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Effect of elevation on photosynthesis of young mango (*Mangifera indica* L.) trees

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Abstract

Anticipating warming related to climate change, commercial mango plantations in China have been shifting from lower to higher elevations. Such a practice may expose mangoes to climatic conditions that could affect photosynthesis. Photosynthesis research on mango has previously examined mature plantations but exploring adequate functions before the time of fruit production is necessary for later crop success. Therefore, we established two main commercial mango cultivars, Tainong No. 1 and Jinhuang, at 450 m and 1,050 m and examined their photosynthetic performance. Our results showed that photosynthetic capacity parameters, including maximum photosynthetic rate, apparent quantum yield, maximum carboxylation rate, and photosynthetic electron transport rate, were significantly different between cultivars due to elevation and positively correlated with leaf nitrogen per area. Moreover, the seasonal gas exchange of the two cultivars showed variations due to elevation, particularly during the warmer seasons. Therefore, elevation affects the photosynthetic performance of these mango cultivars.

Keywords: cultivar; elevation; gas exchange; leaf nitrogen; mango; photosynthesis.

Introduction

Mango (*Mangifera indica* L.) is economically the most important tropical fruit tree (Morton 1987, FAO 2002, 2020), and China is the second largest mango-producing country in the world (FAO 2020). Currently, the country commercially grows more than ten mango cultivars, with Tainong No. 1 and Jinhuang being among the most common cultivars (Gao *et al.* 2019). Cultivar Tainong No. 1 (Haden × Irwin) was originally from Taiwan (Li *et al.* 2013a, Wang *et al.* 2015, Gao *et al.* 2019). Jinhuang (Nang Klang Wan × Keitt) is a polyembryonic cultivar and was originally from China (Luo *et al.* 2012, Wang *et al.* 2015). In the past two decades, commercial mango cultivation has been significantly expanding in the southern part of the country (Gao *et al.* 2011, 2019). Yunnan is one of the

Highlights

- Photosynthesis performance of mango is affected by elevation
- Cultivar Tainong No. 1 showed a higher photosynthesis performance at a higher elevation than Jinhuang
- Leaf nitrogen content has a strong positive relationship with photosynthesis capacity

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Abbreviations: AQY – apparent quantum yield; CD – cold-dry; C_i – intercellular CO_2 partial pressure; E – transpiration rate; g_s – stomatal conductance; HD – hot-dry; J_{max} – photosynthetic electron transport rate; LMA – leaf mas per area; N_a – leaf nitrogen per area; N_m – total nitrogen; P_N – net photosynthetic rate; P_{Nmax} – maximum photosynthetic rate; P_{Nsat} – light-saturated net photosynthetic rate; RM – recently matured leaf; T_{leaf} – leaf temperature; V_{max} – maximum carboxylation rate; VPD – vapor pressure deficit; WW – warm-wet.
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provinces where this expansion has been occurring (Gao *et al*. 2019).

Anticipating warming related to climate change, mango plantations in the country have been consistently shifting from lower to higher elevations (Gao *et al.* 2011, 2019). However, establishing mango plantations at higher elevations could expose trees to climatic conditions that could affect photosynthesis and other related processes (Kingston-Smith *et al.* 1997, Jung *et al.* 1998). The effect of elevation on photosynthesis has been attributed to decreases in air partial pressure of CO_2 as elevation increases (Sakata and Yokoi 2002, Vats and Kumar 2006), whereas its influences on stomatal conductance and transpiration are principally attributed to air temperature and vapor pressure deficit (VPD) (Gale 2004, Körner 2007, Motzer *et al.* 2017, Mujawamariya *et al.* 2018). However, studies on the effects of elevation on photosynthesis of tropical plants have not shown consistent trends (Friend *et al.* 1989, Cordell *et al.* 1999, Kao and Chang 2001, Zhang *et al*. 2005, Premoli and Brewer 2007, Wittich *et al.* 2012, Zhang and Yin 2012, Motzer *et al.* 2017, Mujawamariya *et al.* 2018).

