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Rootstocks influence fruit oleocellosis in 'Hamlin' sweet orange (*Citrus sinensis* L. Osbeck)

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ABSTRACT

Oil spotting or oleocellosis, is a major problem in citrus crops. As the rootstock and fertilization play important roles in citrus growth and fruit development, we investigated the influence of different rootstocks on the growth, mineral nutrition metabolism, water relations, and fruit oleocellosis of eight-year-old field 'Hamlin' sweet orange trees. Trees grafted onto Lichi16-6 trifoliata (*Poncircus trifoliate*) had the greatest rate of oleocellosis (RO), and trees grafted onto Goutou orange (*Citrus aurantium*) had the greatest degree of oleocellosis (DO). In contrast, trees grafted onto Rangpur lime (*Citrus limonia* Osbeck) had the lowest RO and DO. Trees were the most vigorous on Rangpur lime rootstocks, followed by Lichi16-6 trifoliata, and then Goutou orange. In addition, because the scion/stock girth ratio showed significant correlations with the RO and DO, oleocellosis parameters can be a good indicator of scion/stock affinity. The total N, total P, Ca^{2+}, and Mg^{2+} in leaves from trees on Rangpur lime were significantly lower than in leaves from trees on Goutou orange or Lichi16-6 trifoliata. In addition, the RO showed a significant correlation with the leaf Ca^{2+} and S concentrations and with the peel Mg^{2+} concentration. The DO was significantly correlated with the total peel N and S concentrations. In addition, the RO showed a significant correlation with the net assimilation of CO_2 (ACO_2), stomatal conductance (GS), transpiration rate (ET), and water-use efficiency (WUE). However, the DO showed a significant correlation with the GS, ACO_2, and WUE. Taken together, these results indicate that rootstocks affect the development of oleocellosis in 'Hamlin' sweet orange due to their effects on the mineral nutrition balance and water relations.

1. Introduction

'Hamlin' sweet orange originated in the USA, and was introduced into China from Morocco in 1965. It has several advantageous traits, including early fruiting, high productivity, and suitability for both fresh consumption and juice processing. However, the fruits are highly sensitive to oil spotting (oleocellosis) development during ripening.

Oleocellosis occurs during postharvest stage when mechanical damage (Fawcett, 1916) releases oil from the oil glands (Knight et al., 2001). When fruits are very turgid, even slight pressure from bumps and abrasions can result in oil release and spotting. The oil is toxic to surrounding tissue and will inhibit degreening of that tissue. Symptoms appear as irregularly shaped green, yellow, or brown spots that darken over time and make the glands more prominent (Shomer and Erner, 1989). The most effective means of prevention are by avoiding harvesting turgid fruit early in the morning, when dew is present, during foggy conditions, or immediately after rain or irrigation (Wardowski et al., 1997).

A number of reports have described the causes of oleocellosis in different citrus varieties. Nutritional imbalances (Chapman, 1958; Grierson, 1965), climate change from rain to wind (Zaragoza and Alonso, 1975), cold winds (Klotz et al., 1966), sudden changes in relative humidity (Agustí and Zaragoza, 2000), and the development of differential water stress across the rind (Zacarias et al., 2000) are involved in rind breakdown in the 'Navelate' orange. Consequently, the effects of daily variations in the relative humidity and evapotranspiration on the natural occurrence of rind staining have been studied. Moreover, the postharvest induction of oleocellosis in mature fruit indicates that it can occur irrespective of the harvest time, but its occurrence increases with fruit maturity (Alférez and Zacarías, 2001).

Abbreviations: ACO_2, net assimilation of CO_2; DO, degree of oleocellosis; ET, transpiration rate; GS, stomatal conductance; RO, rate of oleocellosis; WUE, water use efficiency.

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Table 1
Effects of three citrus rootstocks on the vegetative growth of seven-year-old 'Hamlin' sweet orange.

Rootstock	Tree height (m)	Canopy diameter (m)	Tree volume (m^3)	Girth		Scion/stock girth ratio
				Scion	Stock	
LC	2.61 b	2.86 a	5.34 b	38.00 a	51.00 a	0.79 b
GT	2.78 b	2.55 b	4.53 c	35.67 b	51.33 a	0.69 c
RL	3.92 a	3.05 a	9.08 a	38.33 a	41.33 b	0.93 a

Note: different lower-case letters in the same row indicate significant differences between treatments ($P < 0.05$). *Abbreviations*: LC = Lichi16-6 trifoliata; GT = Goutouchen sour orange; RL = Rangpur lime.

