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Response of stomatal conductance, transpiration, and photosynthesis to light and CO_2 for rice leaves with different appearance days

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To investigate the dynamics of stomata, transpiration, and photosynthesis under varying light intensities and CO_2 conditions during leaf development, the light response and CO_2 response of stomatal conductance (g_{sw}), transpiration rate (T_r), and net photosynthetic rate (P_n) were observed for rice leaves at different days after leaf emergence (DAE). The results showed that (1) as photosynthetically active radiation (PAR) increased, leaf g_{sw}, T_r, and P_n initially increased rapidly and linearly, followed by a more gradual rise to maximum values, and then either stabilized or showed a declining trend. The maximum g_{sw}, T_r, and P_n were smaller and occurred earlier for old leaves than for young leaves. The g_{sw}, T_r, and P_n all exhibited a linear decreasing trend with increasing DAE, and the rate of decrease slowed down with the reduction in PAR; (2) as the CO_2 concentration (C_a) increased, g_{sw} and T_r decreased gradually to a stable minimum value, while P_n increased linearly and slowly up to the maximum and then kept stable or decreased. The g_{sw}, T_r, and P_n values initially kept high and then decreased with the increase of DAE. These results contribute to understanding the dynamics in g_{sw}, T_r, and P_n during rice leaf growth and their response to varied light and CO_2 concentration conditions and provide mechanistic support to estimate dynamic evapotranspiration and net ecosystem productivity at field-scale and a larger scale in paddy field ecosystems through the upscaling of leaf-level stomatal conductance, transpiration, and photosynthesis.

KEYWORDS

photosynthetic rate, transpiration rate, stomatal conductance, light response, CO_2 response, leaf with different appearance days

1 Introduction

Stomata play a crucial role in regulating water loss through transpiration and carbon dioxide (CO_2) uptake for photosynthesis, significantly influencing water use efficiency and plant productivity (Lawson and Vialet-Chabrand, 2019). Understanding the responses of stomatal conductance (g_{sw}), transpiration rate (T_r), and net photosynthetic rates (P_n) to environmental factors is essential to assess evapotranspiration and net ecosystem productivity in agroecosystems (Bellasio, 2023; Konieczna et al., 2023; Lv et al., 2024). Research into the intricate dynamics of g_{sw}, T_r, and P_n across different environments improves predictive abilities and refines strategies for water utilization and agricultural optimization, which contributes to developing sustainable agricultural strategies aimed at maximizing productivity while minimizing water consumption (Elfadl and Luukkanen, 2006; Katul, 2023; Wu et al., 2023).

Several factors, including crop canopy structure (leaf area index, leaf tilt angle, etc.), leaf nutrient elements (nitrogen, chlorophyll, etc.), soil water-thermal conditions, and meteorological factors (solar radiation, CO_2 concentration, temperature, atmospheric humidity, etc.), have been widely studied for their influence on leaf g_{sw}, T_r, and P_n (Chen et al., 2011; Xu et al., 2015; Liu et al., 2019). The impact of light and CO_2, as the primary energy source and substrate for plant photosynthesis, on leaf g_{sw}, T_r, and P_n have been extensively studied (Baroli et al., 2008, Li F, et al., 2023, Yi et al., 2023). With increased light intensity and CO_2 concentration, leaf P_n initially increase rapidly and then slowly up to the maximum, followed by a declining trend or a stable state, which have been universally acknowledged on various crops (Kabir et al., 2023). Yu et al. (2004) reported that winter wheat g_{sw} decreases with increased CO_2 concentration and increases with increased light intensity, Marín et al. (2014) stated that tobacco T_r is higher at high than at low light intensities, and Kirschbaum and McMillan (2018) showed that increasing atmospheric CO_2 concentrations reduce canopy transpiration. Additionally, the duration (such as cumulative time, thermal time accumulation, or radiant heat accumulation) after leaf emergence also leads to changes in leaf g_{sw}, T_r, and P_n due to changes in both leaf traits (Legner et al., 2014; Scoffoni et al., 2016; Hirooka et al., 2018) and biomass sink–source relations (Kitajima et al., 2002; Xie and Luo, 2003) along with leaf aging from leaf appearance to senescence—for example, Vos and Oyarzun (1987) reported that potato P_n and g_{sw} decreased at near-saturating irradiance with leaf age, Echer and Rosolem (2015) stated that cotton P_n and g_{sw} decreased in the order of 15-, 30-, 45-, and 60-day-old leaves. Locke and Ort (2014) showed that soybean P_n decreased at a specific light intensity. However, the response of g_{sw}, T_r, and P_n to light and CO_2, respectively, are rarely reported for rice leaves with different durations after emergence.

As the most important staple food crop in the world, the three-dimensional canopy structure of rice, describing the elongation process and spatial distribution of various organs (leaves, leaf sheaths, stems, and panicles), has been widely studied (Watanabe et al., 2005; Song et al., 2013). Temporal leaf evapotranspiration and photosynthesis with detailed 3D representation of canopy architecture are necessary to estimate seasonal variation in evapotranspiration and ecosystem productivity at field-scale and a larger scale in paddy field ecosystems, which are often achieved through the upscaling of leaf-level stomatal conductance, transpiration, or photosynthesis (Van der Zande et al., 2009; Chang et al., 2019; Shi et al., 2019). Measured light-saturated rice P_n reaches a maximum at the fully developed stage and then declines gradually as leaves senesce (Wang et al., 2009) or decreases from the top (young leaves) to the base (old leaves) within the rice canopy (Murchie et al., 2002; Jin et al., 2004). The response of P_n to light and CO_2 also changes as rice leaves age (Xu et al., 2019). Thus, it is well known that g_{sw} and T_r, under different light density and CO_2 concentration conditions, also vary among leaves with various durations after leaf emergence. However, the response of g_{sw} and T_r to light and CO_2 is rarely reported for rice leaves with different durations after leaf emergence.

The southern regions of the Yangtze River constitute the primary rice cultivation area in China (You et al., 2011). Understanding how the duration after leaf emergence affects P_n, g_{sw}, and T_r under different light density and CO_2 concentration conditions is essential to unravel the physiological mechanisms of crop transpiration and photosynthesis and to assess seasonal changes in evapotranspiration and ecosystem productivity under different environmental conditions. Therefore, this study aimed to elucidate and analyze the influence of different days after leaf emergence (DAE) on P_n, g_{sw}, and T_r as well as their quantitative relationships with DAE. This will help to understand the dynamic changes in P_n, g_{sw}, and T_r and provide a reference to clarify the mechanism of transpiration and photosynthesis during the growth process of rice leaves.