Field and greenhouse studies on mango have revealed that temporary exposure to suboptimal temperatures caused inhibition of light-saturated photosynthetic assimilation (Allen *et al*. 2000, Allen and Ort 2001). Moreover, depending on the cultivar used, the degree of chilling could negatively impact photosynthesis (Whiley 1993, Allen and Ort 2001, Elsheery *et al.* 2007, 2008; Elsheery and Cao 2008, Damour *et al*. 2009, Normand *et al.* 2015). In addition, previous studies on mango concerning climatic factors largely focused on flowering and fruit production (Rajan 2011, Mathur *et al.* 2012, Normand *et al.* 2015). However, fruit production requires the survival of young trees under climatic conditions in production areas. Once mango plantations are established, only a few modifications can be implemented (Mathur *et al.* 2012). Mangoes also need at least four to five years before reaching optimum fruit production (Rajan 2011, Mathur *et al.* 2012). Therefore, investigating the photosynthetic performance of young mangoes in response to elevation can be a useful tool in predicting the suitability of given commercial mango cultivation at higher elevations. Consequently, this information will contribute to future planting decisions.

Moreover, studies on pre-fruiting mango trees primarily focus on the vegetative growth of plants (Whiley *et al.* 1989, Luvaha *et al.* 2008, Mng'omba *et al.* 2010, Pinto *et al.* 2018). A few studies of gas exchange at this stage have been conducted under controlled conditions (Allen *et al*. 2000, Allen and Ort 2001, Luvaha *et al.* 2007). Overall knowledge of mango field performance in the years before first fruiting is limited, potentially impacting the selection of suitable cultivars for a given site. In this study, we established plots with three-year-old mango cultivars Tainong No 1 and Jinhuang that exhibit locally high fruit production. We planted them at the same elevation currently used locally for mango production as well as at a higher elevation in anticipation of future plantation shifts. We examined photosynthetic performance before first fruiting. We hypothesized that the photosynthetic performance of mango cultivar Tainong No. 1 could be higher at the higher elevation (1,050 m), while the reverse could be true for the cultivar Jinhuang.

Materials and methods

Site description: The study was conducted on two north-facing plots established at elevations of 450 and 1,050 m above sea level (a.s.l.) located between longitude and latitude of 23°25.575'N, 102°15.845'E and 23.40839°N, 102.24649°E, respectively, Honghe County, Yunnan Province, China. Climatic data were retrieved from microclimate stations installed nearby (ca. 20 m) to study plots at both elevations (Fig. 1).

Seedling growth conditions: All subsequent gas-exchange measurements were conducted on three-year-old, local mango cultivars, namely, Tainong No. 1 and Jinhuang. Trees were planted at 450 and 1,050 m a.s.l. with 5 × 5-m spacing on plots with similar soil properties. During the study period, trees were free of shade, irrigated, and fertilized according to local commercial farming practices.

Response of net photosynthesis to PPDF: Net photosynthetic rate (P_N) in response to PPFD was measured on two sun-exposed, recently matured leaves of three replicate trees ($n = 2 \times 3$) per cultivar per elevation. The photosynthesis system (*Li-Cor 6400xt*, USA) was adjusted at series of PPFD of 2,000; 1,800; 1,500; 1,200; 1,000; 800, 600, 500, 400, 300, 200, 150, 100, 50, and 0 μmol m^{-2} s^{-1}, and at a constant CO_2 concentration of 360 μmol mol^{-1}, flow of 500 μmol s^{-1}, and T_{leaf} at 25°C. P_N–PPFD response curve for each leaf was fitted according to Marshall and Biscoe (1980). Maximum photosynthetic rate (P_{Nmax}) and apparent quantum yield (AQY) were derived from the P_N–PPFD response curves. P_N–PPFD measurements were conducted from 8:30–11:30 h local time from 20–23 February 2019.

Response of net photosynthesis to internal CO_2 concentration: Net photosynthetic rate (P_N) in response to internal CO_2 (C_i) at each elevation was measured on two sun-exposed, recently matured leaves of three replicate trees ($n = 2 \times 3$) per cultivar per elevation. The photosynthesis system (*Li-Cor 6400xt*, USA) was adjusted at series of CO_2 concentrations of 400, 300, 200, 100, 50, 400, 600, 800; 1,000; 1,200; 1,800; and 2,000 μmol mol^{-1}, at a constant PPFD of 1,000 μmol m^{-2} s^{-1}, flow of 300 μmol s^{-1}, and T_{leaf} at 25°C. P_N–C_i response curve for each leaf was fitted according to Sharkey *et al.* (2007). Photosynthesis capacity parameters, including maximum carboxylation rate (V_{max}) and photosynthetic electron transport rate (J_{max}) were derived from the P_N–C_i curves. P_N–C_i measurements were conducted from 8:30–11:30 h local time from 24–27 February 2019.