However, on-tree oleocellosis can also occur, resulting in lesions of about 5–8 mm in diameter. This disorder causes a considerable reduction in external fruit quality and fresh fruit exports. Up to 80% of the fruit in more sensitive orchards can be affected (Almela et al., 1990). Our recent research indicates that rootstocks had a significant effect on oleocellosis development under the same field management conditions (Zheng et al., 2010a). However, there is a need to better understand the mechanism that rootstock affected the on-tree oleocellosis development.

The objective of this study was to evaluate the influence of different rootstocks on mineral nutrition metabolism, water metabolism, and fruit oleocellosis of eight-year-old field-grown 'Hamlin' sweet orange trees. The study can also help to develop strategies to reduce or eliminate the occurrence of oleocellosis fruits in citrus industry.

2. Materials and methods

2.1. Plant material

'Hamlin' sweet orange (*Citrus sinensis* L. Osbeck) was obtained from an experimental orchard of eight-year-old trees at the Citrus Research Institute, Southwest University, Chongqing, China (latitude, 29°45′51″N; longitude, 106°22′21″E; altitude, 240 m a.s.l.) grafted onto seven rootstocks, including Lichi16-6 trifoliata (*Poncircus trifoliate*), Goutouchen sour orange (*C. aurantium*), and Rangpur lime (*C. limonia* Osbeck), Volkamer lemon (*C. volkameriana*), 'Guangpi' sour orange (*C. aurantium*), Carrizo citrange [*C. sinensis* (L.) Osbeck × *P. trifoliata* (L.) Raf], 'Sunchusha' mandarin

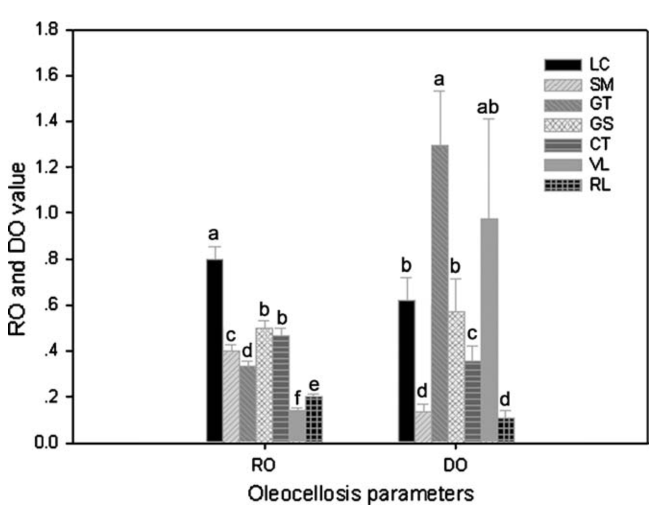

Fig. 1. Effects of various citrus rootstocks on the RO and DO of 'Hamlin' sweet orange. Each value is the mean of six individual replicates (±s.d.). Different lower-case letters in the same columns indicate significant differences between Hamlin with each rootstock ($P < 0.05$). *Abbreviations*: LC = Lichi16-6 trifoliata; GT = Goutouchen sour orange; RL = Rangpur lime; VL = Volkamer lemon; GS = 'Guangpi' sour orange; CT = Carrizo citrange; SM = 'Sunchusha' mandarin.

(*C. reticulate*). The seedlings were budded in spring 2000 by buds taken from virus-free trees of 'Hamlin' sweet orange. The scions of all trees were of the same clonal strain. In March 2001, uniform one-year-old trees were planted in the field at the high density of 3 m × 4 m under a drip irrigation system and grown using standard local commercial practices. Six 8-year-old trees on each rootstock were chosen and labeled for this study.

2.2. Measurement of oleocellosis parameters

To assess the oleocellosis characteristics of fruits at harvest, the citrus oleocellosis parameters ratio of oleocellosis (RO) and degree of oleocellosis (DO) were measured after harvesting according to Zheng et al. (2010b). Samples of 30 fruits per tree were randomly collected at harvest date, and the ratio of the total number of fruits with oleocellosis to total number of measured fruits (TNF) was recorded as RO, and the total number of oleocellosis spots size diameter >0.25 cm and ≤0.25 cm (x_1 and x_2, respectively) were recorded. In addition, the DO per tree was calculated as follows:

$$\text{DO per tree} = \frac{\sum(x_1 \times 0.5 + x_2 \times 0.25)}{\text{TNF}}$$

Note: DO can reflect the total oleocellosis area of each fruit, because the correlation coefficient (R^2) between DO and the total oleocellosis area of each fruit achieved to 0.92 ($n = 20$).

