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ARTICLE

Effects of *Actinidia valvata* Rootstock on Photosynthetic Characteristics, Carbohydrate Metabolism, and Fruit Quality of *Actinidia deliciosa* cv. 'Guichang'

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ABSTRACT: Rootstock plays an important role in commercial horticultural production by influencing scion growth, physiology, and fruit quality. However, information on the effects of different rootstocks on kiwifruit growth and fruit quality remains limited. In this study, *Actinidia valvata* was evaluated as an experimental rootstock and compared with the commonly used *A. deliciosa* rootstock to investigate their effects on photosynthetic characteristics, carbohydrate metabolism, and fruit quality of *A. deliciosa* cv. 'Guichang'. Leaf photosynthetic parameters, fruit quality attributes, carbohydrate contents, and the activities of enzymes related to sucrose and starch metabolism were investigated during fruit development and postharvest ripening. The results showed that vines grafted onto *A. valvata* exhibited higher photosynthetic performance at certain developmental stages. Favorable changes were also detected in several physiological indicators associated with starch and sugar accumulation. In addition, fruits from plants grafted onto *A. valvata* exhibited enhanced activities of key enzymes involved in sucrose and starch metabolism at specific sampling stages. However, for many measured variables and time points, no significant differences were detected between the two rootstocks. Overall, these results suggest that *A. valvata* has potential as an alternative rootstock for 'Guichang' kiwifruit, particularly with respect to carbohydrate metabolism, although its overall performance was broadly comparable to that of *A. deliciosa*.

KEYWORDS: *Actinidia valvata*; rootstock; gas exchange; sucrose metabolism; enzyme activity

1 Introduction

The genus *Actinidia*, which originated in China and comprises approximately 54 species, includes perennial deciduous woody vines that were domesticated during the last century [1,2]. Kiwifruit is valued for its high nutritional quality, as its fruits are rich in vitamins, calcium, iron, potassium, and other essential minerals, and contain 17 amino acids important for human health, along with diverse and attractive flesh colors [3]. Consequently, kiwifruit production and its economic value have expanded remarkably worldwide over the past three decades [4].

In commercial fruit tree production, scion cultivars are commonly grafted onto selected rootstocks that provide anchorage and support water and nutrient uptake. Appropriate rootstock selection can strongly influence flowering, fruit set, yield, fruit quality, and adaptability to local soil and climatic conditions [5]. In major fruit crops, such as apple, citrus, and grape, extensive breeding efforts have been devoted to the selection and development of superior rootstocks that enhance soil adaptation, environmental resilience, and fruit quality for sustainable commercial production [6–10]. Superior rootstock systems can improve scion performance through multiple physiological and biochemical mechanisms, including enhanced tolerance to abiotic stresses such as drought and waterlogging, increased resistance to pests and diseases, and optimized nutrient uptake and translocation, ultimately contributing to improved fruit quality [7,11]. Therefore, identifying and breeding rootstocks that confer improved fruit quality and adaptability to local environments have become key research priorities in fruit tree rootstock development [12].

In kiwifruit production, *A. chinensis* and *A. deliciosa* seedlings have traditionally been used as rootstocks, with *A. deliciosa* being the most widely applied due to its high and uniform germination rate [13,14]. However, these conventional seedling rootstocks often have succulent roots and relatively poor tolerance to drought and flooding stresses, which may restrict their performance under unfavorable soil and climatic conditions [15]. Therefore, screening alternative *Actinidia* species with stronger adaptability and potential beneficial effects on scion growth and fruit quality is of practical importance. Nevertheless, comprehensive studies on kiwifruit rootstock systems remain limited, particularly regarding alternative *Actinidia* species with potential as rootstock candidates [16].

Currently, in addition to *A. chinensis* and *A. deliciosa*, other *Actinidia* species have begun to be used as rootstocks to address challenges faced by the kiwifruit industry, such as drought, waterlogging, and disease stress [16]. Among these species, *A. valvata* has shown promising potential as an alternative rootstock. Previous studies have shown that, compared with traditional rootstocks, *A. valvata* can effectively promote plant growth, improve fruit characteristics, and increase the average fruit weight of the 'Jinmei' kiwifruit cultivar [17]. Further analyses revealed that, under flooding stress, the *A. valvata* root system maintains strong energy metabolism and metabolite accumulation capacity and exhibits enhanced glucose metabolism and respiratory regulation, thereby supporting vigorous plant growth [18]. These characteristics suggest that *A. valvata* may be a valuable alternative rootstock, especially in production areas exposed to excessive rainfall, poor drainage, or other abiotic stress conditions. However, its effects on scion photosynthetic performance, fruit carbohydrate accumulation, and sugar–starch metabolism remain insufficiently understood.

'Guichang', a cultivar belonging to *A. deliciosa*, was discovered in the wild in Guizhou Province during the 1980s [1]. It has become one of the dominant local cultivars and is characterized by long cylindrical fruits, green flesh, a pleasant sweet–acid flavor, and excellent storage capacity under the local climatic conditions of Guizhou [1,19]. The vines also exhibit high productivity and maintain a favorable sugar–acid balance and rich flavor. Traditionally, *A. deliciosa* seedlings have been used as rootstocks in the commercial production of 'Guichang' kiwifruit.

Therefore, this study evaluated the effects of *A. valvata* rootstock on leaf photosynthetic performance, fruit quality, and enzyme activities associated with sucrose and starch metabolism in the scion cultivar *A. deliciosa* cv. 'Guichang', using the traditionally applied *A. deliciosa* rootstock as a reference. This study aimed to clarify the potential of *A. valvata* as an alternative rootstock for 'Guichang' kiwifruit and to provide a theoretical basis for rootstock selection, fruit quality improvement, and the sustainable development of the local kiwifruit industry.

2 Materials and Methods

2.1 General Experimental Site Information

The experiment was conducted from May to September, corresponding to the kiwifruit growth season. The orchards were located in Fuyu Village, Gubao Town, Xiuwen County, Guiyang City, Guizhou Province, China. Kiwifruit vines were trained on T-shaped trellises and planted at a row spacing of 2 m × 4 m (row × plant). All fertilization, irrigation, pruning, and other routine orchard management practices were following standard orchard management. Vines showing visible symptoms of disease, pest damage, mechanical injury, nutrient deficiency, drought stress, or waterlogging stress were excluded. Non-infested vines were therefore defined as vines with normal growth and without visible biotic or abiotic stress symptoms at the time of sampling.