Light-saturated gas exchange: The effect of elevation on seasonal light-saturated gas exchange was assessed at PPFD of 1,000 μmol m^{-2} s^{-1}, and a CO_2 concentration of

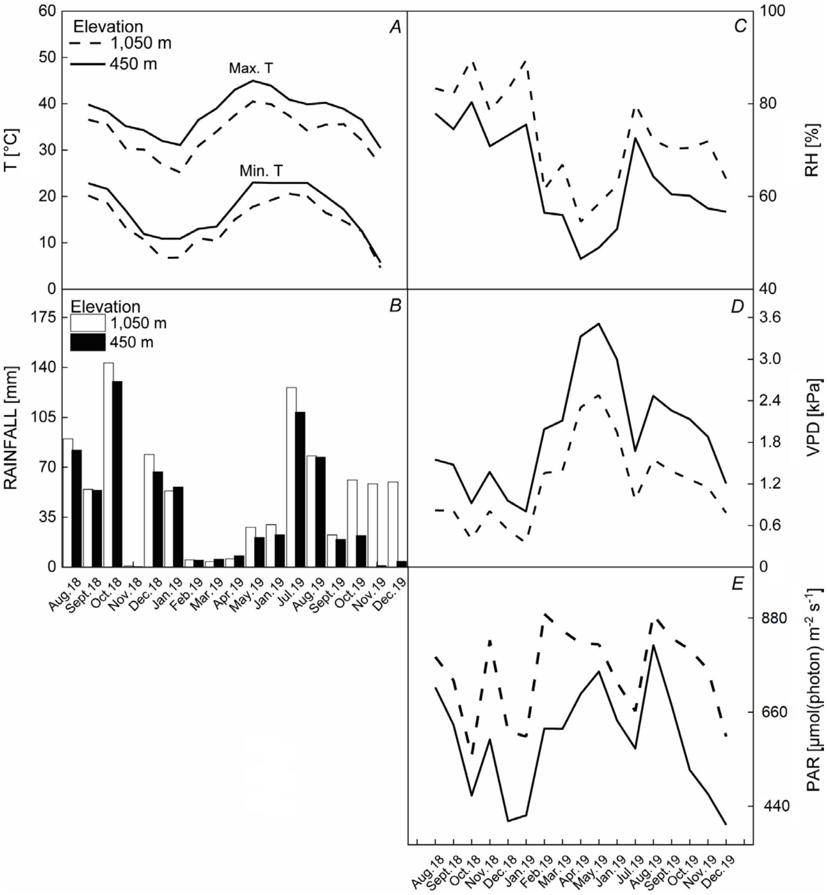

Fig. 1. Monthly maximum and minimum air temperature (T) (*A*); mean monthly rainfall (*B*); relative humidity (RH) (*C*); vapor pressure deficit (VPD) (*D*); and daytime photosynthetically active radiation (PAR) (*E*) during the study period.

360 µmol mol^{-1}. Measurements at the two elevations were carried out on four healthy, sun-exposed, recently matured (RM) leaves on four replicate trees ($n = 4 \times 4$) per cultivar per elevation, for a total of nine days to represent the hot-dry (HD) season (19–21 April 2019), warm-wet (WW) season (17–19 July 2019), and cold-dry (CD) season (15–17 December 2019). Gas-exchange measurements were carried out using a portable photosynthesis system (*Li-Cor 6400xt*, USA) between 8:00 to 11:30 h local time.

Leaf structural traits and nitrogen content: To examine the relationship between photosynthesis capacity with leaf nitrogen content, leaves used for P_N–PPFD and P_N–C_i curves were harvested at the end of the experiment. Leaves were brought to the lab, and leaf area was measured using a leaf area meter (*Li-Cor 3001A*, USA). Then, dry mass was determined after leaves were oven-dried at 70°C for 48 h, and LMA was calculated by dividing leaf dry mass by one-side leaf areas. Then, each leaf excluding the midrib was ground individually using mortar and pestle and sieved using No. 100 mesh. Total nitrogen (N_m) was analyzed twice from 5-mg subsamples using (*Vario MICRO* cube, Germany). Nitrogen per unit area (N_a) was calculated as total nitrogen (N_m) × leaf mass per unit area (LMA).

