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# Scion, rootstock and their interaction affect the photosynthesis of citrus

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# Abstract

Photosynthesis is an essential biological process of the plant. The performance of photosynthesis could remarkably affect the final yield and quality of the fruit. However, the effect of the scion, rootstock and their interaction in the scion-rootstock combinations on photosynthesis of the tree was not clear. In this research, the performance of photosynthesis was analyzed with 21 citrus scion-rootstock combinations derived from three navel oranges (*Citrus sinensis* cv. 'Banfield', 'Chislett' and 'Powell') grafted on seven rootstocks (Swingle citrumelo (*C. paradisi* × *Poncirus trifoliata*), Carrizo citrange (*C. sinensis* × *P. trifoliata*), X639 (*C. reticulata* × *P. trifoliata*), MXT (*C. sinensis* × *P. trifoliata*), Hongju (*C. reticulata*), Ziyang xiangcheng (*C. junos*) and Trifoliate orange (*P. trifoliata*), respectively. Results indicated that photosynthesis was significantly affected by either scion, rootstock or the interaction of scion-rootstock, and rootstock had more effect in the scion-rootstock combinations, but the effects among the rootstocks were variable. The combinations of Swingle demonstrated higher values of photosynthesis indexes. Two of three scions grafted on Swingle had significantly higher net $CO_2$ assimilation rate ($A_{CO2}$). All three scions grafted on Swingle showed the highest electron transport rate (ETR) and quantum yield of PSII (Yield II). Photosynthetic pigments (Chla, Chlb, Car and Chlt) of the three scions were highest on Ziyang xiangcheng. Banfield/Trifoliate, Powell/Trifoliate and Chislett/Ziyang had the highest Rubisco activities. The scion-rootstock interaction made the light quanta enter into other reactions during the processes of photosynthesis. Electron transport rate (ETR) is probably the predominant factor determining the photosynthesis of plant.


# 1. Introduction

Photosynthesis is a vital biological process for plant to convert the light energy into organic matters, which is essential for plant growth (Xiang et al. 2019; Yamori et al. 2016; Yudina et al. 2020). It begins with light absorption of pigments in photosystems, and then continues two stages of light reaction and dark reaction, which react on thylakoid membranes and chloroplast stroma, respectively. During the first stage, the light quantum absorbed by photosynthetic pigments experiences 4 pathways: heat dissipation, fluorescence loss, exciton transferring and electron transportation. The second stage is the process of $CO_2$ assimilation via Calvin cycle, in which the enzyme Rubisco is involved (Xu and Wang 2001).

Photosynthetic pigments such as chlorophylls and carotenoids play indispensable roles in absorbing light quanta, transferring energy, phosphorylation and $CO_2$ assimilation (Scheer 2013; Takaichi 2011; Yang et al. 2015). Non-photochemical quenching (NPQ) is an important process for plant to dissipate and release the excess photons absorbed by Chl antenna (Melis 2009). The parameter of qP reflects the light energy, which dissipate as heat or electron transport (Wu et al. 2019). The maximal quantum yield of PSII photochemistry (Fv/Fm) shows the activity of the PSII components and indicates whether plant is under stresses (Kalaji et al. 2017). Leaf photosynthesis is subject to both stomatal and non-stomatal limitations (Buckley and Diaz-Espejo 2015). The former refers to the restrictions in $CO_2$ supply by diffusion via the stomata to the intercellular spaces of leaves, while the latter is associated with the

diffusion of $CO_2$ from the leaf-intercellular spaces to the sites of the dark reactions of photosynthesis in chloroplasts, and biochemical limitations to photosynthetic efficiency (Salmon et al. 2020). Therefore, many factors such as temperature, light intensity, $CO_2$ concentration, activity of photosynthetic enzymes, and pigments' content can affect plant photosynthesis. Grafting is a technique that joins two plants into a new one. Nowadays, most of fruit trees are propagated by grafting. The growth and performance of the grafted plants is affected by both the rootstock and scion. The interaction of rootstock and scion could affect the efficiency of the photosynthesis (Chen et al. 2022; Zhang et al. 2016; Freitas et al. 2021; Hu et al. 2021). Therefore, selection of superior scion-rootstock combination could improve the plant growth, fruit yield and quality and stress tolerance by enhancement of photosynthesis.

Citrus, the most important fruit crop worldwide, is also propagated by grafting. The influences of citrus rootstocks on tree size, fruit yield and quality (de Carvalho et al. 2021; Ferrer et al. 2022; Kunwar et al. 2021; Tirado-Corbalá et al. 2020; Zhu et al. 2020), and stress tolerance (Silva et al. 2023; Kunwar et al. 2021; Miranda et al. 2020; Sampaio et al. 2021; Ranjbar et al. 2022) of scion cultivars have been extensively studied. However, the research on the effect of scion-rootstock interaction on photosynthesis under natural field conditions are rarely conducted.

The present study investigated the photosynthesis of 21 different citrus scion-rootstock combinations to analyze the effect of scion, rootstock and their interaction on the performance of photosynthesis, aimed to better understanding the performance difference of different scion-rootstock combinations in the physiology and provide a reference for selecting suitable scion-rootstock combinations in citriculture.