2.3. Measurement of growth parameters

In the seventh year after planting (YAP), six trees on each rootstock were chosen and labeled for growth parameters measurement, and in December 2008, the tree height, the canopy diameter in two directions (to obtain the average diameter), and the trunk girth at 10 cm above and below the budding union were measured, and the scion/stock girth ratio was calculated. The canopy volume (m^3) was calculated according to the following equation reported by Wutscher (1995):

$$\text{tree volume} = \frac{\text{tree diameter } 2 \times \text{tree height}}{4}$$

2.4. Fruit peel and leaf nutrient concentrations

In September 2008, 50 expanded function leaves (the fourth leaf of spring tips) and 30 fruit peels (Flavedo and Albedo together) per three as one replicate were randomly collected from 'Hamlin' sweet orange trees grafted on three rootstocks (Lichi16-6 trifoliata, Goutou orange, and Rangpur lime), and six independent replicates for 'Hamlin' sweet orange trees grafted on each rootstock. The tissues were rinsed briefly with deionized water, oven-dried at 60 °C for at least 48 h, weighed, and ground to a fine powder. The tissue N concentration was measured using a Thermo-Finnigan EA 1112 elemental analyzer (Thermo-Finnigan, Milan, Italy). The tissue K^+,

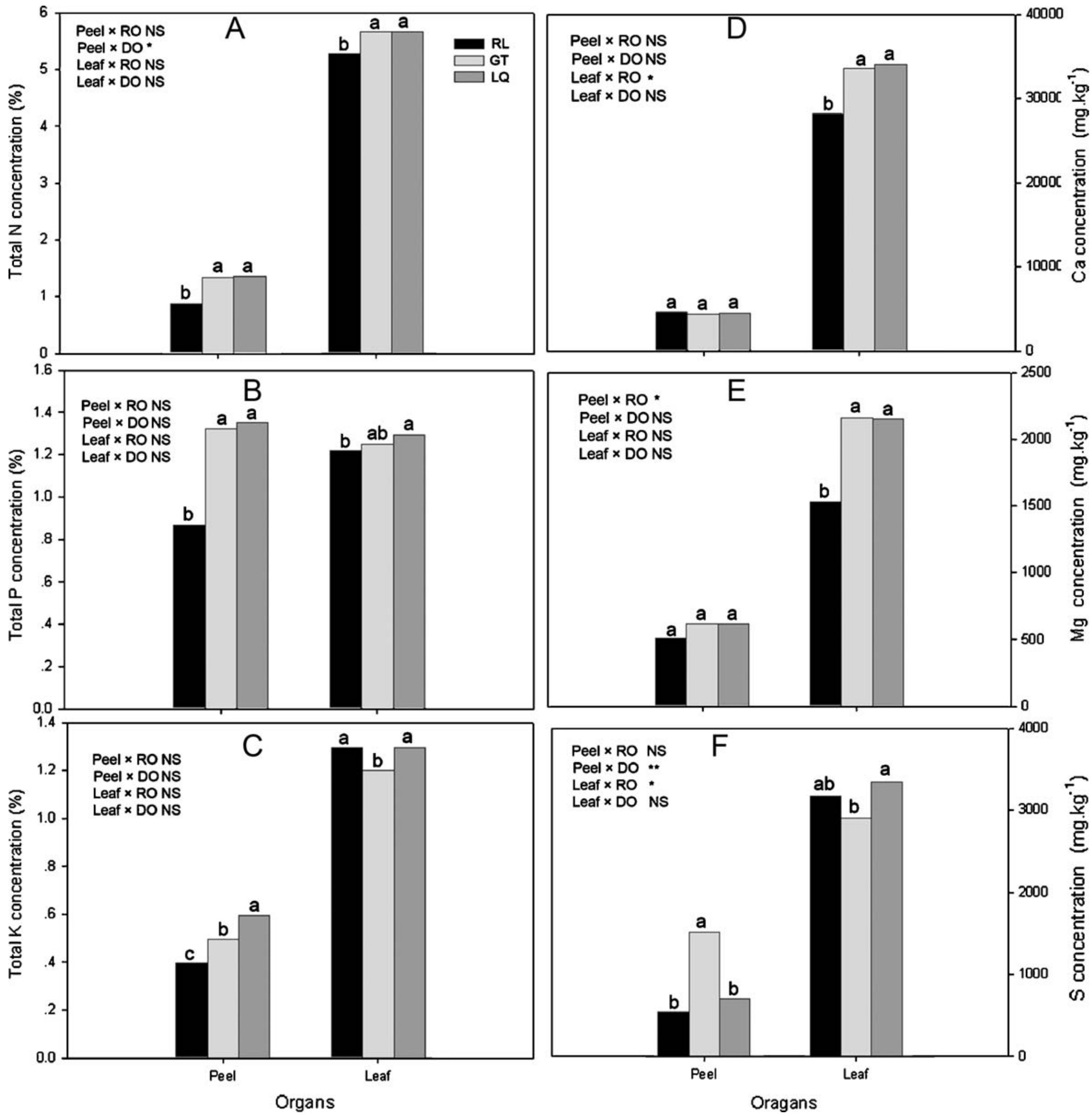

Fig. 2. Effect of the rootstock on the mean mineral nutrient concentrations in leaf and peel ($n = 6$), and correlation between mineral nutrient concentrations in leaf and peel and the fruit RO and DO of 'Hamlin' sweet orange. (A) Total N, (B) Total P, (C) Total K, (D) Ca^{2+}, (E) Mg^{2+} and (F) S. Each value is the mean of six individual replicates ($n = 6$). Different lower-case letters in the same columns indicate significant differences between Hamlin with each rootstock ($P < 0.05$). Ns, *, and ** indicate no significance or significant differences at $P < 0.05$ and 0.01, respectively, for the two-way interaction between the rootstock and mineral nutrient concentrations in leaf and peel. Abbreviations: LC = Lichi16-6 trifoliata; GT = Goutouchen sour orange; RL = Rangpur lime.