Data analysis: Data are presented as the mean (± SE) of photosynthesis parameters. *T*-test was performed to test whether means were statistically significant using *Statistix version 8.1* at $p \leq 0.001$, $p \leq 0.01$, and $p \leq 0.05$. Linear regression was used to detect the relationship between photosynthesis capacity parameters, including maximum carboxylation rate (V_{max}), photosynthetic electron transport rates (J_{max}), apparent quantum yield (AQY), and maximum photosynthetic rate (P_{Nmax}) derived from P_N response to light and CO_2 curves to leaf nitrogen per area (N_a). *OriginPro 2021*, *version 9.8.0.2* was used for curve fitting and plotting.

Results

Elevation affected the maximum carboxylation rate (V_{max}) and photosynthetic electron transport rate (J_{max}) of both mango cultivars. Cultivar Tainong No. 1 showed significantly higher V_{max} and J_{max} compared to cultivar Jinhuang at 1,050 m. However, at 450 m, cultivar Jinhuang showed significantly higher V_{max} and J_{max} compared to cultivar Tainong No. 1 (Fig. 2).

Elevation influenced the apparent quantum yield (AQY) and maximum photosynthetic rate (P_{Nmax}) of both mango cultivars. Cultivar Tainong No. 1 showed significantly higher AQY and P_{Nmax} compared to cultivar Jinhuang at 1,050 m. However, cultivar Jinhuang showed significantly higher AQY and P_{Nmax} compared to cultivar Tainong No. 1 at 450 m (Fig. 3).

Photosynthesis capacity parameters of mango cultivars Tainong No. 1 and Jinhuang including apparent quantum

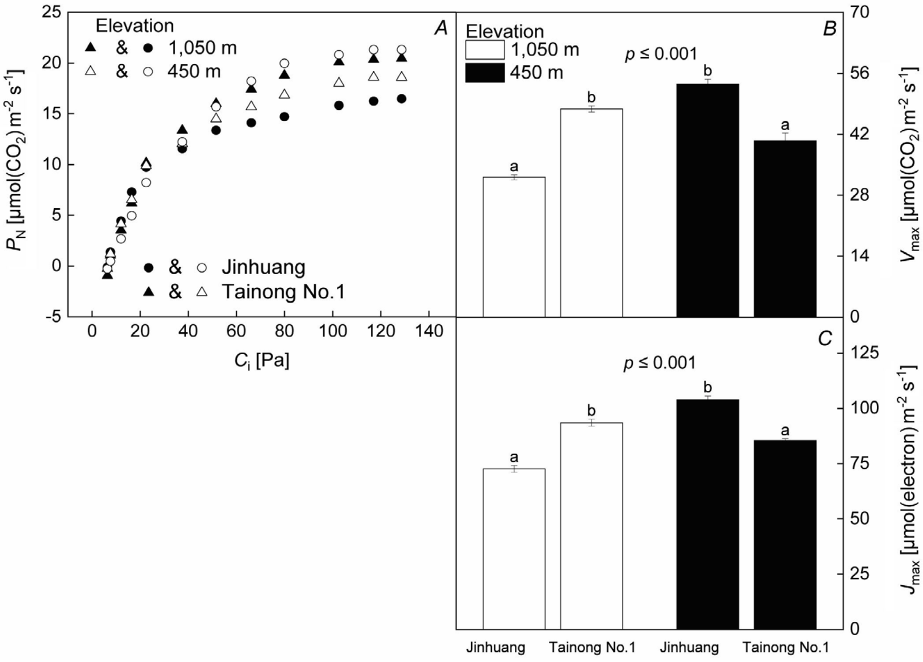

Fig. 2. Net photosynthetic rate (P_N) in response to internal CO$_2$ partial pressure (C_i) (P_N–C_i) (*A*); maximum carboxylation rate (V_{max}) (*B*); and photosynthetic electron transport rate (J_{max}) (*C*) of mango cultivars Tainong No. 1 and Jinhuang grown at 1,050 m and 450 m. Mean ± SE. *Different letters* indicate the difference between means is statistically significant at $p \leq 0.001$.