## 2. Materials and methods

# 2.1 Plant materials

Three late-ripening navel orange scion cultivars [*Citrus sinensis* cv. Powell (PW), Chislett (CH) and Banfield (BF)] grafted on seven citrus rootstocks, including Swingle citrumelo (SW, *C. paradisi* × *Poncirus trifoliata*), Carrizo citrange (CA, *C. sinensis* × *P. trifoliata*), X639 (*C. reticulata* × *P. trifoliata*), MXT (*C. sinensis* × *P. trifoliata*), Hongju (HJ, *C. reticulata*), Ziyang xiangcheng (ZY, *C. junos*) and Trifoliate orange (TO, *P. trifoliata*), respectively, were used as plant materials in this study. The 13-year-old experimental plants of the 21 scion-rootstock combinations were grown in the same orchard in Fengjie County, Chongqing, Southwest China. The planting density is 3.0 m × 4.0 m. Mature and healthy leaves from the third to sixth nodes of spring shoots in the out-layer of tree canopy were chosen for determining the parameters of photosynthesis, chlorophyll fluorescence, the content of pigments, and the activity of Rubisco. Three healthy plants of each scion-rootstock combination were randomly selected as three biological repeats, and three technique replicates were set for each biological repeat.

# 2.2 Measurement of leaf photosynthesis and chlorophyll fluorescence

Measurement of photosynthesis was carried out at 8:30 – 11:00 am on sunny days in summer. Photosynthetic gas exchange was measured using a GFS-3000 portable gas exchange system with a standard cuvette and a 3056-FL PAM-Fluorometer (Walz, Efferich, Germany). The reference $CO_2$ concentration was kept at 400 mg.$L^{-1}$. The measurement was carried out with temperature and relative humidity setting at 27°C and 65%, respectively. Net $CO_2$ assimilation rate ($A_{CO2}$), stomatal conductance ($G_{H2O}$), intercellular $CO_2$ concentration (Ci) and transpiration rate (E) were measured with GFS-3000 portable gas-exchange system (Heinz Walz GmbH, Effeltrich, Germany) with 1000μmol $m^{-2}$ $s^{-1}$ PAR (photosynthetic active radiation). The data was directly exported with GFS-Win software after the measurement stabilized.

Chlorophyll fluorescence was measured with photosynthetic gas exchange system at midnight under fully dark-adapted conditions. Energy partitioning parameters, presented as equations below, were calculated according to the method of Hendrickson et al. (2004). Effective quantum yield of PSII of a light-adapted sample (Yield II) reflecting the proportion of light absorbed by PSII, was determined according to the following expression Yield II = (Fm'-F)/Fm', where Fm' is the light-adapted maximum fluorescence and F is steady-state fluorescence. ETR (Electron transport rate) was calculated as: ETR = PAR×Yield II×0.84×0.5 (Genty et al. 1989). The leave's initial parameter of PSII fluorescence – dark fluorescence yield (Fo) and the maximum fluorescence (Fm) were measured after dark adaptation. Effective quantum yields of PSII and non-photochemical quenching (NPQ) of fluorescence were measured when the leaf acclimated full light to 1000 μmol photon $m^{-2}$ $s^{-1}$ actinic light. Maximum quantum yield of photosystem PSII was calculated as Fv/Fm = (Fm-Fo)/Fm according to Genty et al (1989).

Non-photochemical quenching of fluorescence (NPQ) and qP were calculated using following equations (Bilger and Bjorkman 1990; Kalaji et al. 2014; Kooten and Snel 1990):

NPQ=(Fm-Fm')/Fm'=Fm/Fm'-1

qP = 1-(F-Fo'calc)/(Fm'-Fo'calc)

# 2.3 Photosynthetic pigments determination

The photosynthetic pigments of leaves were extracted with 95% (v/v) ethanol. The contents of chlorophyll a (Chla), b (Chlb), total chlorophyll (Chlt) and carotenoids (Car) of the extracts were determined at maximum absorption peaks of 665 nm, 649 nm and 470 nm, respectively, according to the method described by Li (2000). The content of each pigment was calculated as follows:

Chla (mg/L) = $13.95A_{665}$-$6.88A_{649}$

Chlb (mg/L) = $24.96A_{649}$-$7.32A_{665}$

Chlt (mg/L) = Chla + Chlb

Car (mg/L) = (1000$A_{470}$-2.05Ca-114.8Cb)/245

## 2.4 Determination of Rubisco activity

Activity of the important photosynthetic enzyme Rubisco was detected according to the manual of the Kit (Suzhou Grace Biotechnology Co. Ltd., China). One hundred microgram fresh leaves of each sample were weighed and fully pulverized. 1 mL extracting solution was added, mixed and then centrifuged at 4℃, 12,000rpm for 10 min. The supernatant was transferred to a fresh tube for enzyme activity determination. The activity of enzyme was detected based on an enzymatic method coupled to NADH oxidation of the extract before and after activation with $CO_2$ and $MgCl_2$ by spectrophotometer at 340 nm. The activation state was calculated as the ratio of the initial activity to the final activity (i.e., fully activated state) (Yamori et al. 2012). The activity of the enzyme was calculated as: activity (μmol $s^{-1}$ $Kg^{-1}$ FW) = 10.72 ×△A/0.1, △A = A1-A2. FW indicated as the fresh weight of leaf samples.