Mg^{2+}, Ca^{2+}, and P concentrations were determined by inductively coupled plasma emission optical spectrometry (Iris Intrepid II; Thermo Electron Corporation, Franklin, MA) after acid digestion in HNO_3:H_2O_2 (5:3, v/v).

2.5. Leaf gas exchange parameters

The net assimilation of CO_2 (ACO_2), stomatal conductance (GS), intercellular CO_2 concentration (Ci), transpiration rate (ET), and instantaneous leaf water use efficiency (WUE = ACO_2/ET) were measured using a portable photosynthesis system on September 16, 2008 (model LCA-4; ADC BioScientific, Hoddesdon, Hertfordshire, UK) and a PLC-4N leaf chamber (11.35 cm^2) configured as an open system. All measurements were made in the morning from 08:00 to 10:00 am to avoid high temperatures and low humidity in the afternoon. During all measurements, leaf temperature was 31 ± 1 °C and leaf-to-air vapor pressure difference was 1.6 ± 0.4 kPa within the cuvette.

2.6. Data analysis

All statistical analyses were performed using SPSS 17.0 (SPSS Inc., Chicago, IL), and the data presented here are expressed as means ± s.d. of six independent replicates for each treatment. One-way analysis of variance was used to compare the means. After analysis using Levene's test, means with equal variance were tested by least-squares determination, whereas means with unequal variance were analyzed using Dunnett's T3 test. Differences at $P < 0.05$ were considered significant.

3. Results

3.1. Oleocellosis

The data of Fig. 1 showed that fruits from trees budded on Rangpur lime had lower values for fruit oleocellosis parameters, including DO and RO, than those on other rootstocks. Whilst, both fruits from trees on Lichi16-6 trifoliata and Goutou orange had significant higher DO than from Rangpur lime (Fig. 1), and the causation of high DO were different. And high DO of fruits from trees on Lichi16-6 trifoliata was due to the higher RO than from other rootstocks, however, high DO of fruits from trees on Goutou orange resulted from the higher average oleocellosis spots size than from other rootstocks. Therefore, trees on Goutou orange, Lichi16-6 trifoliata, and Rangpur lime were selected for further study.