2 Materials and methods

The Japonica Rice NJ46 was transplanted with 13 cm × 25 cm hill spacing on July 1, 2017 and harvested on October 26, 2017 in Kunshan, East China (31°15′50″ N, 120°57′43″ E) under field conditions. The rice field extended approximately 200 m in all directions. The region has a subtropical monsoon climate, with average temperature, mean relative humidity, and seasonal precipitation of 25.9°C, 76.9%, and 450.8 mm during the 2017 rice season. Irrigation, fertilizer, and pesticides were applied according to local farming practice (Guo et al., 2017; Li JP, et al., 2023; Lv et al., 2024). To record DAE for subsequent data collection, three latest-emerged leaves on approximately 20 rice plants were tagged at 2-day intervals during tillering, jointing, and booting stages. Using a photosynthesis system (LI- 6800; LI-COR, Lincoln, NE, USA) equipped with a red/blue LED light source (LI-6800–02B) and a charged CO_2 cartridge (CO_2 source), the response of leaf stomatal conductance (g_{sw}), transpiration rate (T_r), and net photosynthetic rate (P_n) to photosynthetically active radiation (PAR) and atmospheric CO_2 concentration (C_a) were measured for tagged leaves at various DAE values at booting and heading stages. The chamber temperature and relative humidity were set as 30°C and 70%, and the measurements were conducted under saturated soil moisture conditions at 8:00–12:00 a.m. on randomly selected sunny days during jointing and heading stages. For the response of g_{sw}, T_r, and

P_n to PAR, the C_a and PAR were set at 400 µmol mol^{-1} (approximate atmospheric CO_2 concentration) and 2,000 µmol m^{-2} s^{-1}, and such a condition was maintained for 15 min for adaptation and stabilization of leaf photosynthesis prior to measurement. Then, leaf g_{sw}, T_r, and P_n were recorded automatically at 120-s intervals at 19 PAR levels (in decreasing order of 2,000, 1,950, 1,900, 1,800, 1,600, 1,400, 1,200, 1,000, 800, 600, 400, 300, 200, 150, 100, 70, 50, 30, and 0 µmol m^{-2} s^{-1}). For the response of g_{sw}, T_r, and P_n to C_a, the C_a and PAR were set at 400 µmol mol^{-1} and 1,600 µmol m^{-2} s^{-1} [slightly lower than saturation light intensity (Xu et al., 2019) to prevent photo inhibition], and leaf g_{sw}, T_r, and P_n were recorded automatically at 120-s intervals at 14 C_a levels (in the order of 400, 300, 200, 100, 50, 400, 400, 500, 600, 800, 1,000, 1,300, 1,500, and 1,800 µmol mol^{-1}) after a 15-min pre-treatment. Totally, 37 response curves to PAR and 24 curves to C_a were measured, evenly distributed across DAE values ranging from 3 to 55.

3 Results

3.1 Light response of stomatal conductance, transpiration, and photosynthesis for rice leaves with different days after leaf emergence

The g_{sw}, T_r, and P_n values were influenced by both the DAE and PAR (Figure 1). Under dark conditions (PAR = 0 µmol m^{-2} s^{-1}), leaves at different DAE maintained relatively low g_{sw} and T_r and negative P_n. As PAR increased, g_{sw}, T_r, and P_n initially exhibited a linear and rapid increase, and then the increase rate (indicated by dg_{sw}/dPAR, dT_r/dPAR, and dP_n/dPAR) gradually slowed down. When PAR reached a certain light intensity (referred to the saturation light intensity for g_{sw}, T_r, and P_n, respectively), g_{sw}, T_r, and P_n reached their maximum values. Subsequently, with further increases in PAR, there was a declining trend (for leaves at DAE lower than approximately 40 days) or a stable state (for leaves at *DAE* higher than approximately 40 days). The g_{sw}, T_r, and P_n, as well as their increase rates with increasing PAR among leaves at different DAE, exhibited similar values under low PAR conditions and showed more pronounced differences as PAR increased.

Both the maximum g_{sw} and its corresponding saturation light intensity decreased with increasing DAE, with older leaves reaching maximum g_{sw} at lower PAR conditions (Figure 1A). The maximum g_{sw} were 0.517, 0.456, 0.394, 0.364, 0.275, and 0.221 mol m^{-2} s^{-1} for leaves at *DAE* of 1–10, 11–20, 21–30, 31–40, 41–50, and 51–60 days. Young leaves (low DAE) maintained high g_{sw}, facilitating photosynthesis and transpiration under high PAR conditions. The light response curves of leaf T_r were distinctly influenced by DAE (Figure 1B). The T_r at specific PAR values, as well as the saturation light intensity when T_r reached the maximum, considerably decreased with increasing DAE. The average P_n values, respectively, were -1.173, -1.141, -0.990, -0.720, -0.519, and -0.462 µmol m^{-2} s^{-1} for leaves at DAE of 1–10, 11–20, 21–30, 31–40, 41–50, and 51–60 days under PAR = 0 µmol m^{-2} s^{-1} conditions (Figure 1C). The negative P_n observed under no-light conditions represented leaf respiration capacity. The decreased absolute value of P_n with increasing DAE implied that the leaf respiration rate attenuated with an increase in DAE, attributable to the exuberant leaf respiration for young leaves. The maximum P_n values were 32.263, 31.959, 27.645, 22.164, 15.676, and 12.582 µmol m^{-2} s^{-1}, respectively, for leaves at DAE of 1–10, 11–20, 21–30, 31–40, 41–50, and 51–60 days. Young leaves sustained high P_n under high PAR conditions and exhibited vigorous physiological growth.

In any PAR condition, leaf g_{sw} linearly decreased with an increase in DAE, and the decrease rate (indicated by the absolute value of the slope of the linear regression line) increased with enhanced PAR (Figure 2). Under PAR of 0 and 100 µmol m^{-2} s^{-1} conditions, DAE had a negligible impact on leaf g_{sw}, and the leaves consistently maintained a lower g_{sw} value. Under PAR of 200, 400, and 800 µmol m^{-2} s^{-1} conditions, the slopes of g_{sw} against DAE were -0.0018, -0.0038, and -0.0057, respectively; the leaf g_{sw} significantly decreased with increasing DAE, and there are noticeable differences in both leaf g_{sw} and the decrease rate among different PAR intensities. Under conditions of PAR higher than 1,200 µmol m^{-2} s^{-1}, the decrease rate in leaf g_{sw} with DAE was approximately 0.007, and leaf g_{sw} ranged from 0.127 to 0.659 mmol m^{-2} s^{-1}. Leaf g_{sw} significantly decreased with increasing DAE, but the differences in both leaf g_{sw} and the decrease rate were less pronounced among different *PAR* intensities.

Consistent with the variation in leaf g_{sw}, leaf T_r linearly decreased with an increase in DAE under any PAR condition, and the decrease rate increased with enhanced PAR (Figure 3). Under PAR conditions lower than 200 µmol m^{-2} s^{-1}, leaf T_r external environmental demand for leaf evaporation is weak, and leaf T_r remains consistently low, with no significant decrease in leaf T_r with increasing DAE. Under PAR intensities of 400, 800, 1,200, 1,600, and 2,000 µmol m^{-2} s^{-1}, leaf T_r respectively ranged from 1.015 to 4.265, 1.724 to 5.359, 1.938 to 7.790, 2.221 to 7.677, and 2.819 to 9.072 mmol m^{-2} s^{-1}, and the slopes of leaf T_r against DAE, respectively, were -0.0325, -0.0464, -0.0666, -0.0771, and -0.0988. Under high PAR conditions (exceeding 400 µmol m^{-2} s^{-1}), leaf T_r significantly decreased, and the decrease rate becomes more pronounced with increasing PAR. Younger leaves can maintain higher T_r under high light conditions to expedite transpirational cooling, enabling the leaves to remain within the optimal temperature range for physiological activities. As the leaves aged, physiological activity decreased, and leaf adaptability to light intensity decreased, resulting in lower T_r under high light conditions.