## 2.6 Statistical analysis

The significant difference among the scion-rootstock combinations was determined with Duncan's multiple-range test at $p < 0.05$. The impacts of scions and rootstocks were analyzed with two-way ANOVA at $p < 0.0001$ as described by Tietel et al. (2020). Pearson correlation analysis were conducted with rcorr in Package Hmisc, and the correlation matrix were visualized with corrplot in Package corrplot. All the analysis in this study was performed by using R program (https://www.R-project.org/).

# 3. Results

## 3.1 Photosynthetic parameters of citrus scion-rootstock combinations

Scion, rootstock and their interaction significantly affect the photosynthetic parameters (Table 1). The rootstock had the greatest effect with the lowest *p* values on the rate of net $CO_2$ assimilation ($A_{CO2}$) and the stomatal conductance ($G_{H2O}$), while the interaction of scion and rootstock demonstrated the greatest impact on the concentration of intercellular $CO_2$ (Ci) and the rate of transpiration (E). However, the scion showed the lowest but significant effect on $A_{CO2}$, $G_{H2O}$ and E but not significant on Ci. The results indicated that the effect of both rootstock and scion-rootstock interaction is greater than that of scion on the parameters of photosynthesis. The photosynthetic parameters varied among the 21 scion-rootstock combinations. The highest rate of net $CO_2$ assimilation ($A_{CO2}$) were observed in Swingle combined with both Banfield and Chislett (BF/SW, CH/SW) at 11.22 and 10.77μmol $m^{-2}$ $s^{-1}$, respectively, and MXT with Powell (PW/MXT) at 12.27 μmol $m^{-2}$ $s^{-1}$. Hongju, Trifoliate orange and Ziyang xiangcheng combined with the three scions (BF/HJ, CH/TO and PW/ZY) had the lowest $A_{CO2}$ at 6.67, 5.58 and 7.07 μmol $m^{-2}$ $s^{-1}$, respectively. The highest stomatal conductance ($G_{H2O}$) was also found in Banfield and Chislett grafted on Swingle (BF/SW, CH/SW) at 163.92 and 159.31 mmol $m^{-2}$ $s^{-1}$, respectively, and Powell on

Trifoliate orange (PW/TO) at 153.97 mmol $m^{-2}$ $s^{-1}$. The lowest $_{GH2O}$ values of scion were showed in Chislett and Powell on Ziyang xiangcheng (CH/ZY, PW/ZY) at 90.34 and 97.38 mmol $m^{-2}$, respectively, and Banfield on Hongju (BF/HJ) at 96.73 mmol $m^{-2}$, which were significantly lower than that of the scions grafted on the other rootstocks. X639 grafted with both Banfield and Powell (BF/X639, PW/X639) had the highest concentration of intercellular $CO_2$ (Ci) at 353.97 and 355.35μmol $mol^{-1}$, respectively, while Chislett on Trifoliate orange (CH/TO) had the highest Ci at 388.59 μmol $mol^{-1}$. The combinations of BF/TO, CH/HJ and PW/CA had the lowest Ci at 310.34, 304.88 and 304.63 μmol $mol^{-1}$. The highest transpiration rate (E) was detected in the combinations of BF/SW, CH/639, PW/MXT at 4.30, 3.16 and 3.91 mmol $m^{-2}$ $s^{-1}$, respectively, and the lowest E values were obtained in BF/HJ, CH/MXT and PW/ZY at 1.74, 1.68 and 1.78 mmol $m^{-2}$ $s^{-1}$.

Table 1
Photosynthetic parameters of the scion-rootstock combinations

| Scions | Rootstocks | $ACO_2$ | Ci | E | $GH_2O$ |
|---|---|---|---|---|---|
| BF | CA | 7.82 D | 349.04 A | 2.43 C | 132.56 BC |
| | HJ | 6.67 E | 325.48 BC | 1.74 E | 96.73 F |
| | MXT | 8.93 C | 335.68 B | 2.84 B | 122.45 DE |
| | PT | 9.75 B | 310.34 D | 2.74 B | 136.43 B |
| | SW | 11.22 A | 327.50 BC | 4.30 A | 163.92 A |
| | X639 | 7.14 E | 353.97 A | 2.18 D | 117.69 E |
| | ZY | 8.82 C | 322.61 C | 2.21 D | 127.63 CD |
| CH | CA | 7.32 D | 357.05 A | 2.85 B | 110.82 CD |
| | HJ | 10.19 A | 304.88 D | 2.54 C | 120.24 C |
| | MXT | 8.34 C | 306.62 D | 1.68 E | 113.00 CD |
| | PT | 5.58 E | 388.59 A | 2.32 CD | 94.40 D |
| | SW | 10.77 A | 307.75 D | 2.38 CD | 159.31 A |
| | X639 | 9.47 B | 322.22 C | 3.16 A | 146.67 B |
| | ZY | 8.47 C | 349.32 B | 2.28 D | 90.34 D |
| PW | CA | 7.62 E | 304.63 D | 3.00 C | 103.82 C |
| | HJ | 7.97 D | 344.45 B | 2.43 D | 138.04 B |
| | MXT | 12.27A | 329.06 C | 3.91 A | 139.23 B |
| | PT | 10.12 C | 329.39 C | 3.27 B | 153.97 A |
| | SW | 11.69 B | 312.94 D | 3.36 B | 139.73 B |
| | X639 | 8.11 D | 355.35 A | 2.38 D | 134.03 B |
| | ZY | 7.07 F | 336.30 BC | 1.78 E | 97.38l C |
| *p* | scion | 1.29E-09*** | 0.7012 | 4.19E-15*** | 6.05E-09*** |
| | rootstock | 1.74E-27*** | 0.00015** | 1.00E-25*** | 1.68E-23*** |
| | interaction | 8.91E-26*** | 8.47E-08*** | 3.25E-28*** | 1.10E-21*** |

Note: different capitalized letters indicate significant differences at $p < 0.05$; *, ** and *** indicates $p < 0.01$, $p < 0.001$ and $p < 0.0001$, respectively.