2.2 Test Material

'Guichang' (*A. deliciosa*) were grafted onto *A. valvata* ('Av') and *A. deliciosa* ('Ad') rootstocks, respectively. All vines were 6 years old at the time of the experiment. Ten non-infested plants grafted vines were selected for each scion–rootstock combination.

Fruit samplings began 28 days after pollination (DAP) and was conducted at 28-day intervals until the fruits reached physiological maturity, corresponding to a soluble solid content of approximately 7–8%. A total of five sampling points were included, representing key stages of fruit development at 28, 56, 84, 112 and 140 DAP.

After harvest, the fruits were stored at 25°C, and samples were collected every 3 days until the fruits softened and fully ripened. Post-harvest sampling was performed at 4, 7, 10, 13, 16 days after harvest (DAH). For each sampling time, 15–20 non-infested fruits were randomly selected for measurement of fruit dimensions and fruit quality analysis.

Following quality assessment, the fruit skin was removed, and the flesh was cut into small pieces, immediately frozen in liquid nitrogen, and stored at −80°C for subsequent biochemical analyses.

2.3 Determination of Photosynthetic Characteristics

In this study, fully expanded spring leaves of 'Guichang' kiwifruit grafted onto two rootstocks were measured. At this stage, both the petiole and leaf blade had reached their average size for the year. Measurements were conducted from May to September in the morning (08:00–11:00) under clear and calm weather conditions. For each scion–rootstock combination, three healthy leaves per vine were selected from three vines, resulting in a total of nine leaves per treatment. All sampled vines exhibited similar growth status, and measurements avoided the midrib region and newly emerged leaves. The parameters recorded included net photosynthetic rate (*Pn*, $\mu molm^{-2}{\cdot}s^{-1}$), transpiration rate (*Tr*, $mmol{\cdot}m^{-2}{\cdot}s^{-1}$), stomatal conductance (*Gs*, $mol{\cdot}m^{-2}{\cdot}s^{-1}$), and intercellular CO_2 concentration (*Ci*, $\mu mol{\cdot}mol^{-1}$). Leaf photosynthetic parameters were measured using a LI-6800 portable photosynthesis system (LI-COR Biosciences, Lincoln, NE, USA) according to the manufacturer's standard operating procedures.

2.4 Determination of Fruit Quality and Carbohydrate Contents

The soluble solid content (SSC, °Brix) was measured using a PAL-8 portable digital refractometer (ATAGO, Tokyo, Japan). Titrable acid (TA, %) was determined by acid-base titration according to the Experimental Guidance on Postharvest Physiology and Biochemistry of Fruit and Vegetables with slight modifications [20].

The contents of starch, total soluble sugars, sucrose, glucose, and fructose were determined using commercial assay kits purchased from Suzhou Mengxi Biotechnology Co., Ltd. (Suzhou, China), following the manufacturer's instructions. Total soluble sugars refer to the collective pool of soluble carbohydrates present in the fruit tissue. The contents of starch, total soluble sugars, sucrose, glucose, and fructose were expressed as $mg \cdot g^{-1}$ FW. All measurements were performed using three biological replicates.

Fruit fresh weight was measured using an electronic balance with an accuracy of 0.01 g. A 2–3 mm thick equatorial slice from each fruit was weighed to record the fresh weight, then oven-dried at 65°C for 24 h to constant weight, and subsequently reweighed to obtain the dry weight. The measurements were repeated ten times (n = 10). Dry matter content (DMC) was calculated as the ratio of dry weight to fresh weight [21].

2.5 Analysis and Determination of the Related Enzyme Activities in Fruit

Sucrose phosphate synthetase (SPS), sucrose synthase activity in the cleavage direction (SS-C), sucrose synthase activity in the synthesis direction (SS-S), soluble acid invertase (S-AI), neutral invertase (NI), hexokinase (HK), α-amylase, β-amylase and ADP-glucose pyrophosphorylase (AGP) were determined using commercial assay kits (Suzhou Mengxi Biotechnology Co., Ltd., Suzhou, China). All measurements were performed with three biological replicates.

2.6 Data Analysis

Data were preliminarily processed using Microsoft Excel 2010. Statistical analyses were performed using GraphPad Prism 10 (GraphPad Software, San Diego, CA, USA). For each parameter, the data were analyzed using two-way *ANOVA*, with rootstock and sampling time as factors. Because the objective of this study was to evaluate the effect of rootstock at each developmental or ripening stage, multiple comparisons were restricted to differences between the two rootstocks within the same sampling time using the built-in multiple comparisons procedure in GraphPad Prism. Differences were considered statistically significant at $p < 0.05$.

3 Results

3.1 Photosynthesis during Fruit Development as Affected by Rootstock

As shown in Fig. 1, during all sampling points throughout fruit development of 'Guichang' kiwifruit, all parameters were measured on scion leaves. The net photosynthetic rate (*Pn*), transpiration rate (*Tr*), and stomatal conductance (*Gs*) of leaves in both scion-rootstock combinations exhibited a similar pattern, initially increasing and then declining. For Pn and Tr, values in 'Av' were generally higher than those in 'Ad' ($p < 0.05$), with both parameters peaking at 56 DAP (Fig. 1a,b). Intercellular CO_2 concentration (*Ci*) remained relatively stable throughout development, with a significant difference observed between 'Av' and 'Ad' only at 28 DAP ($p < 0.05$); no significant differences were detected at subsequent stages. Gs peaked at 56 DAP for both combinations, and values at 28 and 56 DAP were significantly higher in 'Av' than that in 'Ad' ($p < 0.05$) (Fig. 1c,d). The results showed that, in comparison to 'Ad', the *A. valvata* ('Av') rootstock enhanced leaf photosynthetic capacity of 'Guichang' kiwifruit during the critical early developmental stage of fruitlets (28–56 DAP).