3.2. Growth

As shown in Table 1, the rootstocks had a significantly influence on tree height, canopy diameter, tree volume, scion and stock trunk girth of 'Hamlin' sweet orange trees. In the 2007/2008 seasons, 'Hamlin' sweet orange trees budded on Rangpur lime was significantly taller than those on Lichi16-6 trifoliata or Goutou orange, and there was no significant difference in the heights of the shorter trees on Lichi16-6 trifoliata or Goutou orange. Trees grafted onto Rangpur lime or Goutou orange showed the largest and smallest canopy diameters, respectively. In the end, trees budded onto Rangpur lime had the greatest volume, significantly different from the volumes of those on Lichi16-6 trifoliata and Goutou orange, and trees budded on Lichi16-6 trifoliata and Goutou orange were significantly smaller than those budded on other rootstocks. Those budded on Goutou orange had the smallest volume, differing significantly from those on the other rootstocks studied. Whilst, trees on Rangpur lime and Lichi16-6 trifoliata had greater scion trunk girth than trees on Goutou orange. Trees on Lichi16-6 trifoliata and Goutou orange had greater stock girth than those on Rangpur lime. The ratio between scion and rootstock trunk girth is used as a scion/rootstock affinity indicator, with values close to 1 associated with very good affinity (Bisio et al., 2000). Finally, the greatest affinity was found with Rangpur lime, which showed the highest scion/stock ratio (0.93). The lowest affinity was found with Lichi16-6 trifoliata and Goutou orange (0.79 and 0.69, respectively).

3.3. Mineral nutrient concentrations

Under the same field management conditions, trees on Rangpur lime had lower total N, total P, K^+, and S concentrations in peel, and lower total N, total P, Ca^{2+}, and Mg^{2+} concentrations in leaves than those on Lichi16-6 trifoliata and Goutou orange, whereas the Ca^{2+} and Mg^{2+} concentrations in peel were similar in trees on Rangpur lime, Lichi16-6 trifoliata, and Goutou orange. Trees on Goutou orange and Lichi16-6 trifoliata had higher total N, total P, K^+, and leaf Ca^{2+} and Mg^{2+} concentrations in peel and leaf than trees on Rangpur lime. However, trees on Goutou orange had the highest S concentrations in peel and the lowest S and K^+ concentrations in leaves (Fig. 2). The fruit RO was significantly correlated with the leaf Ca^{2+} and S concentrations and the peel Mg^{2+} concentration, and the fruit DO was significantly correlated with the total N and S concentrations in peel (Fig. 2).

3.4. Leaf gas exchange parameters

Leaves from trees on Goutou orange had the highest GS and ET values, followed by those on Rangpur lime, and the lowest values were in leaves from trees on Lichi16-6 trifoliata. However, leaves from trees on Lichi16-6 trifoliata had the highest WUE, followed by those on Rangpur lime, and the lowest WUE values were in leaves from trees on Goutou orange. Leaves from trees on Rangpur lime showed higher ACO_2 values than trees on Goutou orange or Lichi16-6 trifoliata (Fig. 3). Whilst, all leaf gas exchange parameters (GS, ET, ACO_2, and WUE) had a significant correlation with the RO ($P<0.01$), and the leaf gas exchange parameters (GS, ACO_2, and WUE) also had a significant correlation with the DO (Table 2).

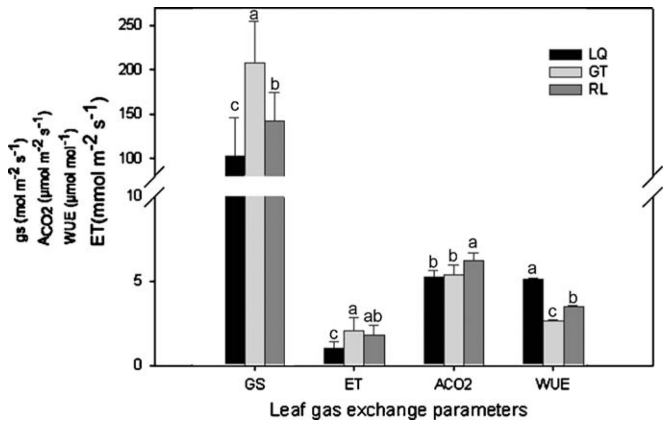

Fig. 3. Effects of three rootstocks on the ACO_2 (mmol m^{-2} s^{-1}), GS (mol m^{-2} s^{-1}), ET (mmol m^{-2} s^{-1}), and water-use efficiency (ACO_2/ET, mmol mol^{-1}) of 'Hamlin' sweet orange leaves. Each value is the mean of six individual replicates (±s.d.). Different lower-case letters in the same columns indicate significant differences between Hamlin with each rootstock ($P<0.05$). Significant differences ($P<0.05$) between treatments are denoted with different lower-case letters. *Abbreviations*: LC = Lichi16-6 trifoliata; GT = Goutouchen sour orange; RL = Rangpur lime.