Under no-light conditions (PAR = 0 µmol m^{-2} s^{-1}), leaf P_n was negative, and P_n linearly increased with DAE (Figure 4). The leaves were unable to perform photosynthesis under zero light intensity, and leaves with low DAE exhibited a stronger metabolic activity, reflected in a higher respiration rate (manifested as negative values). Under a PAR of 100 µmol m^{-2} s^{-1}, leaf P_n remained at approximately 3.6 µmol m^{-2} s^{-1}, with no significant change in leaf P_n with increasing DAE. Under PAR conditions higher than 200 µmol m^{-2} s^{-1}, leaf P_n significantly decreased with increasing DAE, and the magnitude of decrease became more pronounced with enhanced PAR.

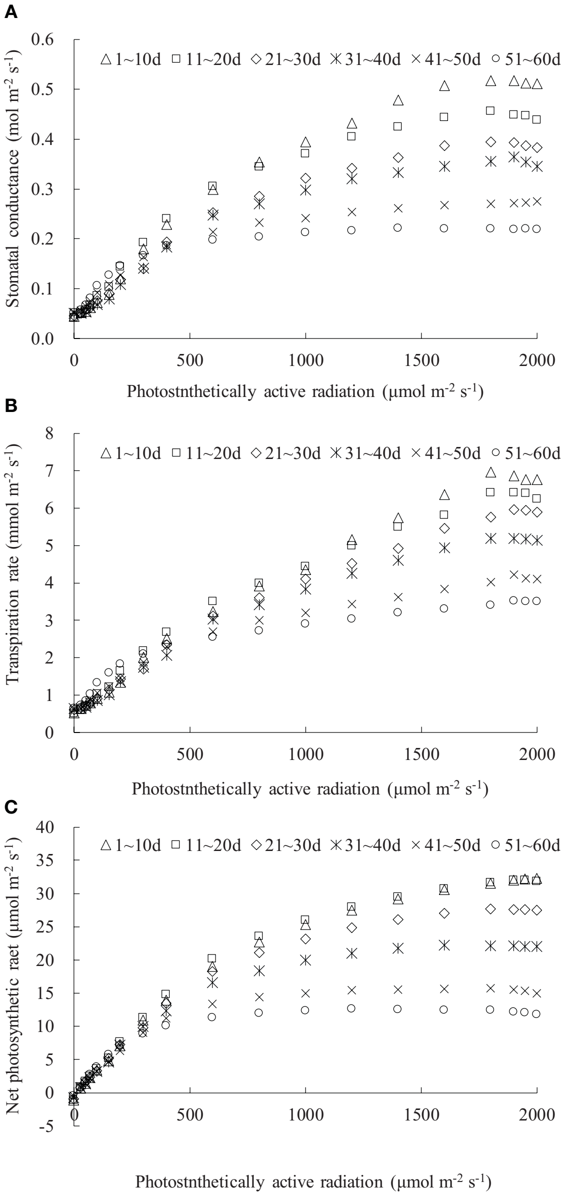

FIGURE 1
(A–C) The light response of stomatal conductance, transpiration rate, and net photosynthetic rate for rice leaves with different ranges of days after leaf emergence ("*m~n* d" in the legend indicates the days after leaf emergence; ranges from *m* to *n*).

3.2 CO_2 response of stomatal conductance, transpiration and photosynthesis for rice leaves with different days after emergence

The C_a considerably influenced g_{sw}, T_r, and P_n in rice leaves (Figure 5). The diffusion of CO_2 from the outside to the inside of the leaf primarily relied on stomata; an increase in C_a led to a reduction in leaf g_{sw}, followed by a decrease in leaf T_r (Figures 5A, B). Leaf g_{sw} and T_r gradually decreased with increasing C_a and DAE, and their decreasing rate slowed down as C_a increased. When C_a increased to approximately 1,500 μmol mol^{-1}, leaf g_{sw} and T_r stabilized at the minimum values. Under the C_a range of 0 to 1,800 μmol mol^{-1}, leaf g_{sw} respectively ranged from 0.103 to 0.693, 0.171 to 0.411, 0.139 to 0.458, 0.133 to 0.404, 0.135 to 0.247, and 0.104 to 0.165 mol m^{-2} s^{-1}, and leaf T_r respectively ranged from 1.426 to 7.895, 2.694 to 5.622, 2.431 to 6.401, 2.423 to 5.912, 2.326 to 3.872, and 1.615 to 2.514 mmol m^{-2} s^{-1} for DAE of 1–10, 11–20, 21–30, 31–40, 41–50, and 51–60 days. Both leaf g_{sw} and T_r decreased with increasing DAE under specific C_a conditions. Leaves at smaller DAE maintained higher g_{sw} and T_r at low C_a, indicating that vigorously growing leaves sustained higher g_{sw} for physiological processes (such as transpiration and photosynthesis) and exhibited robust physiological activity even under low C_a conditions. There was a relatively small difference in leaf g_{sw} and T_r among leaves at different DAE at high C_a concentrations. Leaves with larger DAE (41–50 and 51–60 days) showed limited sensitivity of g_{sw} and T_r to changes in C_a concentration, maintaining consistently lower values regardless of the variations in C_a concentration.