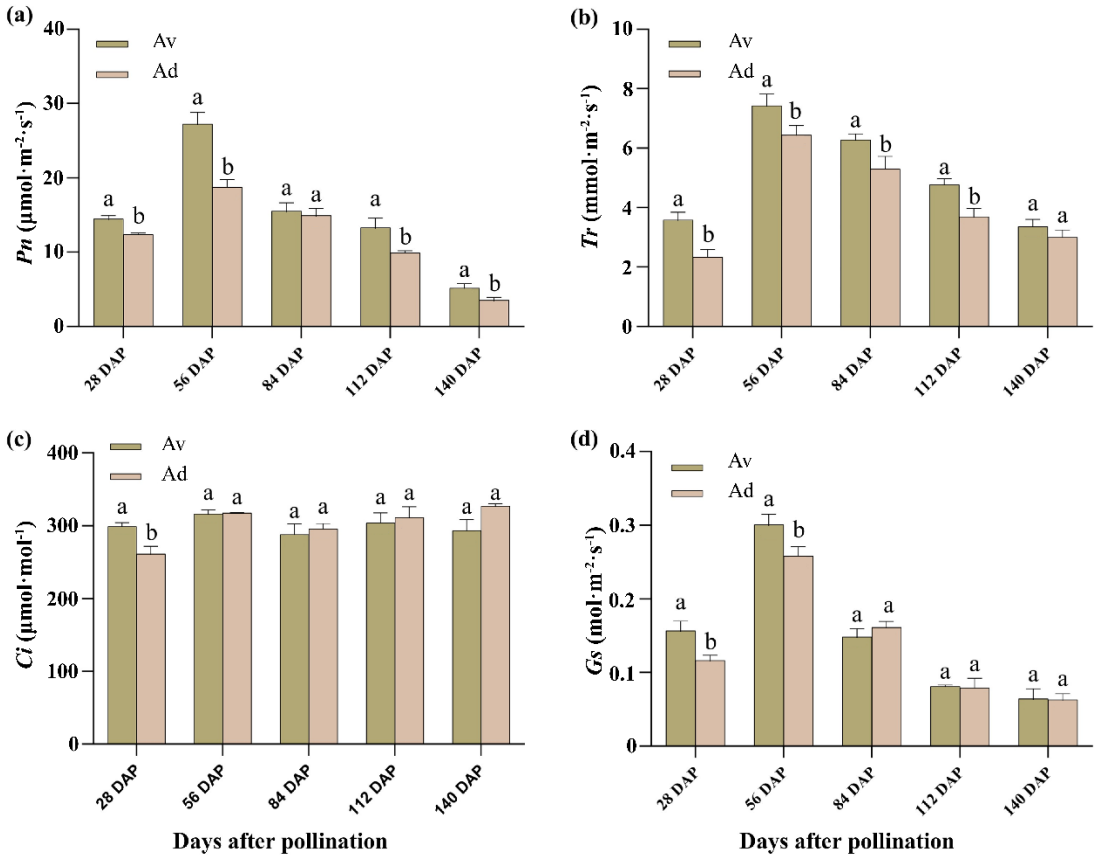

Figure 1: Photosynthetic responses of 'Guichang' kiwifruit grafted onto *Actinidia valvata* 'Av' and *Actinidia deliciosa* 'Ad' rootstocks. (**a**) Net photosynthetic rate (*Pn*); (**b**) transpiration rate (*Tr*); (**c**) stomatal conductance (*Gs*); and (**d**) intercellular CO_2 concentration (*Ci*). Statistical comparisons were performed separately at each sampling time. Different letters above the bars within the same sampling time indicate significant differences at $p < 0.05$. Vertical bars represent the standard error of the mean.

3.2 Carbohydrate Accumulation and Metabolism of 'Guichang' Kiwifruit Fruit in 'Av' and 'Ad' Grafting Combinations during Growth on Vines and Ripening Off Vines

As shown in Fig. 2a, fruit starch content in both scion-rootstock combinations initially increased and then decreased during fruit development, reaching a peak at 112 DAP. Across all sampling stages, starch content in 'Av' was generally higher than in 'Ad', with a significant difference observed ($p < 0.05$).

Regarding sugar accumulation, sucrose and fructose contents increased continuously throughout fruit development and postharvest ripening (Fig. 2b,c). During fruit development on the vine, sucrose content fluctuated in both 'Av' and 'Ad', with several significant differences observed ($p < 0.05$). However, during postharvest ripening, sucrose content in 'Av' showed numerically higher values than that in 'Ad', but the differences were not statistically significant (Fig. 2b).

Fructose content in 'Av' fruits was higher than in 'Ad' throughout fruit development, with significant differences at 28, 56, and 140 DAP ($p < 0.05$). During postharvest ripening, fructose remained higher in 'Av', with a significant difference observed only at 7 DAH (Fig. 2c).

Glucose content in both combinations generally increased until 56 DAP, decreased thereafter, and rose again after 112 DAP, reaching another peak at 126 DAP before stabilizing. At 28 DAP, glucose content was

significantly higher in 'Ad' than in 'Av' ($p < 0.05$), whereas at 56 DAP, 'Av' exhibited significantly higher glucose levels than 'Ad' ($p < 0.05$) (Fig. 2d).

Overall, these results indicate that the *A. valvata* ('Av') rootstock enhances starch accumulation during fruit development and promotes sucrose and fructose accumulation during postharvest ripening. Superior performance was observed at key developmental stages (28, 56, 84, and 140 DAP) and the early postharvest phase (7 DAH), suggesting the potential of 'Av' rootstock to improve fruit quality through optimized carbohydrate metabolism.