# 3.2 Chlorophyll fluorescence of citrus scion-rootstock combinations

Scion, rootstock and scion-rootstock interaction all had significant effects on electron transport rate (ETR), but rootstock had the greatest contributions to ETR than the other two factors with the lowest p values. Among the 7 rootstock varieties, Swingle possessed the highest rate of electron transport with all the three scions (BF/SW, CH/SW, PW/SW) at 132.24, 158.39 and 154.59μmol electrons $m^{-2}$ $s^{-1}$, respectively. Ziyang xiangcheng with Chislett and Powell (CH/ZY, PW/ZY), Hongju with Banfield (BF/HJ) had the lowest ETR at 90.22, 83.00 and 81.88μmol electrons $m^{-2}$ $s^{-1}$, respectively, which were significantly lower than that of the scions with the other rootstocks. Only rootstock had significant effect on the quantum yield of the PSII (Yield II). Swingle grafted with the three scions (BF/SW, CH/SW, PW/SW) also possessed the highest quantum yield of the PSII (Yield II) at 0.32, 0.38 and 0.38, respectively, while Ziyang xiangcheng with Chislett and Powell (CH/ZY, PW/ZY) and Hongju with Banfiled (BF/HJ) had the lowest values at 0.22 and 0.20, and 0.20, respectively. Both scion and scion-rootstock interaction had significant effect on the maximal quantum yield of PSII photochemistry (Fv/Fm) and non-photochemical quenching of fluorescence (NPQ). Trifoliate orange grafted with Banfield (BF/TO), Carrizo with both Chislett and Powell (CH/CA, PW/CA) showed significantly lower Fv/Fm ratios at 0.74, 0.68 and 0.77, respectively. The highest NPQ values were measured in the combinations of BF/CA, CH/ZY and PW/SW at 3.06, 3.09 and 3.22, respectively, while the lowest values were in BF/PT, CH/CA and PW/639 at 1.50, 1.13 and 2.40, respectively. The combinations of BF/TO, CH/HJ and PW/MXT demonstrated the highest values of qP at 0.26, 0.31 and 0.31, respectively. Only scion-rootstock interaction showed significant effect on qP (Table 2). Among the 21 scion-rootstock combinations, the combinations of BF/TO, CH/HJ and PW/MXT had the highest qP values at 0.26, 0.31 and 0.31, respectively. And Chislett and Powell grafted on Carrizo and X639 (CH/CA, PW/X639) had the lowest values at 0.11 and 0.14, respectively. Banfield grafted on MXT, Swingle and X639 all had the lowest qP at 0.17, significantly lower than that on Trifoliate orange and Carrizo (Table 2).

Table 2
Chlorophyll fluorescence of the scion-rootstock combinations

| Scions | Rootstocks | Yield II | ETR | Fv/Fm | qP | NPQ |
|---|---|---|---|---|---|---|
| BF | CA | 0.28 BC | 116.31 B | 0.83 A | 0.22 A | 3.06 A |
| | HJ | 0.20 B | 81.88 D | 0.80 AB | 0.21 A | 2.62 A |
| | MXT | 0.31 A | 125.69 A | 0.84 A | 0.17 B | 2.90 A |
| | TO | 0.28 AB | 114.71 B | 0.74 B | 0.26 A | 1.50 B |
| | SW | 0.32 A | 132.24 A | 0.83 A | 0.17 B | 2.70 A |
| | X639 | 0.28 AB | 112.33 B | 0.82 A | 0.17 B | 2.29 AB |
| | ZY | 0.23 AB | 94.42 C | 0.80 AB | 0.19 AB | 2.71 A |
| CH | CA | 0.27 BC | 110.82 D | 0.68 B | 0.11 B | 1.13 D |
| | HJ | 0.29 ABC | 120.24 C | 0.81 A | 0.31 A | 2.98 AB |
| | MXT | 0.27 BC | 113.00 D | 0.79 A | 0.17 AB | 2.03 D |
| | TO | 0.23 C | 94.09 E | 0.82 A | 0.22 AB | 2.57 ABC |
| | SW | 0.38 A | 158.39 A | 0.77 AB | 0.20 AB | 1.89 BCD |
| | X639 | 0.36 AB | 146.67 B | 0.80 A | 0.29 A | 2.68 ABC |
| | ZY | 0.22 C | 90.22 E | 0.81 A | 0.24 AB | 3.09 A |
| PW | CA | 0.28 BC | 116.75 C | 0.77 B | 0.21 AB | 2.56 AB |
| | HJ | 0.24 C | 100.31 D | 0.82 A | 0.24 AB | 2.84 AB |
| | MXT | 0.36 AB | 145.48 B | 0.82 A | 0.31 A | 3.13 A |
| | TO | 0.27 BC | 110.92 C | 0.82 A | 0.22 AB | 3.08 A |
| | SW | 0.38 A | 154.59 A | 0.82 A | 0.30 A | 3.22 A |
| | X639 | 0.22 C | 90.85 E | 0.83 A | 0.14 B | 2.40 B |
| | ZY | 0.20 C | 83.00 F | 0.81 A | 0.17 B | 2.77 AB |
| *p* | scion | 0.5235 | 0.00275* | 0.0068* | 0.2838 | 0.0033* |
| | rootstock | 7.68E-06*** | 1.95E-26*** | 0.0114 | 0.2214 | 0.0606 |
| | interaction | 0.0169 | 7.85E-18*** | 0.0014* | 0.0071* | 0.0004** |

