a "hysteresis loop" relationship between Pn and ecological factors Ta, PAR, and VPD (Figure 4, left panel), primarily because the daily peaks of ecological factors lagged behind the peak of Pn in time (Figure 4, right panel). By dividing the daily response process into three stages (06:00–12:00, 12:00–16:00, and 16:00–22:00), we found that in Stage 1, Pn increased with strengthening ecological factors, showing a positive correlation; in Stage 2, Pn decreased despite further strengthening of ecological factors, showing a negative correlation; and in Stage 3, Pn continued to decrease as ecological factors weakened, again showing a positive correlation.

Analysis of the responses of grape leaf Pn to physiological factors showed no hysteresis loop phenomenon with T, Gs, and Ci (Figure 5, left panel), mainly because physiological factors and Pn shared the same trend throughout the day, with their peaks occurring at approximately the same time (Figure 5, right panel). Grape leaf Pn showed linear relationships with both T and Gs, with R^2 values above 0.85, indicating that these two factors can well explain the dynamic variation of grape leaf Pn. In contrast, Pn exhibited an exponential relationship with Ci, with an R^2 of approximately 0.53.

3 Discussion

3.1 Analysis of Grape Leaf Net Photosynthetic Rate Variation

As a fundamental plant function, photosynthesis plays a crucial role in plant growth and development and the global carbon-water cycle (Yu et al., 2004; Linus et al., 2020). The diurnal variation of plant photosynthesis can be generally categorized as single-peak, double-peak, multi-peak, or flat patterns (Wang et al., 2020). Net photosynthetic rate is an important indicator of plant growth and production. In this study, the diurnal variation of grape leaf Pn in Northwest China' s arid region from June to September showed an overall single-peak pattern of increasing then decreasing, without exhibiting photosynthetic "midday depression." This is consistent with previous studies on the photosynthetic characteristics of *Atraphaxis bracteata* and *Apocynum venetum* in arid sandy areas and *Artemisia ordosica* in semi-arid regions (Ning et al., 2014; Li et al., 2015). Generally, photosynthetic midday depression in plants results from two causes: stomatal limitation and non-stomatal limitation (Chandra, 2018). Stomatal limitation refers to the decline in Pn caused by partial stomatal closure that restricts CO diffusion and assimilation under conditions of strong radiation, high temperature, and high vapor pressure deficit, as leaves reduce transpiration to maintain water balance. Non-stomatal limitation involves the decline in Pn due to enhanced photorespiration and photoinhibition resulting from prolonged light energy excess. Regular irrigation of the vineyard (Figure 6) maintained abundant soil water resources, preventing partial stomatal closure under extreme environmental factors. Han (2020) found no photoinhibition in Northwest China' s arid oasis plants in a study on carbon-water coupling mechanisms. Therefore, the grape leaf Pn in this study did not decline due to stomatal or non-stomatal limitations. Instead, Pn increased from morning to noon as radiation intensified and temperature rose, providing basic energy for photosynthesis and activating photosynthetic enzymes, then decreased as radiation and temperature declined.

Changes in environmental hydrothermal conditions and plant growth and development inevitably alter photosynthetic activity (Cheng et al., 2018). From June to August, as suitable environmental temperature and humidity conditions were met and leaf structure and function improved, photosynthesis strengthened. In August, during the berry maturation stage, both the daily peak and mean values of Pn were highest, indicating maximum organic matter accumulation that contributes to grape fruit plumpness and sweetness. By September, as radiation and temperature decreased and leaves gradually senesced, photosynthetic capacity declined. Subsequently, grape leaves turned yellow, gradually fell, and entered dormancy for winter burial to prevent freezing and wind damage.

3.2 Analysis of Relationships Between Grape Leaf Net Photosynthetic Rate and Physiological-Ecological Factors

Under natural conditions, plant photosynthesis is jointly regulated by physiological and ecological factors (Gago et al., 2013). In this study, grape leaf Pn in

Northwest China' s arid region was extremely significantly correlated with all physiological-ecological factors in each month. Path analysis results were generally consistent with correlation analysis, indicating that transpiration rate and stomatal conductance were the most important factors affecting grape leaf Pn variation from June to September, while other factors also exerted direct and indirect effects. This aligns with findings by Diao et al. (2014) that stomatal conductance was the most important factor affecting *Sapindus mukorossi* Pn variation, and with Jiang et al. (2019) reporting that *Rhus chinensis* photosynthesis in different growth periods was mainly affected by stomatal conductance, photosynthetically active radiation, and transpiration rate. As a crucial hub for gas exchange during photosynthesis, stomata directly regulate both Pn and transpiration rate (Medlyn, 2001). Throughout the day, stomata maintain minimal transpiration while maximizing carbon assimilation in response to changing environmental factors, resulting in close interrelationships and mutual constraints.

The relationship between plant Pn variation and physiological-ecological factors has been widely studied (Bassow et al., 1998; Fang et al., 2021), but few studies have examined the relationship between Pn and these factors in different time periods throughout the day. This study found significant differences in grape leaf Pn responses to physiological-ecological factors across different daytime periods, which helps better understand the variation mechanisms of grape leaf Pn under different environmental conditions. The hysteresis loop relationship between grape leaf Pn and ecological factors occurred because in Stage 1, Pn increased with strengthening ecological factors but peaked earlier; in Stage 2, Pn began to decline despite further strengthening of ecological factors; and in Stage 3, Pn continued to decline as ecological factors weakened. The regression slope in Stage 1 was significantly higher than in Stage 3 (Figure 4), indicating that morning Pn was more sensitive to ecological factor changes than afternoon Pn. During Stage 2, air temperature was high (above 30 °C overall), while the optimal temperature for photosynthesis is generally 25-30 °C (Xu, 2021). Excessive temperature can inactivate or denature photosynthetic enzymes and even alter leaf stomatal aperture, preventing grape leaf Pn from continuing to increase with further strengthening of environmental factors. The absence of a hysteresis loop between grape leaf Pn and physiological factors was mainly because stomata synchronously regulate Pn and transpiration rate, resulting in good temporal synchronization and similar variation trends between transpiration rate, stomatal conductance, and Pn. This study conducted a unified analysis of time-lag effects between grape leaf Pn and physiological-ecological factors during the main growing season; future research could conduct more detailed monthly and seasonal analyses to further enhance understanding of plant physiological processes and their relationships with influencing factors.

In summary, the diurnal variation of grape leaf Pn from June to September under natural field conditions showed a single-peak pattern of increasing then decreasing. The ranking of both daily peak and mean Pn values across months was August > July > June > September. Grape leaf Pn was primarily influenced by physiological factors (transpiration rate and stomatal conductance) but also affected by the combined influence of other factors. Therefore, when regulating specific physiological or ecological factors to improve photosynthesis during cultivation, it is essential to consider both the direct effects of the factor itself and its indirect effects through altering other factors. The ecological environment in arid regions is fragile, and scientific management of grape cultivation and production will bring long-term benefits to local farmers.

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