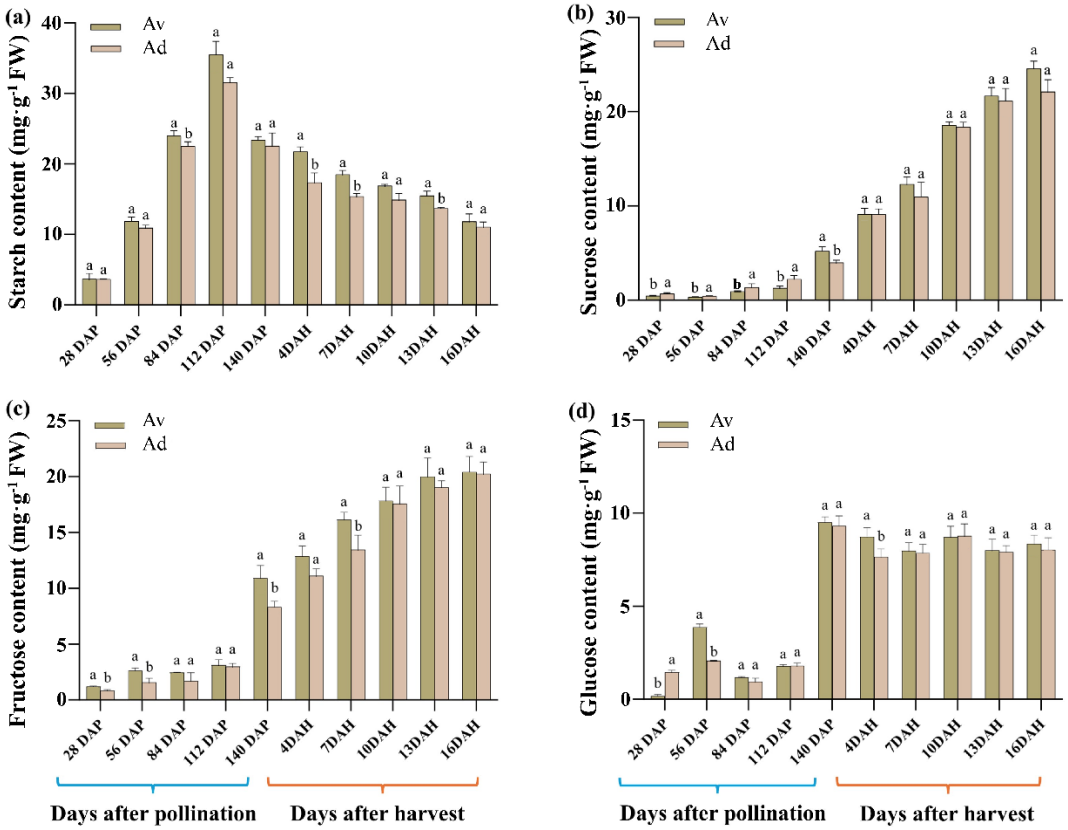

Figure 2: Effects of two rootstocks (*Actinidia valvata* 'Av' and *Actinidia deliciosa* 'Ad') on carbohydrate accumulation of 'Guichang' kiwifruit during on-vine fruit development and carbohydrate metabolism during postharvest ripening: (**a**) Starch content; (**b**) sucrose content; (**c**) Fructose content; (**d**) Glucose content. Different letters at the same sampling times indicate that a significance found at $p < 0.05$ between the two used rootstocks in the same period. Vertical bars represent the standard error of the mean.

3.3 Fruit Quality of 'Guichang' Kiwifruit in 'Av' and 'Ad' during On-Vine Growth and Off-Vine Ripening

DMC, SSC, total soluble sugar, TA, and sugar-acid ratio of 'Guichang' kiwifruit grafted onto the two rootstocks generally increased during fruit development on the vine and postharvest ripening (Fig. 3). Fruit weight was consistently higher in 'Av' than in 'Ad' at all sampling stages (Fig. 3a).