Note: different capitalized letters indicate significant differences at $p < 0.05$ among the seven scion-rootstock combinations within a scion; *, ** and *** indicates $p < 0.01$, $p < 0.001$ and $p < 0.0001$, respectively.

## 3.3 Photosynthetic pigments’ content of citrus scion-rootstock combinations

Among the scion, rootstock and scion-rootstock interaction, only rootstock had significant effect on the content of chlorophylls, while none of the three ones had significant effect on the carotenoids content. As shown in Table 3, among the 7 rootstocks, the effect of Ziyang xiangcheng on photosynthetic pigments was distinguishing. The highest contents of Chla, Chlb and Chlt were all observed in the combinations of Ziyang xiangcheng gfated with three scions (BF/ZY, CH/ZY, PW/ZY).

Table 3
Content of photosynthetic pigments of the scion-rootstock combinations

| Scions | Rootstocks | Chla | Chlb | Car | Chlt |
|---|---|---|---|---|---|
| BF | CA | 12.7 A | 5.5 AB | 2.4 AB | 18.2 A |
| | HJ | 12.4 A | 5.4 AB | 2.7 A | 17.8 AB |
| | MXT | 12.3 A | 5.4 AB | 2.5 AB | 17.8 AB |
| | TO | 12.1 B | 5.1 B | 2.5 AB | 17.2 B |
| | SW | 11.1 C | 4.6 C | 2.3 B | 15.7 C |
| | X639 | 12.9 A | 5.5 AB | 2.6 AB | 18.4 A |
| | ZY | 13.7 A | 6.2 A | 2.4 AB | 19.8 A |
| CH | CA | 12.1 C | 5.2 B | 2.3 BC | 17.2 C |
| | HJ | 11.2 C | 4.6 C | 2.3 BC | 15.8 C |
| | MXT | 11.2 C | 5.0 BC | 2.1 C | 16.1C |
| | TO | 11.4 C | 4.7 C | 2.1 C | 16.2 C |
| | SW | 11.2 C | 4.5 C | 2.2 BC | 15.7 C |
| | X639 | 12.7 B | 5.4 B | 2.4 AB | 18.1 B |
| | ZY | 14.3 A | 6.6 A | 2.8 A | 21.0 A |
| PW | CA | 11.8 CD | 5.1 CD | 2.4 AB | 16.9 DE |
| | HJ | 11.5 E | 5.2 CD | 2.2 B | 16.7E |
| | MXT | 11.8 DE | 5.2 CD | 2.2 B | 17.0 CD |
| | TO | 11.4 E | 4.8 D | 2.2 B | 16.2 E |
| | SW | 12.9 BC | 5.6 BC | 2.3 AB | 18.5 BC |
| | X639 | 13.1 AB | 5.8 B | 2.5 AB | 18.9 B |
| | ZY | 14.0 A | 6.4 A | 2.6 A | 20.4 A |
| *p* | scion | 0.3020 | 0.1502 | 0.0213 | 0.2589 |
| | rootstock | 7.21E-06*** | 5.04E-08*** | 0.0157 | 1.32E-06*** |
| | interaction | 0.5623 | 0.3350 | 0.0719 | 0.4847 |

Note: different capitalized letters indicate significant differences at $p < 0.05$; *, ** and *** indicates $p < 0.01$, $p < 0.001$ and $p < 0.0001$, respectively.

## 3.4 Rubisco activity of the citrus scion-rootstock combinations

Only rootstock had significant effect on the activity of Rubisco, but the effect was highly varied among the rootstocks. As shown in Fig. 1, among the 7 rootstocks, Trifoliate orange with Banfield and Powell (BF/TO, PW/TO), and Ziyang xiangcheng with Chislett (CH/ZY) possessed the highest Rubisco activities at 1390.53, 1570.03 and 1350.34μmol $s^{-1}$ $Kg^{-1}$ FW, respectively. Carrizo with Banfield and Chislett (BF/CA, CH/CA), and Hongju with Powell (PW/HJ) had the lowest activities at 788.00, 554.50, and 784.39 μmol $s^{-1}$ $Kg^{-1}$ FW, respectively.