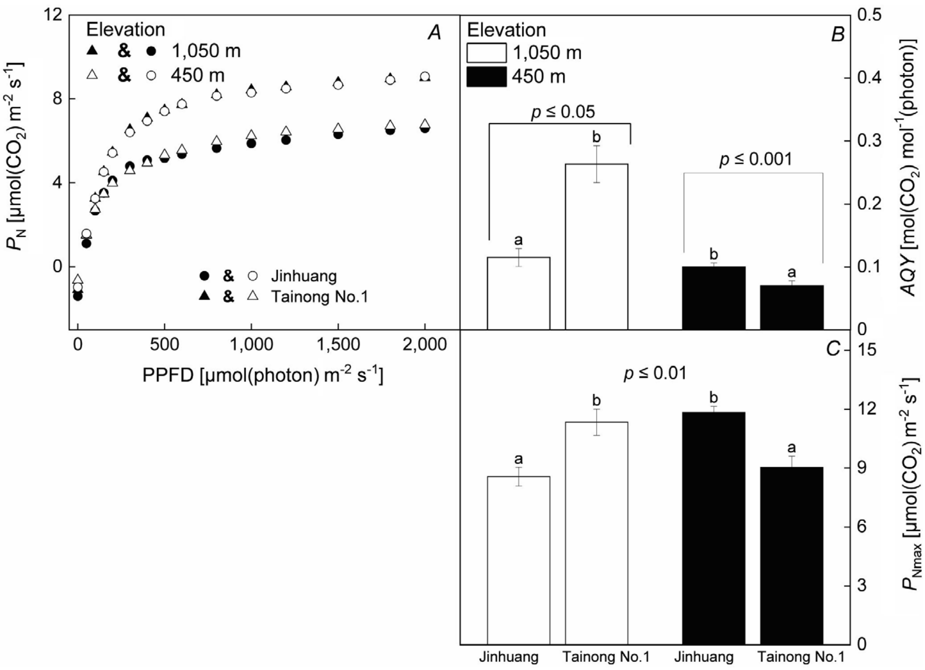

Fig. 3. Net photosynthetic rate (P_N) in response to photosynthetic photon flux density (PPFD) (P_N–PPFD) (*A*); apparent quantum yield (AQY) (*B*); and maximum photosynthetic rate (P_{Nmax}) (*C*) of mango cultivars Tainong No. 1 and Jinhuang grown at 1,050 m and 450 m. Mean ± SE. *Different letters* indicate the statistically significant difference between means.

yield (AQY) (R^2 = 0.88, 0.54, 0.88, 0.54) (Fig. 4*A*,*B*), maximum photosynthetic rate (P_{Nmax}) (R^2 = 0.86, 0.86, 0.73, 0.98) (Fig. 4*C*,*D*), maximum carboxylation rate (V_{max}) (R^2 = 0.91, 0.8, 0.81, 0.84) (Fig. 4*E*,*F*), and photosynthetic electron transport rate (J_{max}) (R^2 = 0.89, 0.84, 0.88, 0.95) (Fig. 4*G*,*H*) at both 1,050 m and 450 m showed positive linear relationships with leaf nitrogen per area (N$_a$). Moreover, the total leaf nitrogen (N$_m$) content of the cultivars Tainong No.1 and Jinhuang was significantly higher at 1,050 m compared to 450 m ($p<0.001$) (Fig. 5). However, no significant differences in N$_m$ were observed between the two cultivars.

Cultivar Tainong No. 1 showed significantly higher light-saturated photosynthesis (P_{Nsat}) at 1,050 m compared to cultivar Jinhuang during hot-dry (HD) and warm-wet (WW) seasons. Conversely, Jinhuang showed significantly higher P_{Nsat} at 450 m during HD and WW seasons. However, neither cultivar showed statistically significant differences in P_{Nsat} due to elevation and P_{Nsat} was generally low during the cold-dry season (Fig. 6*A*). Moreover, intercellular CO$_2$ (C_i) also showed no statistical difference between cultivars due to elevation except during the cold-dry season at 1,050 m, where cultivar Tainong No. 1 showed lower C_i compared to Jinhuang.