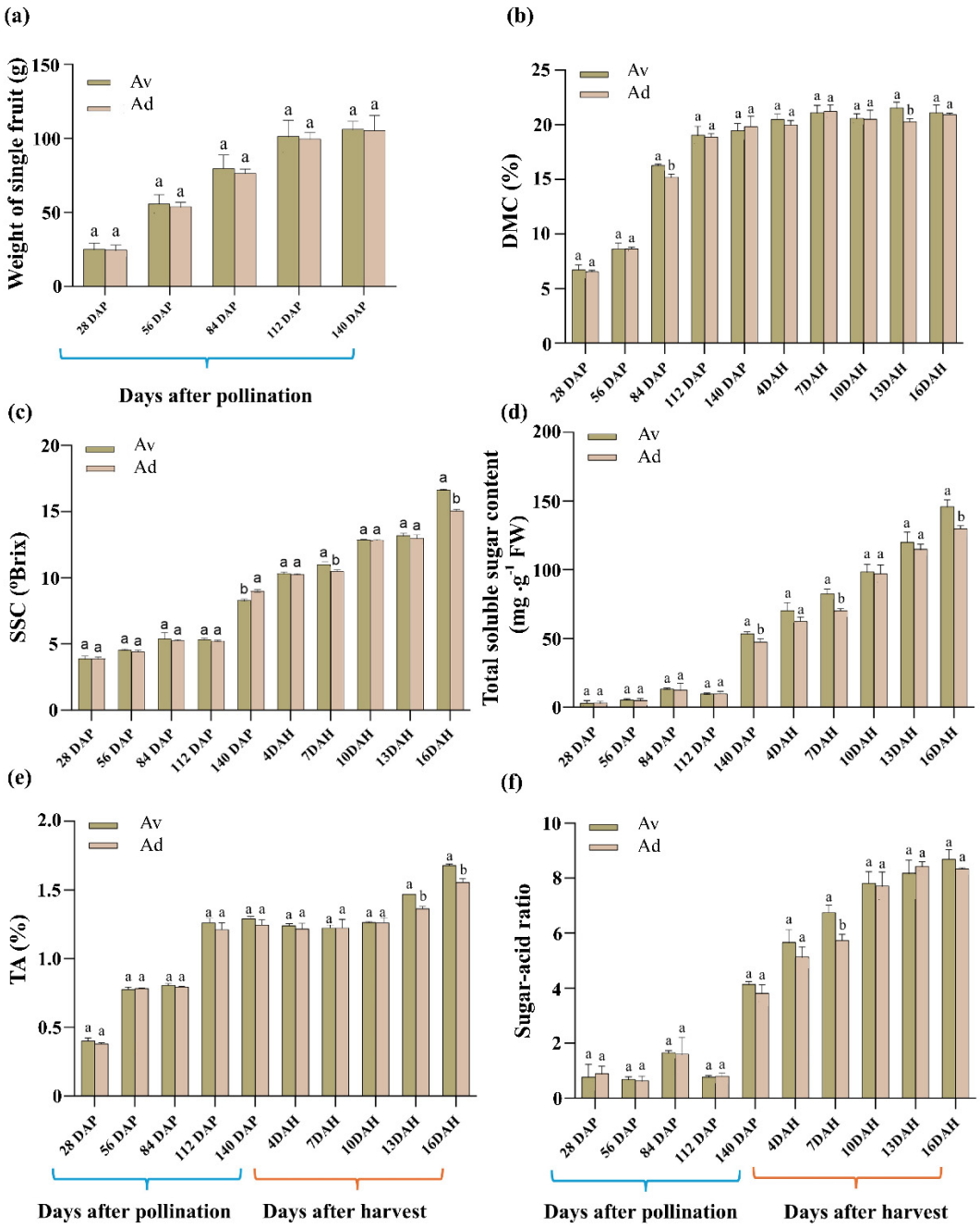

Figure 3: Effect of two rootstocks (*Actinidia valvata* 'Av' and *Actinidia deliciosa* 'Ad') on fruit quality of 'Guichang' kiwifruit; (**a**) Average fruit weight; (**b**) Dry matter content (DMC); (**c**) Soluble solids content (SSC); (**d**) Total soluble sugar content; (**e**) Titrable acid (TA); (**f**) Sugar-acid ratio. Different letters in the same column of the same sampling time indicate that a significant difference was detected at $p < 0.05$. Vertical bars represent the standard error of the mean.

For DMC, no significant differences were observed between the two rootstocks throughout fruit development, although a sharp increase occurred at 112 DAP, after which values stabilized (Fig. 3b). SSC and soluble sugar contents showed no significant differences at early developmental stages but increased

rapidly after 112 DAP. At 16 DAH, SSC in fruits grafted onto 'Av' was significantly higher than in those on 'Ad' ($p < 0.05$) (Fig. 3c,d).

TA values differed slightly between the two rootstocks, with 'Av' exhibiting significantly higher TA than 'Ad' at 13 and 16 DAH ($p < 0.05$) (Fig. 3e). The sugar–acid ratio of 'Av' fruits tended to be higher than that of 'Ad' at 16 DAH, although the difference was not statistically significant (Fig. 3f).

Overall, differences in fruit quality-related parameters between 'Av' and 'Ad' varied depending on the measured parameter and sampling stage, with more pronounced differences in SSC and TA during the late postharvest ripening stage.

3.4 Activities of Sucrose- and Starch-Metabolizing Enzymes in 'Guichang' Kiwifruit in 'Av' and 'Ad' during On-Vine Growth and Off-Vine Ripening

Enzyme activities in fruits grafted onto the two rootstocks ('Av' and 'Ad') exhibited similar temporal patterns during fruit development on the vine and postharvest ripening (Fig. 4). SS-C activity increased until 56 DAP, decreased to a minimum at 112 DAP, and then rose again during fruit development on the vine. During postharvest ripening, SS-C activity generally declined. Across most sampling points, SS-C activity in 'Av' fruits was higher than in 'Ad', with many differences being statistically significant ($p < 0.05$) (Fig. 4a).

SS-S activity decreased until 56 DAP, increased until at 112 DAP, and subsequently decreased again on the vine, reaching its lowest level at 4 DAH. During postharvest ripening, SS-S activity gradually increased, with significant differences observed only at 10 and 13 DAH (Fig. 4b).

Sucrose phosphate synthase (SPS) activity increased from 28 DAP to 10 DAH, peaking at 10 DAH, followed by a slight decline and subsequent stabilization. Greater fluctuations were observed in fruits on 'Ad' rootstock, whereas SPS activity in 'Av' fruits remained consistently higher than in 'Ad' at corresponding sampling points (Fig. 4c).

Soluble acid invertase (S-AI) activity was higher in 'Av' fruits than in 'Ad', with significant differences at 56–140 DAP, 7 DAH, and 16 DAH ($p < 0.05$) (Fig. 4d). Neutral invertase (NI) activity remained relatively stable during fruit development on the vine but fluctuated sharply during postharvest ripening. NI activity in 'Av' fruits was significantly lower than in 'Ad' at 84 DAP and 7–13 DAH ($p < 0.05$) (Fig. 4e).

Hexokinase (HK) activity generally increased during fruit development and postharvest ripening, with minor fluctuations. HK activity in 'Av' fruits was significantly higher than in 'Ad' during late fruit development and ripening ($p < 0.05$) (Fig. 4f).

β-Amylase activity in 'Av' fruits was higher than in 'Ad' during fruit development and at harvest, but declined below 'Ad' levels during postharvest ripening (Fig. 5a). α-Amylase activity increased continuously, with 'Av' fruits exhibiting higher activity than 'Ad' during development and ripening; significant differences were detected at 56–112 DAP and 10 DAH ($p < 0.05$) (Fig. 5b).

ADP-glucose pyrophosphorylase (AGP) activity increased sharply, peaking at 112 DAP, and then declined prior to harvest. During postharvest ripening, AGP activity remained relatively stable, with significant differences observed only at 56 and 112 DAP ($p < 0.05$) (Fig. 5c).

Overall, the *A. valvata* ('Av') rootstock affected the activities of key carbohydrate-metabolizing enzymes in 'Guichang' kiwifruit, including enzymes involved in sucrose synthesis (SS-S and SPS), sucrose cleavage or hydrolysis (SS-C, S-AI, and NI), starch biosynthesis (AGP), and starch degradation (α-amylase and β-amylase). These enhanced enzyme activities contributed to greater carbohydrate accumulation during fruit development and postharvest ripening, thereby supporting improved sugar content and overall fruit quality. In contrast, some enzymes such as neutral invertase (NI) exhibited lower activity in 'Av' fruits,

suggesting a possible modulation of sucrose hydrolysis pathways. Collectively, these findings indicate that *A. valvata* rootstock positively regulates carbohydrate metabolism in 'Guichang' fruits, promoting sugar accumulation and potentially enhancing flavor and quality during both developmental and ripening stages.