3.5. RO and DO curve estimation with leaf gas exchange parameters

To better elucidate the relationships between the fruit oleocellosis parameters (RO and DO) and leaf gas exchange parameters, curve fitting was performed to establish regression models between fruit RO and DO and leaf gas exchange parameters (GS, ET, ACO_2, and WUE). RO models with GS, ET, and WUE were $y=4.54000-0.05112x+0.00015x^2$ with $R^2=0.922$, $y=2.60617-2.28518x+0.54049x^2$ with $R^2=0.909$, and $y=1.57232-0.89042x+0.14563x^2$ with $R^2=0.889$, respectively. DO models with GS, ET, and WUE were $y=5.78930-0.07741x+0.00027x^2$ with $R^2=0.943$, $y=3.23760-3.85440x+1.26553x^2$ with $R^2=0.520$, and $y=7.61840-3.75557x+0.46743x^2$ with $R^2=0.822$, respectively (Fig. 4). These results show that the RO and DO decreased significantly when the GS, ET, and WUE varied from 140 to 180 mol m^{-2} s^{-1}, from 1.5 to 2.0 m m^{-2} s^{-1}, and from 3.0 to 4.0 mmol mol^{-1}, respectively. Whilst, the disorder in fruit was due to losing balance of tree water metabolism. However, RO and DO models with ACO_2 were $y=\exp(-9.49240+47.92362/x)$ with $R^2=0.754$, and $y=74927.99389\exp(-2.11593x)$ with $R^2=0.644$ (Fig. 5), respectively. These results show that the RO and DO decreased significantly with increasing ACO_2.

4. Discussion

Oleocellosis has been observed during not only post-harvest storage (Alférez and Zacarías, 2001) but also in the on-tree stage. On-tree oleocellosis is thought to be caused by unfavorable climatic conditions, an insect piercing an oil gland, or rubbing by twigs triggered by wind. However, the causal factors and mechanism of action of oleocellosis are unknown.

Table 2
Correlation between oleocellosis parameters (RO and DO) and leaf gas exchange parameters.

Pearson correlation	GS	ET	ACO_2	WUE
RO	−0.694**	−0.855**	−0.773**	−0.847**
DO	−0.642**	−0.399	−0.647**	−0.512*

Note: Each oleocellosis parameters (RO and DO) and leaf gas exchange parameters data corresponds to the mean (±s.e.) of 30 fruits and 10 leaves, respectively.

* Indicates significant differences at $P<0.05$ ($n=18$).