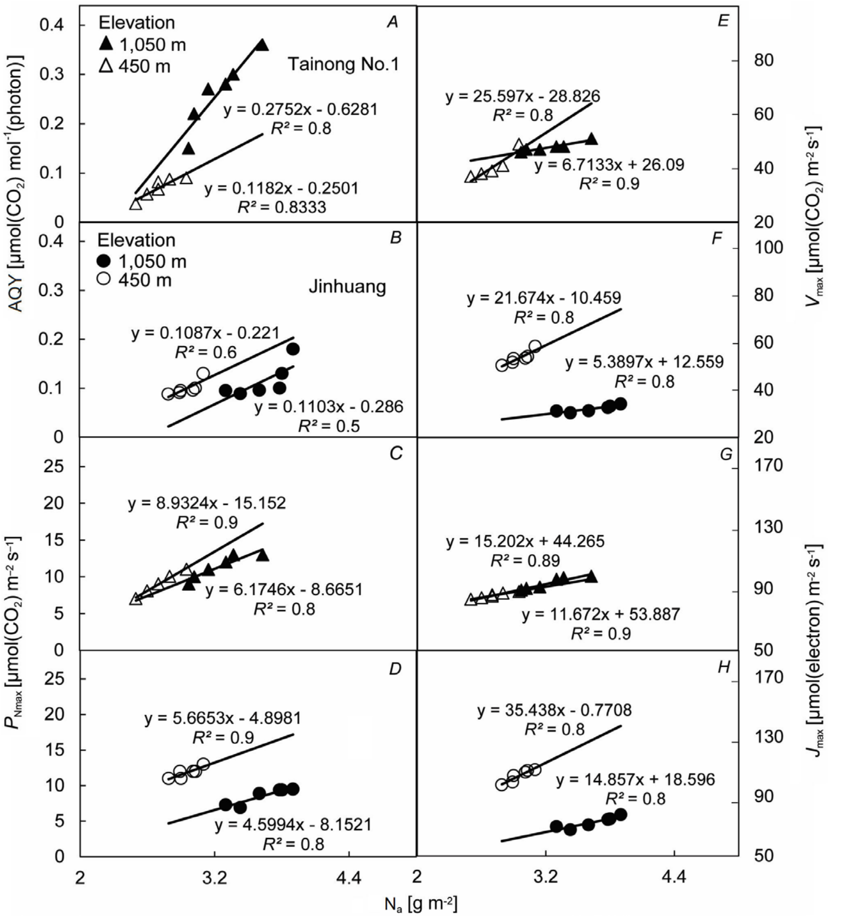

Fig. 4. Relationships of apparent quantum yield (AQY) (*A*,*B*); maximum net photosynthetic rate (P_{Nmax}) (*C*,*D*); maximum carboxylation rate (V_{max}) (*E*,*F*); and photosynthetic electron transport rate (J_{max}) (*G*,*H*) with leaf nitrogen per area (N_a) of mango cultivars Tainong No. 1 and Jinhuang grown at 450 m and 1,050 m.

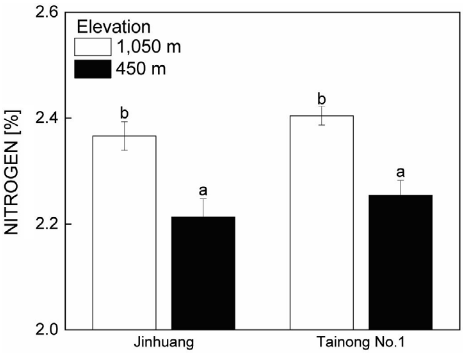

Fig. 5. Mean (± SE) total nitrogen content of leaves of mango cultivars Tainong No. 1 and Jinhuang grown at 450 m and 1,050 m. *Different letters* indicate the difference between means is statistically significant at $p<0.001$.

Seasonal stomatal conductance (g_s) of Jinhuang and Tainong No. 1 showed significant difference due to elevation during the warm-wet season where Jinhuang showed higher g_s at 450 m, while Tainong showed higher g_s at 1,050 m. In addition, Tainong No. 1 showed significantly higher g_s compared to Jinhuang at 450 m during the hot-dry season. Furthermore, g_s was generally low during the cold-dry season while it was high during the hot-dry seasons at 450 m; however, no significant difference between cultivars was observed due to elevation (Fig. 6*C*).

Furthermore, cultivar Tainong No. 1 showed a significantly higher transpiration rate (*E*) compared to cultivar Jinhuang at 1,050 m during HD and WW seasons (Fig. 6*D*). The opposite was true at 450 m. At 450 m, cultivar Jinhuang showed significantly higher *E* compared to cultivar Tainong No. 1 (Fig. 6*D*). Furthermore, both cultivars showed higher *E* during the hot-dry season at both elevations and lower *E* during the cold-dry season; nevertheless, there were no significant differences between cultivars due to elevation (Fig. 6*D*).