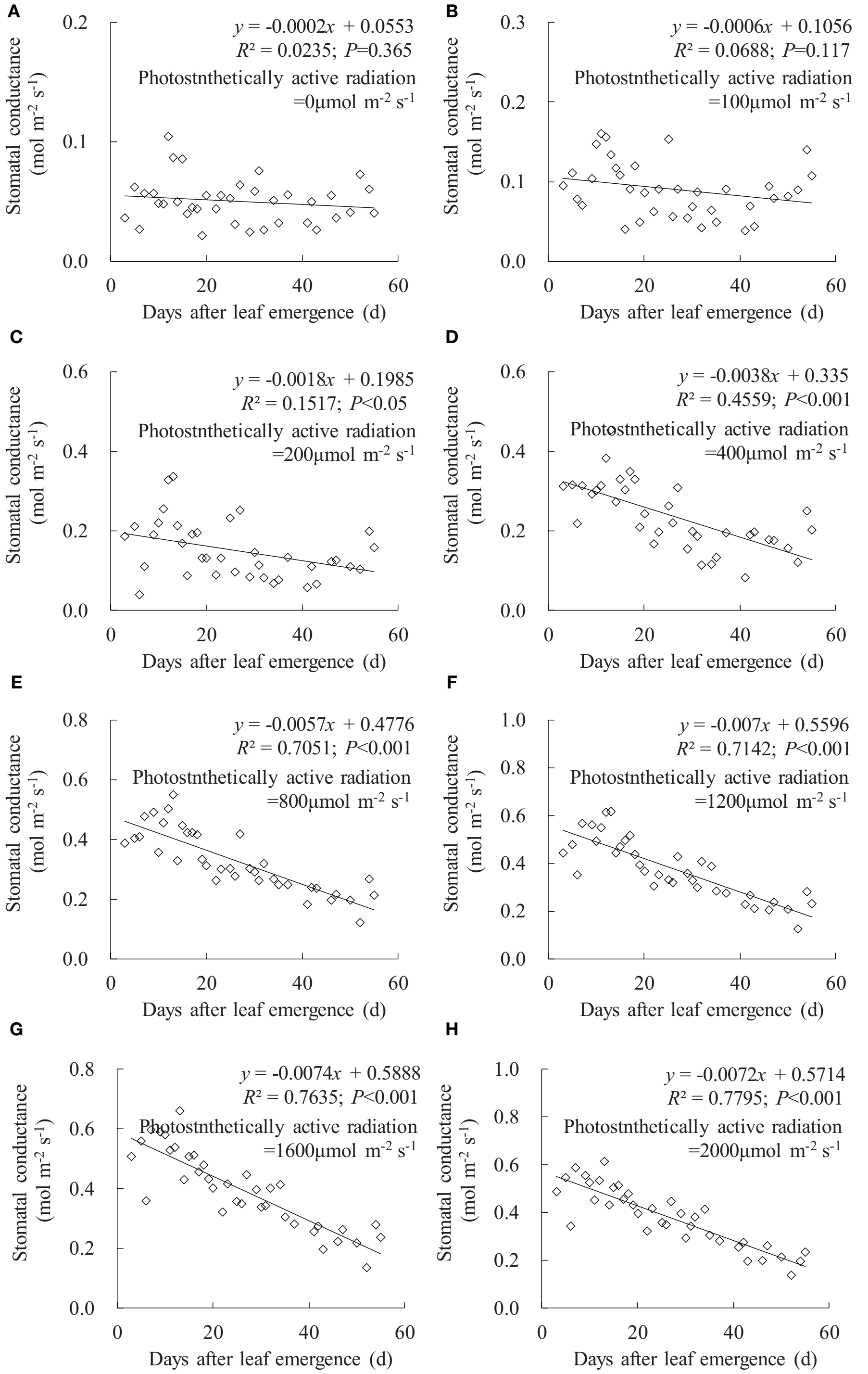

FIGURE 2
(A–H) Impact of days after leaf emergence on stomatal conductance under different photosynthetically active radiation conditions.

The leaf P_n at different DAE exhibited a similar trend with changing atmospheric C_a (Figure 5C). The increase rate of leaf P_n (indicated by dP_n/dC_a) gradually slowed down with increasing DAE. As C_a increased, rice leaf P_n initially increased rapidly in a linear fashion, and the increase rate subsequently decreased, and leaf P_n gradually reached its maximum value, resulting in either a stable or a declining P_n. Under CO_2 concentrations lower than 50 µmol mol^{-1}, leaf photosynthesis was constrained by the available CO_2 concentration; larger stomatal conductance could not compensate for the impact of low CO_2 concentration, resulting in lower leaf photosynthesis than respiration, leading to CO_2 emission (negative P_n values). Within the C_a range of 0 to 1,800 µmol mol^{-1}, leaf P_n ranged from -0.437 to 41.866, -0.419 to 39.614, -0.491 to 40.345, -0.639 to 29.344, -0.485 to 19.135, and -0.504 to 10.657 µmol m^{-2} s^{-1} for DAE of 1–10, 11–20, 21–30, 31–40, 41–50, and 51–60 days, respectively. As DAE decreases, both the peak value of P_n

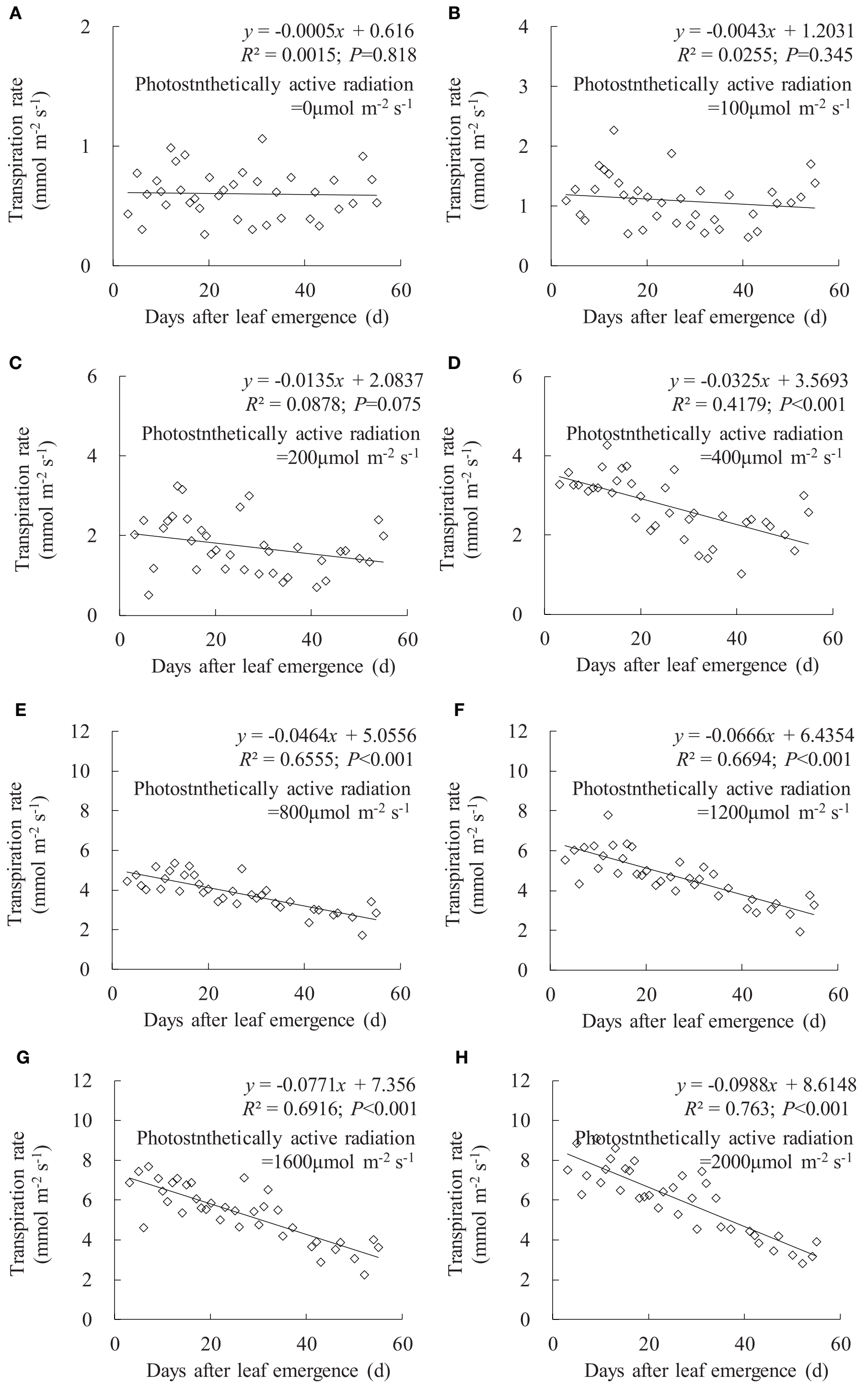

FIGURE 3

(A–H) Impact of days after leaf emergence on transpiration rate under different photosynthetically active radiation conditions.

and the carboxylation rate (the slope of the linear segment) increased, indicating that leaves with smaller DAE possessed a stronger photosynthetic capability.