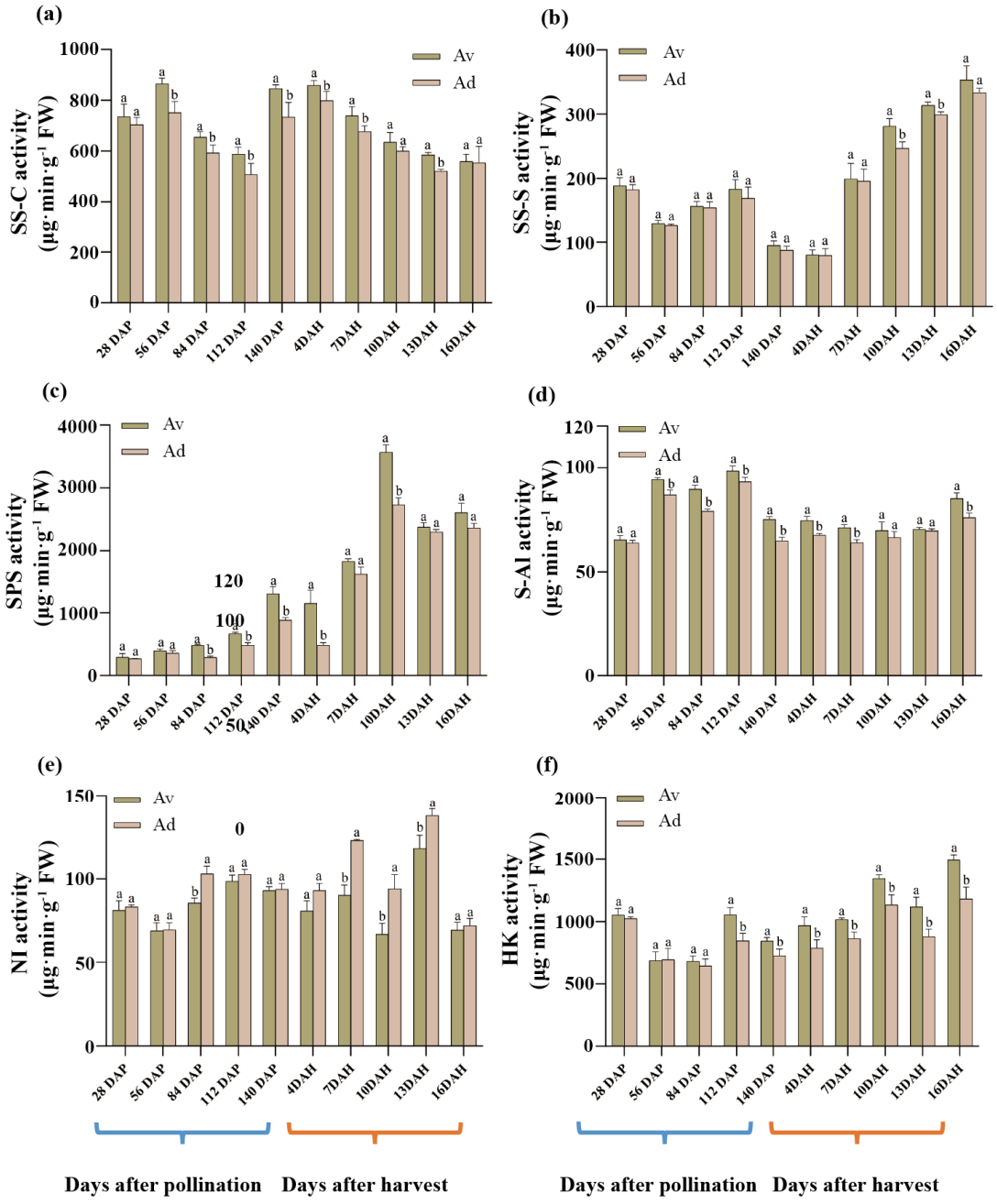

Figure 4: Variation patterns of sucrose- and starch metabolism-related enzyme activities in 'Guichang' kiwifruit grafted on two rootstocks (*Actinidia valvata* 'Av' and *Actinidia deliciosa* 'Ad'): (**a**) Sucrose synthase cleavage (SS-C); (**b**) Sucrose synthase synthesis (SS-S); (**c**) Sucrose phosphate synthetase (SPS); (**d**) Soluble acid invertase (S-AI); (**e**) Neutral invertase (NI); (**f**) Hexokinase (HK). Different letters at the same sampling times indicate that a significant difference is found at $p < 0.05$. Vertical bars represent the standard error of the mean.