# 4. Discussion

The scion, rootstock and their interaction can significantly affect the morphological and physiological performance of the plant (Liu et al. 2023). The capacity of photosynthesis, which is essential for synthesis of carbohydrates to support the plant growth also influenced (Jover et al. 2012). In this study, significant differences on the performance of photosynthesis were observed among the citrus scion-rootstock combinations. Liao et al (2016) reported that a citrus variety ‘Huangguogan’ grafted on Trifoliate orange, Hongju and Xiangcheng, which are the same three rootstocks investigated in our research, had different photosynthetic performances. In the present research, investigation of photosynthetic capacity was conducted in the 21 combinations made by three scions and seven rootstocks to illustrate the effect of scion, rootstock and scion-rootstock interaction on performance of the photosynthesis, and reveal their contributions of the scion, the rootstock and their interaction.

Fourteen photosynthesis indexes were investigated. Among the photosynthetic parameters, the content of chlorophylls (Chla, Chlb and Chlt) were significantly influenced by the rootstocks only. In the present research we found that the content of photosynthetic pigments (Chla, Chlb, Chlt, and Car) of the combinations was the highest in the combinations using Ziyang xiangcheng as rootstock (Table 3), indicating that the largest quantity of light quanta was absorbed in these combinations at the beginning of photosynthesis. Theoretically, approximately 30% light quanta absorbed by the photosystem could be transferred and conserved as biochemical energy (Xu and Wang 2002; Melis 2009). The rest of light quanta is dissipated by other processes. The parameters such as NPQ and qP were suggested as important indicators for photoprotection against photoinhibition (Choi 2021). Non-photochemical quenching (NPQ), which is significantly influenced by both the scion and scion-rootstock interaction (Table 2), indicating the dissipation of excess energy by fluorescence, and preventing deleterious photochemical reactions (Melis 2009), differed significantly among the combinations. NPQ value of the combinations using Ziyang xiangcheng as rootstock was relatively high among the 21 scion-rootstock combinations (Table 2), indicating the that large quantities of light quanta have been dissipated as fluorescence. qP, significantly influenced by the interaction of scion and rootstock (Table 2), indicates the light energy, which dissipate as heat or electron transport (Wu et al. 2019). qP value of the combinations using Trifoliate orange as rootstock is also relatively high among the combinations (Table 2), which

means that a big portion of light quanta has been dissipated as heat. Fv/Fm ratio, one parameter of chloroplast fluorescence, is an important index to present the maximum potential ability of photosynthesis, the activity of the PSII components and an index to indicate plant is whether under stress conditions (Kalaji et al. 2017). For most of the plants under stress-free environment, Fv/Fm is close to 0.83 (Choi 2021). If the ratio is lower than this value, it indicates that the plant is under stressful conditions (Kalaji et al. 2017). In our study, Fv/Fm ratio of most combinations was close to 0.83, indicating that the plants are under good growing conditions. However, Fv/Fm ratios of some combinations such as Chislett and Powell on Carrizo rootstock (CH/CA, PW/CA) and Banfield on Trifoliate orang (BF/TO), were much lower than 0.83, also significantly lower than that of in other combinations, indicating that trees of those three combinations were probably under stressful conditions. Gonza´lez-Mas et al (2009) also indicated that Fv/Fm value of 'Navelina' navel orange grafted on Carrizo was significantly lower than that on other rootstocks due to its least tolerance to calcareous condition. However, the cause of this stress in our results was unknown. It is likely due to that under natural field conditions, plants usually experience fluctuating light condition in timescales of seconds, minutes and hours (Slattery et al. 2018).

Photosynthesis is the largest biological synthesis reaction on earth that converts the light energy into organic matters for plant (Xu and Wang 2002). In this research we found that the rate of net $CO_2$ assimilation ($A_{CO2}$) of the grafted citrus plants, was significantly influenced by the scion, the rootstock and their interaction among the citrus scion-rootstock combinations (Table 1). It is also influenced by many factors such as the concentration of intercellular $CO_2$ (Ci), the rate of transpiration (E) and the stomatal conductance ($G_{H2O}$) during the photosynthetic process. Compared with other combinations, the combinations of CH/CA and BF/TO possessed lower $A_{CO2}$ and Ci, but higher $G_{H2O}$, suggesting that their photosynthesis was probably affected by non-stomatal limitation. However, the combination PW/CA had relatively lower $A_{CO2}$, also low Ci and $G_{H2O}$, showing that its photosynthesis was possibly influenced by stomatal limitation.

Electron transport is the most important process that converts the light energy into biochemical biomass (Xu and Wang 2002). Rate of electron transport (ETR) is an essential parameter to reflect the internal characteristics of photosynthetic system and the photosynthesis of plants under various conditions (Long et al. 2013). It was found that there was significant and positive relationship between ETR and photosynthesis in maize ($r = 0.8743^{**}$) (Wu et al. 2019). In this research, like the rate of net photosynthesis ($A_{CO2}$), ETR was also significantly influenced by all the scion, rootstock and their interaction (Table 2). The combinations which possessed the highest photosynthesis rate also had the highest electron transport rate (ETR) (Table 1, 2), suggesting that ETR was probably a predominate factor in determining the variation of photosynthesis among the scion-rootstock combinations. Coefficient analysis also indicated that net $CO_2$ assimilation rate ($A_{CO2}$) positively and significantly correlated to electron transport rate (ETR) with $r = 0.7791^{**}$ (Fig. 2), which further demonstrated their close relationship. Rubisco is the rate-limiting enzyme of Calvin cycle and could determine the rate of net photosynthesis (He et al. 2020; Xu and Wang 2002). In the study of Liao et al (2016), the combination