The relationships between g_{sw}, T_r, and P_n and DAE could be fitted using quadratic regression equations (Figures 6–8). Under C_a of 50, 200, 400, 600, 1,000, and 1,800 μmol mol^{-1}, leaf g_{sw} respectively ranged from 0.132 to 0.535, 0.122 to 0.474, 0.134 to 0.478, 0.129 to 0.390, 0.111 to 0.316, and 0.046 to 0.224 mmol m^{-2} s^{-1}. Leaf g_{sw} decreased along with increasing C_a. As DAE increased, leaf g_{sw} initially remained at higher values and subsequently

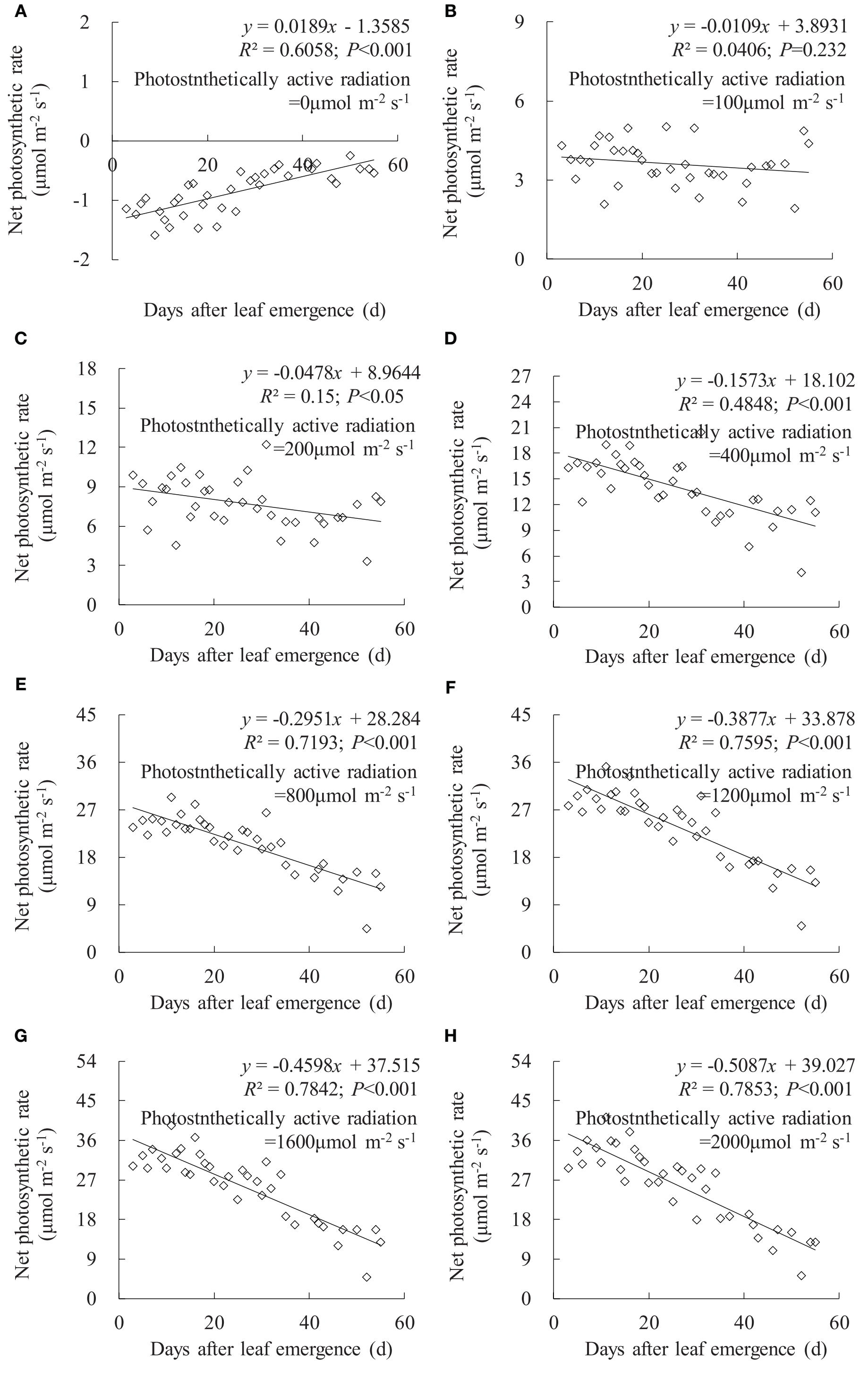

FIGURE 4
(A–H) Impact of days after leaf emergence on net photosynthetic rate under different photosynthetically active radiation conditions.

gradually decreased. Young leaves (small DAE) maintained higher g_{sw} to facilitate physiological activities at low C_a conditions. High CO_2 concentrations (especially at a C_a of 1,800 μmol mol^{-1}) inhibited stomatal aperture, and the leaf g_{sw} at different DAE consistently remained at lower values.

Leaf T_r exhibited a similar trend to leaf g_{sw} (Figure 7). Under C_a of 50, 200, 400, and 600 μmol mol^{-1}, leaf T_r for different DAE respectively ranged from 1.876 to 7.007, 1.743 to 7.810, 1.905 to 6.467, and 1.815 to 6.202 mmol m^{-2} s^{-1}. Leaf T_r decreased with increasing C_a, and rice leaves at small DAE maintained a higher T_r at low C_a. As DAE increased, leaf T_r initially remained at higher values and then gradually decreased. At C_a of 1,000 and 1,800 μmol mol^{-1}, the impact of DAE on T_r diminished, and high CO_2 concentration inhibited stomatal aperture and transpiration.