Discussion

Photosynthetic capacity parameters differed between mango cultivars studied depending on the elevation. Cultivar Tainong No. 1 had a higher V_{max}, J_{max}, AQY – moles of CO_2 fixed per mole photons (Ehleringer and Björkman 1977, Ehleringer and Pearcy 1983, Oberhuber *et al.* 1993), and P_{Nmax} at 1,050 m, while this was true for Jinhuang at 450 m. Similar studies on tropical plant species have also reported higher V_{max}, J_{max}, AQY, and P_{Nmax} at a higher elevation (Laisk *et al.* 1997, Shi *et al.* 2006, Fujimura *et al.* 2010, Liu *et al.* 2012, Dusenge *et al.* 2015).

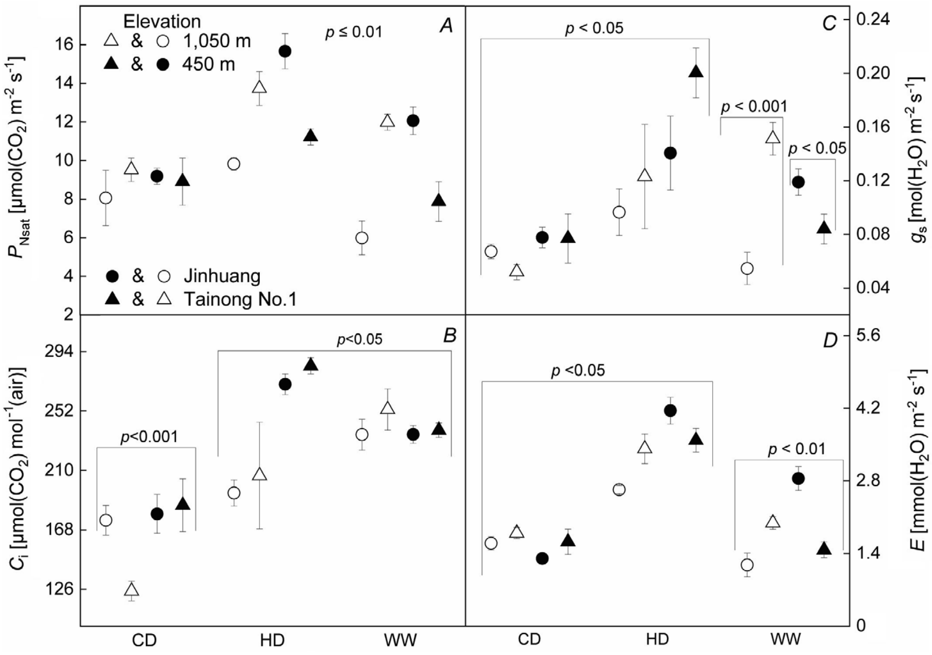

Fig. 6. Mean (± SE) seasonal light-saturated photosynthetic rate (P_{Nsat}) (*A*); intercellular CO$_2$ concentration (C_i) (*B*); stomatal conductance (g_s) (*C*); and transpiration rate (E) (*D*) of mango cultivars Tainong No. 1 and Jinhuang grown at 1,050 m and 450 m during cold-dry (CD), hot-dry (HD), and warm-wet (WW) seasons.

Seasonal light-saturated photosynthesis (P_{Nsat}) of cultivar Tainong No. 1 was higher at 1,050 m, while this was true for cultivar Jinhuang at 450 m during hot-dry and wet-warm seasons. The 1,050 m elevation had lower temperatures compared to the 450 m elevation (Fig. 1*A*). This signified that cultivar Tainong No. 1 performed better in cooler climates, while Jinhuang performed better in warmer climatic conditions, which was also reported by Elsheery *et al.* (2007). Studies have also shown both decreases (Kao and Chang 2001, Zhang *et al.* 2005, Mujawamariya *et al.* 2018) and increases (Friend *et al.* 1989, Premoli and Brewer 2007, Mujawamariya *et al.* 2018) in P_{Nsat} with elevation depending on elevation and plant species studied.

Stomatal conductance (g_s) differed across elevations during the hot-dry season along with transpiration rate (E) during hot-dry and warm-wet seasons between studied mango cultivars. Additionally, g_s and E were generally low during cold-dry at both elevations and no difference was observed between cultivars. Previous studies on tropical plants have shown that g_s and E typically decrease with an increasing elevation, which is typically attributed to the decrease in temperature and vapor pressure deficit (VPD) with elevation (Sendall *et al.* 2009, Motzer *et al.* 2017, Mujawamariya *et al.* 2018). Furthermore, C_i was generally consistent between cultivars at both elevations. Comparable results of seasonal fluctuation in C_i have also been reported by Munjonji *et al.* (2021).