Huangguogan/Xiangcheng, which possessed higher photosynthesis capacity, also had the highest Rubisco activity. However, this relationship was not observed in this study conducted in natural field conditions. In this investigation, the activity of Rubisco was significantly influenced by the rootstock only, not by scion and scion-rootstock interaction (Fig. 1). The activity of Rubisco was the highest in the combinations of PW/TO, BF/TO and CH/ZY, but the rate of net photosynthesis ($A_{CO2}$) was obtained in the combinations of PW/MXT, BF/SW and CH/SW. The inconsistence between the activity of Rubisco and the rate of net photosynthesis in the scion-rootstock combinations could imply that there are some other factors have influenced the photosynthesis. Heat and fluorescence dissipation indicated with qP and NPQ significantly influenced by scion-rootstock interaction in Table 2 have demonstrated the speculations. However, how they were influenced by the scion-rootstock interaction is rarely known. Interestingly, we found that those combinations using Trifoliate orange as rootstock with high Rubisco activity combinations had the highest total soluble solid (TSS) content and fruit yield efficiency in our previous study (Zhu et al. 2020). This may imply that Rubisco, the most important enzyme in Calvin cycle, is probably a predominate factor influence of the fruit quality and yield efficiency through regulating the carbohydrates accumulation.

## 5. Conclusion

The results of this research showed that rootstock, scion and their interaction had significant effect on the rate of net photosynthesis ($A_{CO2}$) and the rate of electron transport (ETR), causing significant difference on the performance of photosynthesis among the combinations. Either scion, rootstock or scion-rootstock interaction has influenced the other photosynthetic indexes, which made the light quanta enter into other reactions during the processes of photosynthesis, thus make the different performances of the scion-rootstock combinations.

## Declarations

# Authors' contributions

**Shiping Zhu**: Designing, Funding acquisition, Conceptualization, Writing: original draft – review & editing, Supervision. **Mengyu Liu**: Investigation, Methodology, Data curation, Writing –Writing, reviewing & editing. **Guotao Luo**: Data curation, Writing –Writing, reviewing & editing. **Zhou Hu**: Methodology, Data curation. **Xiaonan Zhang**: Investigation. **Jinsong Xiang, Rong Yang, Shixue Hu**: Resources and Investigation. **Xiaodong Cai**: Validation, Writing – review & editing. **Xin Yu**: Investigation, Data curation, Writing – reviewing & editing.