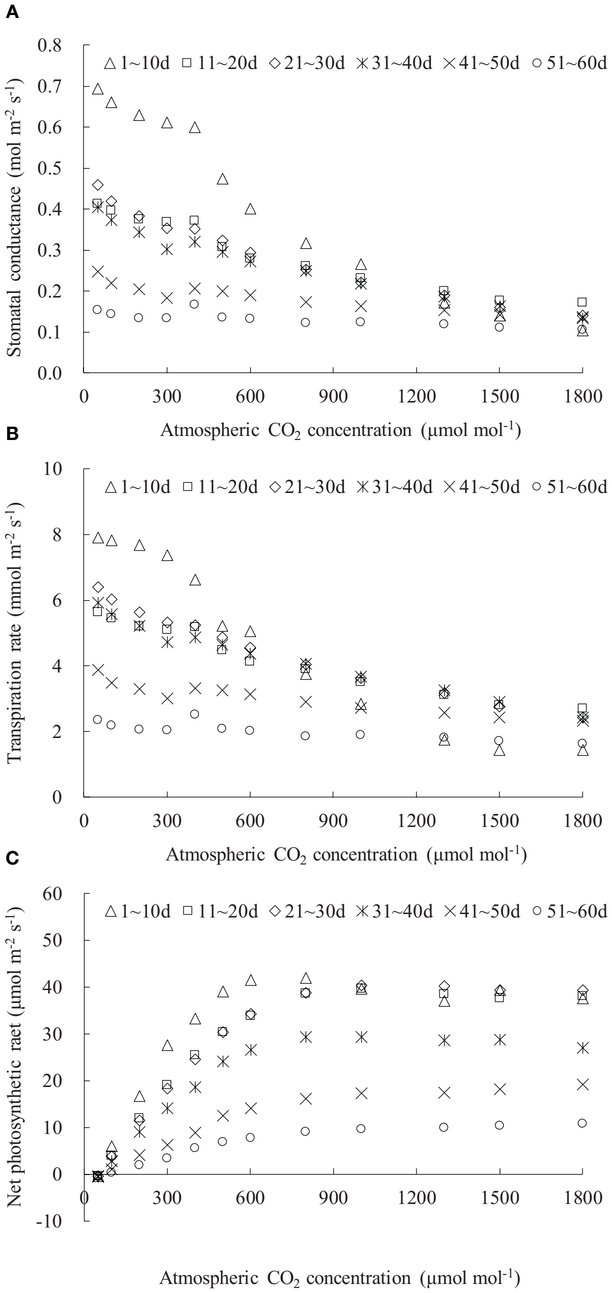

FIGURE 5

(A–C) CO_2 response of stomatal conductance, transpiration rate, and net photosynthetic rate of rice leaves with different ranges of days after leaf emergence ("*m*~*n* d" in the legend indicates the days after leaf emergence; ranges from *m* to *n*).

The variation in leaf P_n with DAE under different C_a is depicted in Figure 8. At C_a of 50 µmol mol^{-1}, the leaf P_n at different DAE consistently remained at approximately -0.5 µmol m^{-1} s^{-1}. This is primarily attributed to the limitation of photosynthetic capacity by low CO_2 concentrations, where leaf respiration exceeded photosynthesis, resulting in CO_2 release. At C_a of 200, 400, 600, 1,000, and 1,800 µmol mol^{-1}, leaf P_n respectively ranged from 1.690 to 13.114, 5.484 to 27.375, 6.694 to 41.858, 8.576 to 47.116, and 9.304 to 47.137. Leaf P_n rapidly increased with rising C_a, reaching its peak at approximately 1,000 µmol mol^{-1} C_a, with no considerable difference between 1,000 and 1,800 µmol mol^{-1} C_a. When C_a exceeded 200 µmol mol^{-1}, leaf P_n remained relatively high at smaller DAE and gradually decreased with further increases in DAE. This indicated that vigorously growing leaves exhibited higher P_n, and leaf photosynthetic capacity decreased as leaves age, leading to a decline in carbon assimilation.

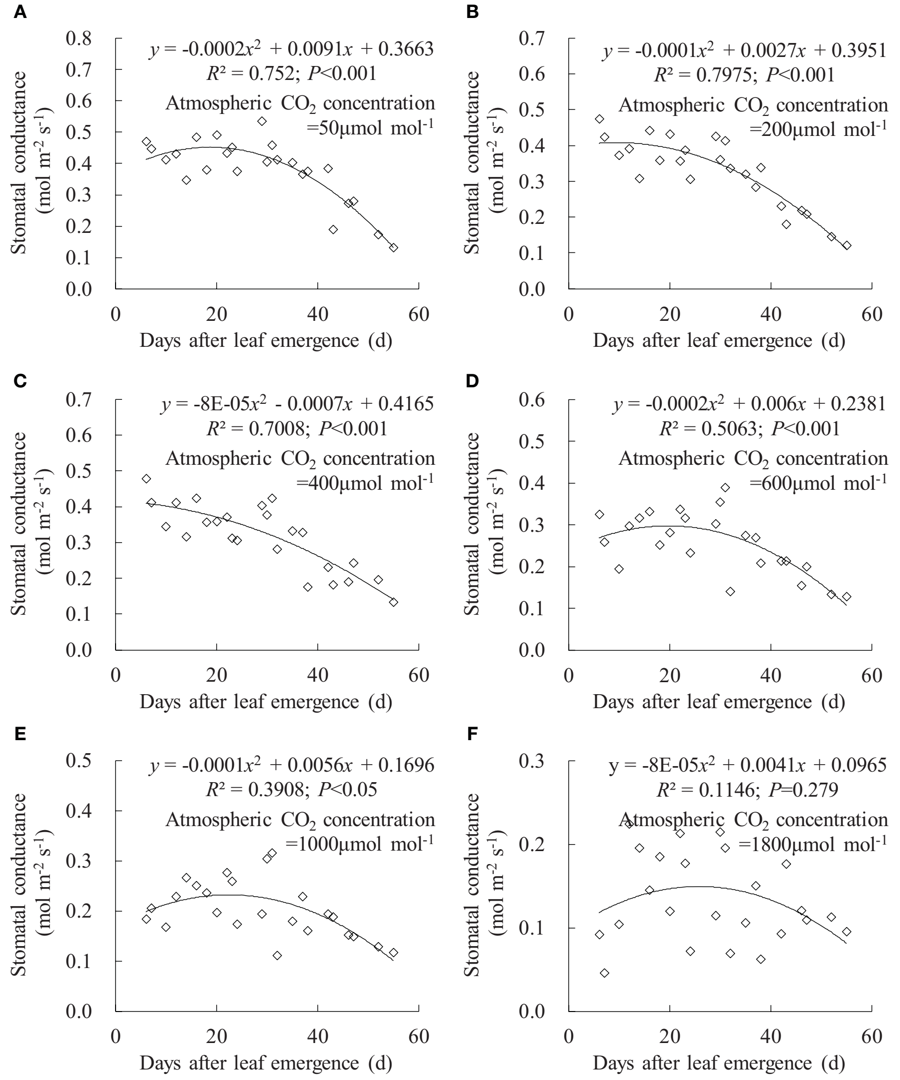

FIGURE 6
(A–F) Impact of days after leaf emergence on stomatal conductance under different atmospheric CO_2 concentration conditions.