Studies have established that mangoes grow well in hot and dry climates; however, photosynthetic performance depends on cultivar and location of growth (Allen *et al.* 2000, Allen and Ort 2001, Elsheery *et al.* 2007, Elsheery and Cao 2008, Damour *et al.* 2009, Lu *et al.* 2012). Furthermore, physiological responses of mango cultivars to the environment are related to the evolutionary center of origin of cultivars (Morton 1987, Whiley 1993). Thus, variation in the photosynthesis performances, g_s, and E of the two cultivars could also be due to their adaptation to climatic conditions of their respective growing areas. In this case, cultivar Tainong No. 1 is predominantly grown in the dry subtropics featuring hot summers and cooler winters. Cultivar Jinhuang, however, is grown in continuously hot humid tropics (Mukherjee 1972, Gao *et al.* 2011). Jinhuang, a polyembryonic cultivar, suffers more from the low temperature at 1,050 m than cultivar Tainong No. 1, resulting in a reduction of photosynthetic performance at 1,050 m, cooler location, which was also observed by Elsheery *et al.* (2007, 2008).

Furthermore, we found a strong positive correlation between photosynthetic capacity parameters including P_N, J_{max}, carboxylation, and AQE with leaf nitrogen per area (N_a). Studies have demonstrated that nitrogen is the macronutrient with the strongest direct relationship with photosynthesis in plants (Urban *et al*. 2006, Kattge *et al.* 2009, Zhang *et al.* 2017). Nitrogen application can enhance associated enzyme activities, thereby increasing the photosynthetic capacity of leaves (Shangguan *et al.* 2000, Pal *et al.* 2005, Li *et al.* 2013b). In contrast, photosynthetic capacity can be reduced at lower nitrogen concentrations (Pal *et al*. 2005, Li *et al*. 2013b). Moreover, nitrogen affects plant photosynthetic efficiency by affecting the maximum net photosynthetic rate and other associated parameters (Urban *et al.* 2006, Kattge *et al.* 2009). Previous studies have revealed that optimal nitrogen availability highly influences leaf P_N, J_{max}, carboxylation, and AQE (Evans 1989, Cordell *et al.* 1999, Shi *et al.* 2006, Bote *et al.* 2018, Wang *et al.* 2018, Fei *et al.* 2019). Moreover, studies on mango and other tree species have also reported that leaf nitrogen content and partitioning both exert direct impacts on photosynthetic capacity (Körner 1989, Kenzo *et al.* 2006, Urban *et al.* 2006, Kositsup *et al.* 2010, Domingues *et al.* 2014, Xu *et al.* 2015).

The variations in leaf nitrogen per area (N_a) observed in Fig. 6 resulted from the effect of elevation on the leaf total nitrogen (N_m) contents of Tainon No. 1 and Jinhuang (Fig. 5). Previous studies on field-grown plants have also repeatedly reported that leaf nitrogen content varies across ecological gradients associated with elevation (Morecroft and Woodward 1996, Macek *et al*. 2012, He *et al*. 2016, Ram *et al*. 2020). This variation due to elevation has principally been attributed to exposure to low temperatures (Morecroft and Woodward 1996, Soethe *et al*. 2008, He *et al*. 2016, Du *et al*. 2017). Furthermore, plants grown at low temperatures in laboratory conditions also showed higher leaf nitrogen (Sun *et al*. 2011). The higher leaf nitrogen of mango leaves at higher elevation could be present to maintain photosynthetic efficiency in constraining environmental conditions as also reported in other tree species (Körner 1989, Liu *et al*. 2012).

This study was limited to examining photosynthesis and seasonal gas exchange of two mango cultivars before first flowering and fruiting. We suggest that assessing the effects of elevation on photosynthesis and associated traits in other commercial mango cultivars during the time of flowering and fruit production could add value to our findings. Nevertheless, our study demonstrated that elevation influences photosynthesis performance and seasonal gas exchange of two primary commercial cultivars. This suggests that shifting mango plantations to higher elevations should consider selecting specific cultivars for environmental suitability.

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