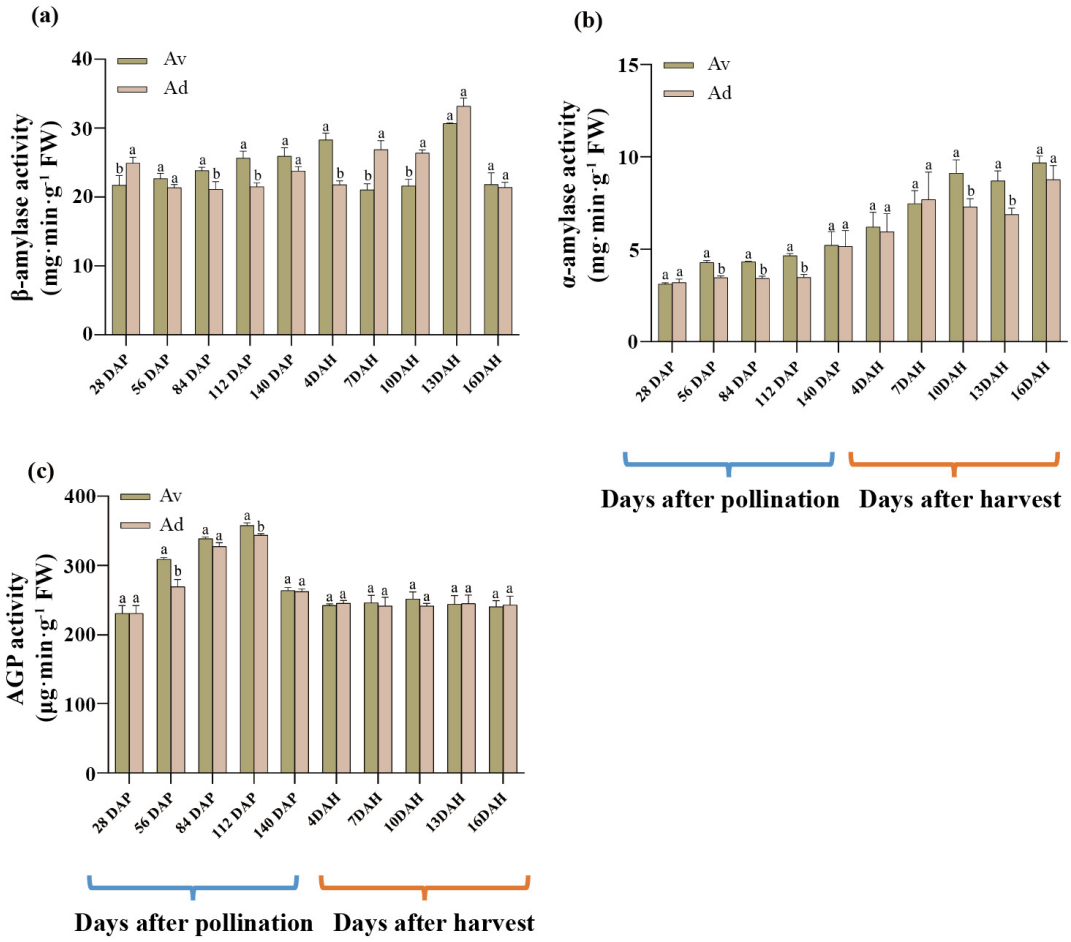

Figure 5: Variation patterns of sucrose- and starch metabolism-related enzyme activities in 'Guichang' kiwifruit grafted on two rootstocks (*Actinidia valvata* 'Av' and *Actinidia deliciosa* 'Ad'): (**a**) β-amylase; (**b**) α-amylase; (**c**) ADPG enzyme (AGP). Different letters at the same sampling times indicate that a significant difference is found at $p < 0.05$. Vertical bars represent the standard error of the mean.

4 Discussion

4.1 Photosynthetic Characteristics of 'Guichang' Kiwifruit as Affected by Rootstock

In modern horticulture, the use of novel germplasm as rootstock resources represents an important strategy for improving scion performance. Rootstocks can regulate scion physiological status, environmental adaptability, and fruit quality-related traits, partly through effects on gas exchange and carbon assimilation in the scion [22,23]. Therefore, photosynthetic parameters, including Pn, Tr, Ci, and Gs, were used in this study to evaluate rootstock-induced differences in leaf photosynthetic performance.

In this study, *Pn*, *Tr*, and *Gs* in both rootstock groups initially increased and then declined during fruit development of 'Guichang' kiwifruit. Notably, fruits grafted onto *A. valvata* ('Av') exhibited higher photosynthetic efficiency during the early fruit development stage (28–56 DAP), a critical period for rapid fruitlet growth. Enhanced photosynthesis at this stage is likely beneficial for achieving larger fruit size and improved fruit quality, traits that are particularly important for commercial marketing [24–26].

Interestingly, during fruit development up to harvest at 140 DAP, the leaf Pn and Tr values in 'Av' were generally higher than those in 'Ad' at most sampling points, suggesting that 'Av' tended to maintain

relatively greater leaf photosynthetic activity throughout the fruit growth cycle. Specifically, Pn was significantly higher in 'Av' at 28, 56, 112, and 140 DAP, while no significant difference was observed at 84 DAP. Similarly, Tr was significantly higher in 'Av' from 28 to 112 DAP, whereas the difference was not significant at 140 DAP. After 84 DAP, Pn and Tr declined in both rootstocks, which may be related to high temperature stress, as daytime temperatures reached up to 38°C—levels above 35°C are known to impose substantial stress on kiwifruit [27]. In addition, the stage-dependent changes in Ci and Gs suggest that differences in photosynthetic performance between 'Av' and 'Ad' may be associated with dynamic regulation of gas exchange during fruit development.

Collectively, these findings demonstrate that *A. valvata* ('Av') rootstock enhances leaf photosynthetic performance during key developmental stages, supporting fruit growth and quality. The physiological mechanisms underlying these effects warrant further investigation.

4.2 Fruit Quality and Carbohydrate Metabolism

Fruit weight, DMC, SSC, TSS (total soluble solid), TA and sugar-acid ratio are important indicators to evaluate kiwifruit quality [4]. Rootstock selection plays an important role in modulating these traits in grafted scion varieties. Previous studies have shown that grafting 'Hongyang' onto certain rootstocks significantly increased average fruit weight, while 'Jinmei' grafted onto *A. valvata* exhibited higher DMC, highlighting the potential of rootstocks to optimize scion growth and fruit characteristics in kiwifruit cultivation [17]. Similarly, 'Jianxiang' grafted onto *A. valvata* produced the highest dry matter among tested combinations [28].

Here, neither A. *valvata* nor A. *deliciosa* significantly affected fruit DMC, indicating that the tested rootstocks had limited influence on this parameter under the present experimental conditions. Therefore, no clear rootstock-related modulation of DMC could be inferred from the present data. Nevertheless, rootstocks may affect other fruit quality-related traits, such as volatile metabolite composition [29].