4 Discussion

4.1 Effect of days after leaf emergence on the light response

As PAR was enhanced, leaf g_{sw}, T_r, and P_n initially exhibited a linear and rapid increase, followed by a gradual slowdown in the increase rate, eventually reaching a maximum value and then stabilizing or slightly decreasing thereafter (Figure 1). Similar trends have been observed in the flag leaves of winter wheat (Inoue et al., 2004; Carmo-Silva et al., 2017). Under no-light conditions *(PAR* = 0 μmol m^{-2} s^{-1}), the leaves were unable to undergo photosynthesis, resulting in metabolic CO_2 emission (with leaf P_n showing as a negative value). Leaves at smaller DAE released more CO_2 due to their vigorous metabolic activity (Pantin et al., 2012). Under low-light conditions, limited atmospheric evaporative capacity and insufficient PAR for photosynthesis led to lower g_{sw}, T_r, and P_n regardless of the variations in DAE. As PAR intensified, leaf stomatal opening widened, leading to an increase in g_{sw}. Larger stomatal apertures allowed a greater influx of CO_2 (providing an ample supply for leaf photosynthesis) and output of water vapor through the stomata; thus, leaf P_n and T_r increased. Simultaneously, the increased atmospheric evaporative capacity caused by enhanced PAR also resulted in higher T_r. Leaves with larger DAE reached the light saturation point earlier, and g_{sw}, T_r, and P_n, under saturated light conditions, decreased with increasing DAE, suggesting that young leaves could maintain larger stomatal apertures for efficient transpiration and photosynthesis under high light intensity (high T_r and P_n). As the leaves aged, their adaptation to high light weakened, and leaves with larger DAE could not fully utilize high light intensity for photosynthesis.

Under a specific PAR condition, g_{sw}, T_r, and P_n showed a consistent linear decrement with the increase in DAE (Figures 2–4). This finding was congruent with the decline in g_{sw} and P_n with potato leaf senesced (Vos and Oyarzun, 1987). Echer and Rosolem (2015) also asserted that cotton leaf DAE had nominal impact on leaf P_n under low PAR, while P_n was notably higher in 15- and 30-day-old

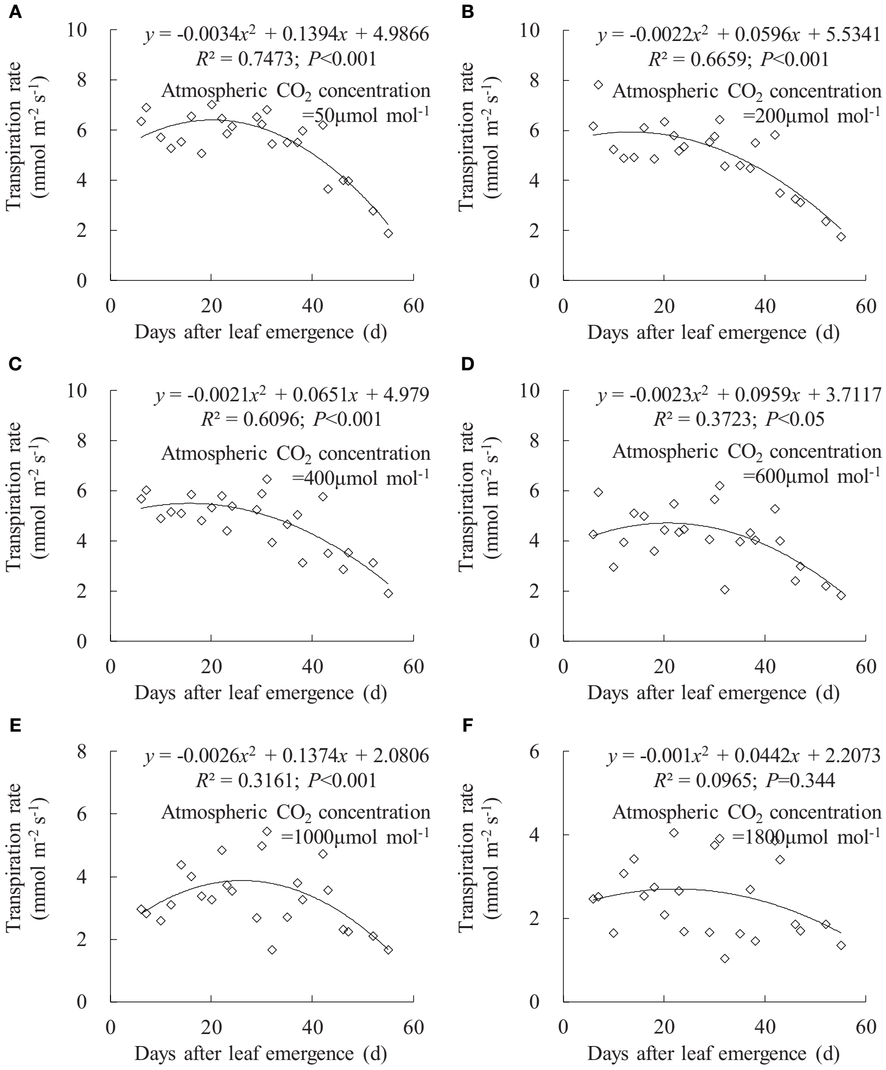

FIGURE 7
(A–F) Impact of days after leaf emergence on transpiration rate under different atmospheric CO_2 concentration conditions.

leaves compared to 45- and 60-day-old leaves when PAR exceeded a threshold, with both T_r and g_{sw} reduced as the leaves aged and the light intensity waned. Hossain et al. (2007) and Jin et al. (2004) reported that rice g_{sw}, T_r, and P_n, at particular PAR, decreased significantly with lowering leaf position, which was consistent with the current research, as newly emerged rice leaves appeared in the upper canopy, implicating a reduction in leaf DAE as leaf position decreased. Generally, rice leaf photosynthesis was highly related to leaf nitrogen level, efficiencies of radiant energy utilization, electron transport, and photophosphorylation, and these values decreased with leaf aging (or downward leaves) (Murchie et al., 2002; Suzuki et al., 2009; Okami et al., 2016; Yang et al., 2016), which also agreed with the decreased P_n. In contrast, Wang et al. (2009) reported that the measured light-saturated rice g_{sw}, T_r, and P_n reached the maximum at the last second fully developed leaf and then declined gradually in downward leaves at nine-leaf age (an indicator representing the developmental progress of plants) stage (tillering stage correspondingly). Xu et al. (2019) also stated that light-saturated rice P_n peaked at around 10 days after leaf emergence and then decreased as leaves aged. The discrepancy with the current study might be attributed to low-frequency measurement for photosynthetic characteristics under smaller DAE, as the measurement was inconvenient due to the small leaf area before they were fully expanded. Additionally, the measurement in the current study began at DAE of 3 days, at which time the leaves had a large leaf area. Consequently, the study did not monitor the increase in leaf g_{sw}, T_r, and P_n during the leaf expansion process.