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# Figures

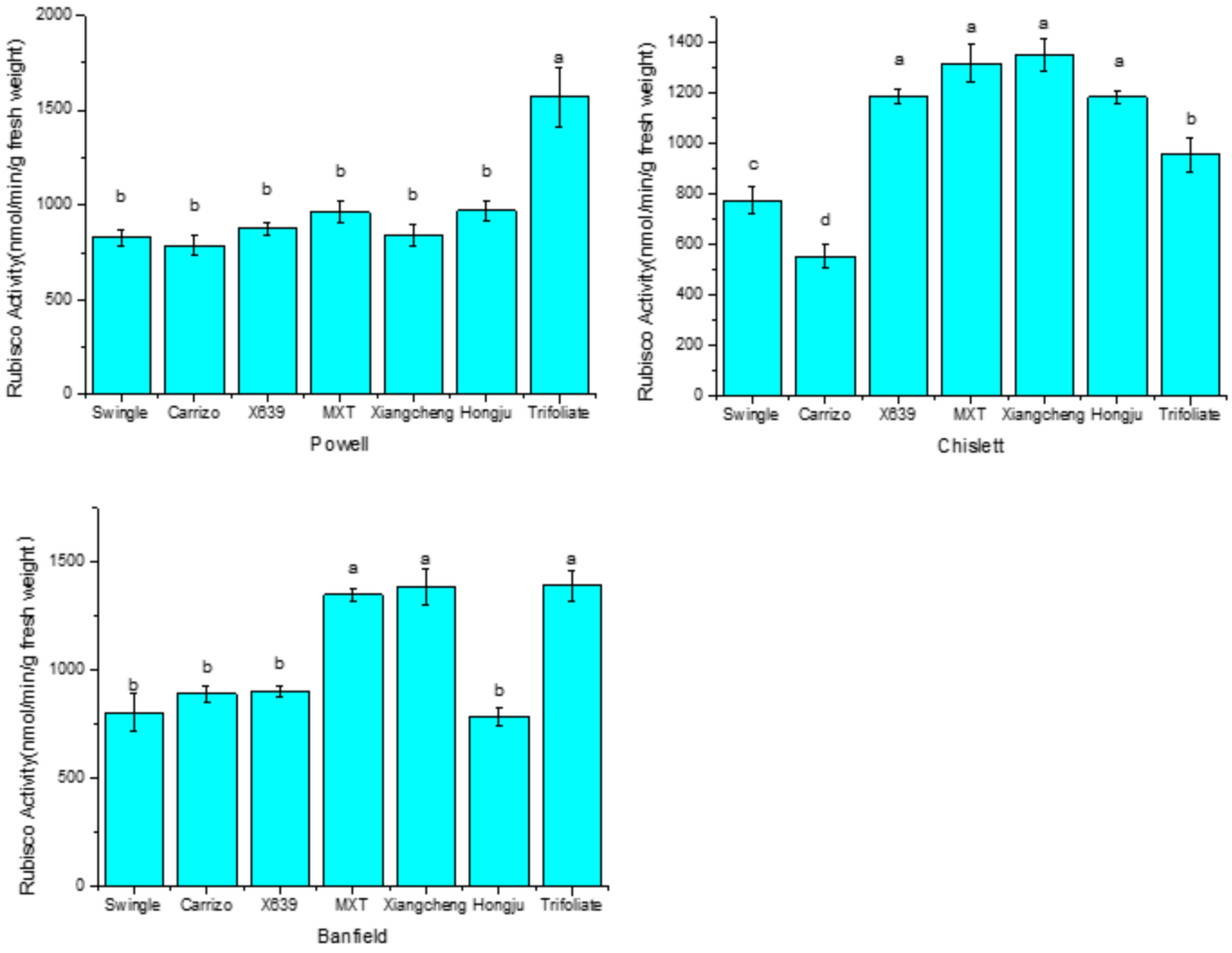



**Figure 1**

Rubisco activity of the citrus scion-rootstock combinations of three scions

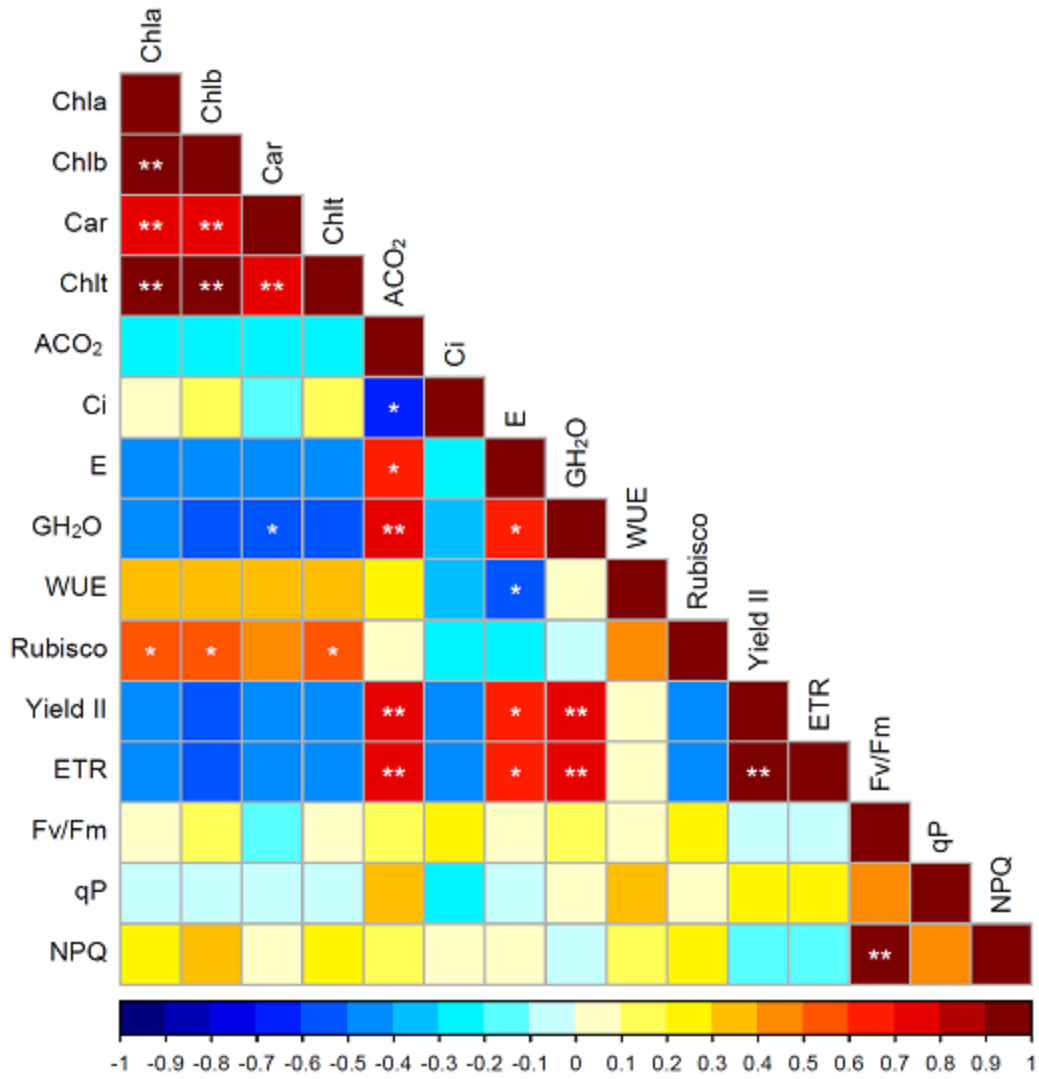



**Figure 2**

Correlation analysis of the parameters related to photosynthesis of 21 scion-rootstock combinations

Note: * and ** indicated the correlation with significant differences at $p<0.05$ and $p<0.01$, respectively.

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