Evaluation of fruit quality at multiple developmental stages on-vine and during postharvest ripening revealed that fruits from the 'Av' graft combination exhibited higher SSC, soluble sugar, TA, and sugar–acid ratio than those from 'Ad'. Previous studies have shown that different rootstocks can influence kiwifruit growth and fruit quality [30]. In the present study, these improvements may be partly associated with the relatively higher photosynthetic performance observed in 'Av', especially the generally higher Pn and Tr values at most developmental stages. Rootstock-induced differences in photosynthetic performance have also been reported in kiwifruit and other fruit crops [22,23]. Enhanced photosynthetic activity may increase assimilate supply to developing fruits, thereby contributing to sugar accumulation and fruit quality formation [31]. These findings suggest that *A. valvata* has potential as a rootstock for improving scion physiological performance and fruit quality under the soil and climate conditions of Guizhou, although further studies are needed to clarify the underlying mechanisms, including root characteristics, nutrient uptake, and source–sink relationships.

Fruit sugar accumulation is closely related to photosynthetic carbon assimilation and assimilate transport from source leaves to developing fruits. Photosynthetically produced sucrose is transported via the phloem to fruits, where it is metabolized into glucose and fructose or temporarily stored as starch, thereby influencing fruit sweetness and quality [32]. In this study, the relatively higher photosynthetic performance of 'Av', especially the generally higher Pn and Tr values at most developmental stages, may have contributed to greater assimilate supply for carbohydrate accumulation in fruits. Previous research on rootstock effects has often focused on graft union position, bud development, or root traits, whereas the influence of rootstocks on fruit carbohydrate content and metabolism has received relatively less

attention [33,34]. Consistent with this physiological framework, starch content in 'Av' fruits was generally higher than that in 'Ad' from 28 to 112 DAP and during postharvest ripening. After 112 DAP, starch content declined in both graft combinations, probably due to starch degradation and conversion into soluble sugars during ripening [35]. Moreover, sucrose and fructose contents during postharvest ripening were higher in 'Av' fruits than in 'Ad', supporting the view that rootstocks can influence carbohydrate composition and sugar accumulation in kiwifruit [36]. These differences may be associated with sugar metabolism-related processes, including starch degradation and sugar conversion [37,38]. Overall, these results suggest that *A. valvata* rootstock may improve fruit carbohydrate accumulation partly through enhanced photosynthetic performance and assimilate supply.

4.3 Effect of 'Av' on Sucrose and Starch Metabolism of 'Guichang' Kiwifruit

Comprehensive analysis of SS-C, SS-S, SPS, NI, S-AI, and HK activities indicates that these enzymes collaboratively regulate sugar accumulation and degradation in kiwifruit [39]. During early fruit development, S-AI and SS-C activities increased rapidly, resulting in elevated glucose and fructose contents. This is consistent with the hydrolysis of phloem-transported sucrose by S-AI and SS-C into glucose and fructose, which serve as essential carbon sources for cell division and growth during the fruitlet stage, facilitating subsequent rapid fruit expansion [40]. In contrast, SS-S activity remained low during on-vine development but increased slightly during postharvest ripening, coinciding with the stage of relatively high sucrose accumulation. This suggests that SS-S may be involved in sucrose accumulation during postharvest ripening, consistent with previous reports showing a positive association between sucrose synthase activity and sucrose accumulation [41]. NI activity was generally low throughout fruit development, increasing only during the S-AI active phase and post-ripening stage, indicating minimal contribution to sugar accumulation [42]. These results support the notion that S-AI and NI are key enzymes governing sucrose metabolism, consistent with previous results [43].

During postharvest ripening, SPS activity in fruit on 'Av' rootstock was significantly higher than those on 'Ad', concomitant with higher sucrose content. This suggests that SPS plays a critical role in sucrose synthesis during soft ripening and directly reflect the sucrose synthesis ability of plants [44]. HK is one of the key enzymes in glucose metabolism and is responsible for catalyzing the phosphorylation of glucose and fructose, converting it into glucose-6-phosphate or fructose-6-phosphate, into glycolysis or other metabolic pathways [45,46]. Higher HK activity in 'Av' during early fruit development likely accelerates sugar metabolism, supplying energy and metabolic intermediates for cell division and growth. Elevated HK activity during ripening further enhances hexose availability, promoting efficient sugar conversion and utilization [46]. In conclusion, *A. valvata* used as rootstock can increase the SS-C, S-AI, HK, and SPS activities of 'Guichang' kiwifruit, accelerate sucrose decomposition and the formation of fructose and glucose in the early stage of fruit development, and accelerate sucrose synthesis in the fruit ripening process off vines, thus increasing the sugar content of fruit, all of these could result in improving fruit taste.

During the early growth stage, fruit primarily accumulate starch, which subsequently converts into soluble sugars upon reaching a certain level of accumulation [47]. AGP serves as the first key enzyme in plant starch synthesis [48]. Our study demonstrated that AGP activity was significantly higher in fruits grafted onto 'Av', leading to accelerated starch synthesis and higher starch content compared with 'Ad' fruits [35]. Starch degradation is mediated by α-amylase and β-amylase, both critical for regulating starch metabolism [49,50]. In 'Guichang' fruits, α-amylase activity increased in 'Av' during ripening, suggesting enhanced cleavage of internal starch chains and the generation of oligosaccharide intermediates. In contrast, β-amylase activity increased in 'Ad' at 4–7 days after harvest, indicating a possible role in releasing maltose

units from starch-derived substrates and contributing more directly to soluble sugar production. These findings highlight the influence of rootstock on starch metabolism, with amylase activities playing pivotal roles during maturation and sugar accumulation.

Overall, *A. valvata* rootstock promotes starch accumulation during early development, supporting subsequent sugar formation and fruit quality enhancement.

5 Conclusion

In summary, *Actinidia valvata* ('Av') rootstock enhanced leaf photosynthetic performance in 'Guichang' kiwifruit at certain developmental stages and was associated with favorable changes in fruit starch and soluble sugar accumulation. Fruits grafted onto 'Av' also showed higher activities of several key enzymes involved in sucrose and starch metabolism, including SS, SPS, invertase, HK, AGP, and α-amylase, at specific sampling points. However, many measured variables did not differ significantly between *A. valvata* and *A. deliciosa* ('Ad'), indicating that both rootstocks are suitable for 'Guichang' kiwifruit cultivation under the conditions examined. Overall, 'Av' may serve as a promising alternative rootstock, while 'Ad' remains a reliable option. Further studies are needed to compare their adaptability and performance under abiotic stress conditions.

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