4.2 Effect of days after leaf emergence on the CO_2 response

As C_a increased, leaf g_{sw} and T_r gradually decreased, while P_n increased linearly and rapidly, and the amplitude of variations in g_{sw}, T_r, and P_n decelerated, eventually leading to a stabilization of minimal g_{sw} and T_r and an elevation of P_n to its peak, subsequently maintaining stability or experiencing a slight decline (Figure 5). Yasutake et al. (2016) found that 1,000 µmol mol^{-1} C_a significantly increased sweet pepper P_n but decreased g_{sw} and T_r compared with 400 C_a. Ahmed et al. (2022) reported that P_n increased and g_{sw} and T_r decreased in the order of 500, 1,000, and 1,500 µmol mol^{-1} C_a. This was consistent with the decreased g_{sw} and T_r and increased P_n with leaf aging observed in the current study. Inamoto et al. (2022) showed that the increase in Oriental Hybrid Lily P_n was greater in the low C_a range (380 to 1,000 µmol mol^{-1}) and lower in the high C_a range (1,000 to 2,000 µmol mol^{-1}), which agreed with the amplitude of variations in P_n.

Under specific C_a, the leaf g_{sw}, T_r, and P_n remained at a relatively high level when DAE was less than approximately 25 days and then gradually decreased with the further increase in DAE (Figures 6, 7, 8). Chlorophyll activity, Rubisco activity, RuBP regeneration capacity, and nitrogen content (positively correlated with the photosynthetic potential of leaves) generally exhibited an increasing trend during the leaf expansion phase, followed by the maintenance of relatively high values, and then decreased as the leaves aged (Murchie et al., 2002; Suzuki et al., 2009; Gunasekera et al., 2013), which might be the primary reasons for the variation in g_{sw}, T_r, and P_n. At lower C_a concentrations, leaves at a smaller DAE maintained higher g_{sw} to facilitate atmospheric CO_2 entering for transpiration and photosynthesis. Leaves at a greater DAE had weaker adaptability to external environments, maintaining lower levels of g_{sw}, T_r, and P_n regardless of C_a level. When C_a exceeded a certain level, C_a exerted a suppressive effect on stomatal conductance to reduce transpiration, but the photosynthetic rate did not decrease.

5 Conclusions

This study investigated the dynamics of stomatal conductance g_{sw}, transpiration rate T_r, and net photosynthetic rate P_n in rice leaves across

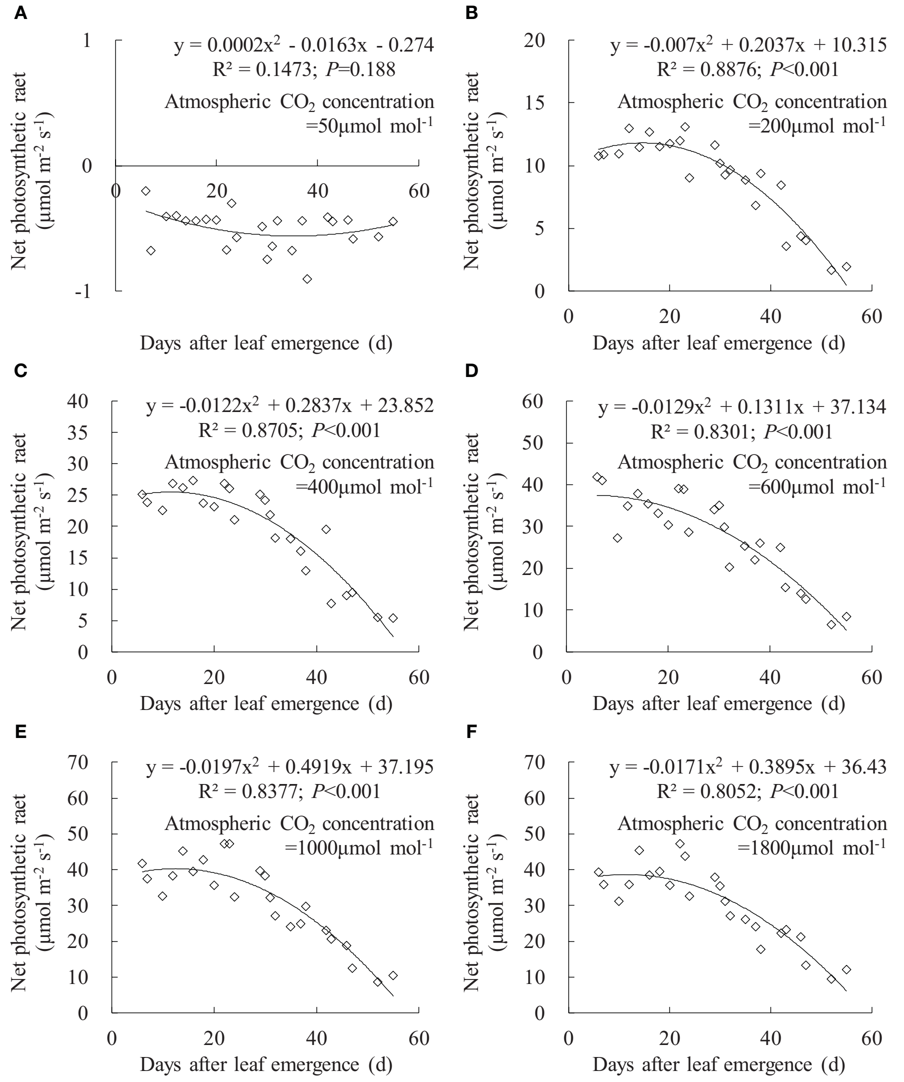

FIGURE 8
(A–F) Impact of days after leaf emergence on net photosynthetic rate under different atmospheric CO_2 concentration conditions.

varying light intensities and CO_2 conditions during leaf development. The key conclusions drawn from the findings are as follows:

(1) Response to photosynthetically active radiation PAR: Increasing PAR led to an initial rapid and linear increase in g_{sw}, T_r, and P_n, followed by a more gradual rise to maximum values, with subsequent stabilization or decline. Notably, old leaves reached their maximum g_{sw}, T_r, and P_n earlier and at smaller magnitudes compared to young leaves. Additionally, a linear decreasing trend in g_{sw}, T_r, and P_n with increasing DAE was observed, with the decrease rate slowing down with reduced PAR.

(2) Response to atmospheric CO_2 concentrations C_a: With increasing C_a, g_{sw} and T_r decreased gradually to a stable minimum value, while P_n exhibited a linear and slow increase up to a maximum before stabilizing or decreasing. Under specific C_a conditions, rice leaf g_{sw}, T_r, and P_n initially remain at higher values and then gradually decrease with increasing DAE.

These conclusions provided crucial mechanistic insights to estimate dynamic evapotranspiration and net ecosystem productivity at both field-scale and larger scales in paddy field ecosystems by upscaling leaf-level physiological processes. This knowledge can inform more accurate predictions and management strategies to optimize agricultural practices and enhance the sustainability of rice cultivation amidst changing environmental conditions.

Data availability statement

The datasets presented in this article are not readily available because the authors do not have permission to share data. Requests to access the datasets should be directed to YL, lvyuping@yzu.edu.cn.

Author contributions

YL: Conceptualization, Funding acquisition, Writing – original draft. LG: Investigation, Writing – original draft. RM: Formal analysis, Validation, Writing – review & editing. XL: Writing – review & editing. JX: Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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