** Indicate significant differences at $P<0.01$ ($n=18$).

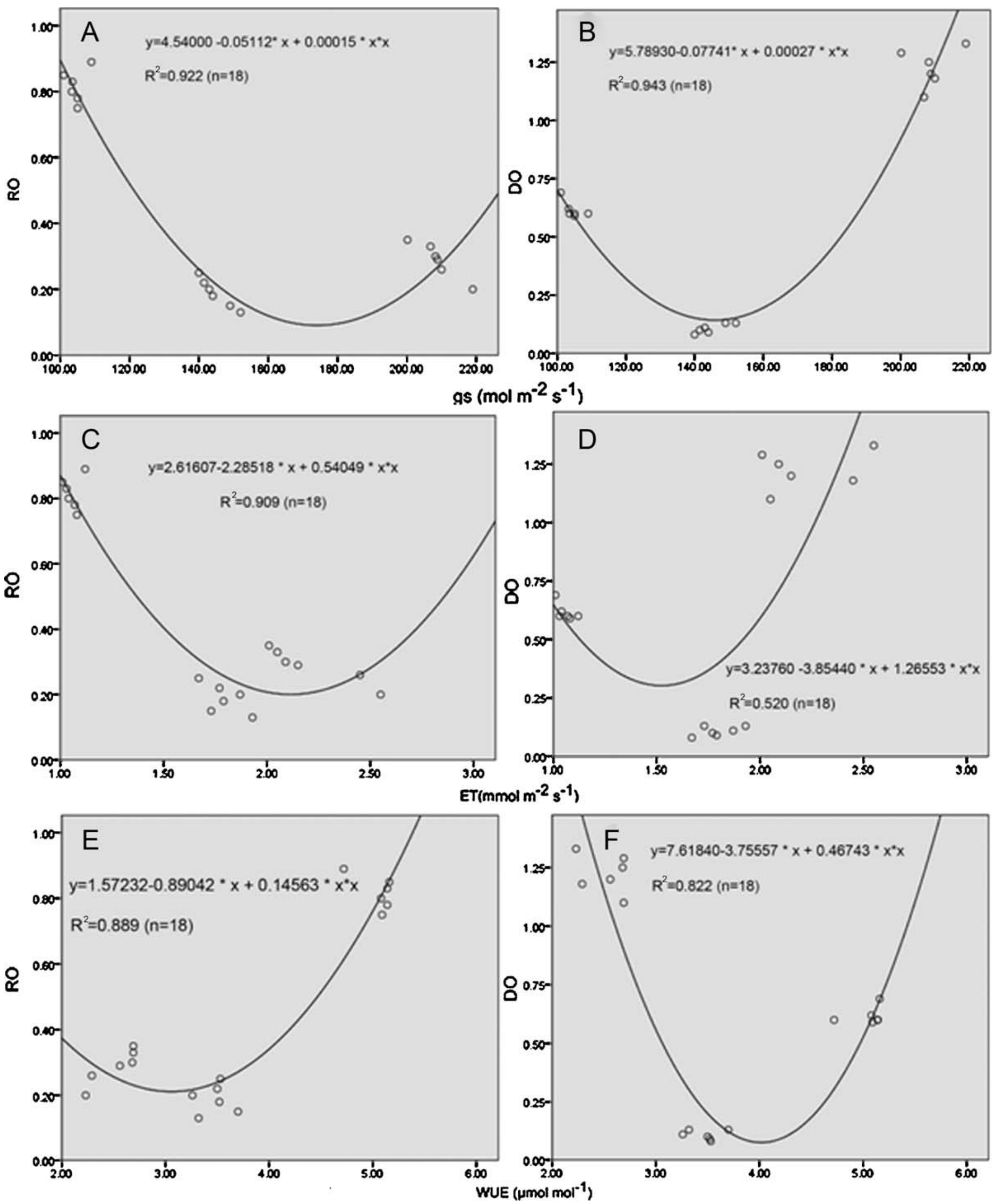

Fig. 4. Fruit RO and DO models with GS, ET, and WUE of 'Hamlin' sweet orange leaves. (A) RO model with GS. (B) DO model with GS. (C) RO model with ET. (D) DO model with ET. (E) RO model with WUE. (F) DO model with WUE.

4.1. Tree growth and oleocellosis

It is clear that the rootstock affect the overall tree performance (Cantuarias-Avilés et al., 2010) (Table 1). Our results indicate that the scion/rootstock affinity had a significant influence not only on scion and rootstock growth (tree height, canopy diameter, and tree volume) but also on oleocellosis development (RO and DO) (Table 1 and Fig. 1). Trees on Rangpur lime showed significantly increased tree height, canopy diameter, and tree volume, and the scion/stock girth ratio was 0.93. In contrast, trees on Goutou orange showed significantly reduced tree height, canopy diameter, and tree volume, and the scion/stock girth ratio was only 0.69 (Table 1). The fruit RO and DO were significantly higher in trees on Goutou orange than in trees on Rangpur lime (Fig. 1). These results indicated that the RO and DO can be used as scion/rootstock affinity indicators like the scion/stock girth ratio (Bisio et al., 2000), and the development of oleocellosis may be due to the scion/stock affinity.

4.2. Mineral nutrition and oleocellosis

As reported previously, the rootstock significantly influenced the nutritional status of scions (Wutscher and Shull, 1976; Georgiou, 2000, 2002) (Fig. 2), Our results indicate that the total N, total P, Ca^{2+}, and Mg^{2+} in leaves from trees on Rangpur lime were

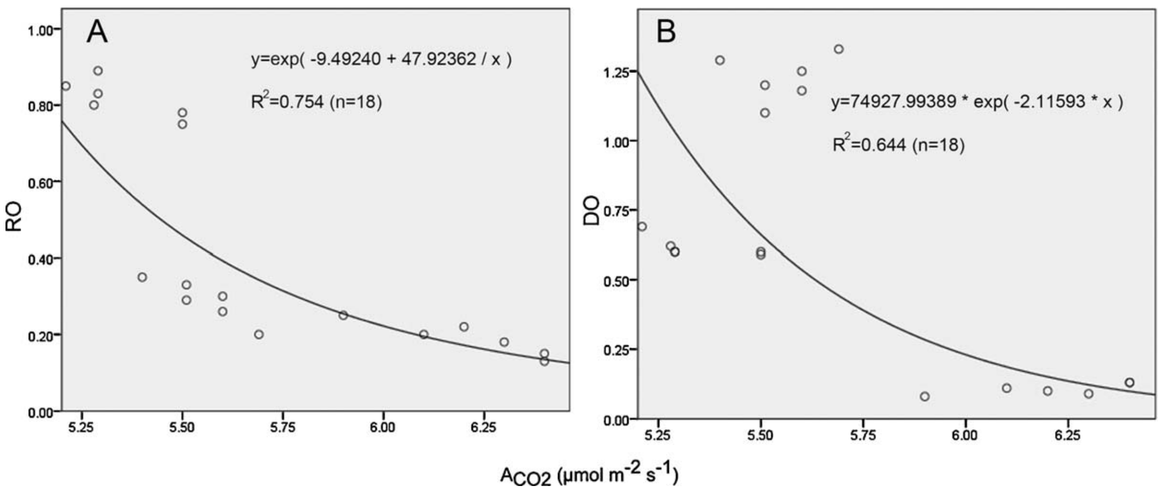

Fig. 5. Fruit RO and DO models with ACO_2 (mmol m^{-2} s^{-1}) of 'Hamlin' sweet orange leaves. (A) RO model with ACO_2. (B) DO model with ACO_2.

significantly lower than in leaves from trees on Goutou orange and Lichi16-6 trifoliata, likely reflecting differences in the capacities of the rootstocks for water and mineral uptake and the physical characteristics of the root systems (Castle and Krezdorn, 1975). Whilst, the fruit RO showed a significant correlation with the Ca^{2+} and S concentrations in leaves and the Mg^{2+} concentration in peel, the fruit DO showed a significant correlation with the total N and S concentrations in peel (Fig. 2). The most interesting is that the lower RO and DO values of fruit from trees on Rangpur lime were due to the significantly lower leaf Ca^{2+} concentrations as compared to fruits from trees on Goutou orange and Lichi16-6 trifoliata, and not to the Ca^{2+} concentrations in peel (Fig. 2D).

4.3. Leaf gas exchange parameters and oleocellosis

As previously reported, Ca^{2+} signal transduction pathways are involved in water metabolism by regulating stomatal movements (Michael, 2000). Our results indicate that the significant increase in Ca^{2+} and decrease in K^+ in leaves from trees on Goutou orange as compared to trees on Rangpur lime resulted in significantly lower WUE, higher GS and ET significantly in leaves from trees on Goutou orange than from trees on Rangpur lime (Fig. 3), and that will lead to leaves' water loss seriously and water stress of plant. However, leaves from trees on Lichi16-6 trifoliata with the highest WUE, lowest GS and ET will result in high temperature of leaves. Finally, fruits from trees on Goutou orange had a significantly higher DO than those on Rangpur lime and Lichi16-6 trifoliata, and fruits from Rangpur lime showed lower RO and DO values than trees on Goutou orange or Lichi16-6 trifoliata (Fig. 1). Whilst, in our other studies, spraying low calcium fertilizers concentration ($\leq$0.25%) to crown trees with different Ca^{2+} level soil background (relatively scarce and abundant) that led leaf gas exchange parameters (GS, ET and WUE) to intermediate levels resulted in decreasing the oleocellosis (RO and DO) significantly (Zheng et al., 2009). These results partially disagree with Martínez-Romero et al. (1999), and they found calcium treatment could make the fruit less susceptible to mechanical damage due to increasing fruit firmness by its role in cross-linking pectic substances in the cell wall with the increasing Ca^{2+} in peel (Klein and Lurie, 1994; Conway et al., 1997). It may be due to water metabolism that controlled by Ca^{2+} in leaves playing a more important role in on-tree oleocellosis regulation than cell wall metabolism that controlled by Ca^{2+} in peel.

Based on our data and those of other studies, we conclude that water relations and the mineral nutrition balance are involved in the regulation of oleocellosis development. These results provide a theoretical basis for the development of techniques to control oleocellosis. However, the mechanisms how water metabolism and mineral nutrition metabolism especially for Ca^{2+} of plant take part in control RO and DO are still needed to study further.

Acknowledgements

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