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Reduced Phosphate Availability Improves Tomato Quality Through Hormonal Modulation in Developing Fruits

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Abstract
Nutrient management is one of the most important agricultural practices to ensure yield and fruit quality. The aim of this study was to examine the effect of N and P availability in the yield and quality of tomato fruits (*Solanum lycopersicum* var. Meyity), and the hormonal mechanisms underlying these effects. Fruit yield and quality (in terms of sugar accumulation and titratable acidity) at harvest, together with the hormonal profiling of developing fruits were evaluated. While low N caused a reduction of sugars, reduced P availability increased sugars and reduced acidity in fruits. These changes were not accompanied by significant reductions in yield. Enhanced *trans*-zeatin content at early stages of fruit development and during color break might be associated with an increased sink activity. Furthermore, jasmonic acid, salicylic acid and 1-aminocyclopropane-1-carboxylic acid (the ethylene precursor) concentrations increased at early stages of fruit development, thus suggesting a complex hormonal crosstalk induced by low P availability. In conclusion, a reduction of P availability increased tomato sugar contents, while yield was not negatively impacted. These results have implications to alleviate the depletion of natural P reserves to arrive at a more sustainable horticulture.

Keywords Cytokinins · Nitrogen · Phosphorus · Salicylic acid · Soluble sugars

Introduction

Tomato plants are one of the highest produced and consumed horticultural crops worldwide because of the organoleptic properties and nutritive value of their fruits (De Pablo and Battistuzzi 2012). Consequently, cultivation of tomato plants is one of the best studied and optimized agricultural practices nowadays, despite there is still strong interest in evaluating factors that influence tomato yield and quality to arrive at a more sustainable horticulture in the current frame of global change. In this respect, nitrogen (N) and phosphorous (P) are the two major mineral nutrients required for plant growth and development that are applied in crop fertilization and previous studies have already shown that the nutritional value of tomatoes can be improved by growing them in the greenhouse by applying different agronomic techniques that influence fruit yield and quality (Erba et al. 2013). These previous findings support the idea that there is still room to improve not only yields, but most particularly fruit quality, and that this goal must be achieved associated with more sustainable agricultural practices.

On one hand, N is essential for the synthesis of nucleic acids, proteins and phospholipids. Moreover, it is required for the synthesis of other compounds such as co-enzymes, photosynthetic pigments and secondary metabolites (Adams 1986; Amtmann and Armengaud 2009; Maathuis 2009). On the other hand, P plays an essential role in plants, as it is a component of nucleic acids and phospholipids. But above all, it is a constituent of adenosine triphosphate (ATP), an energy-rich phosphate compound crucial in plant metabolism. Consequently, both N and P deficiency can reduce plant growth and yield, and consequently, these nutrients

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are often over applied in agriculture. However, the excess of fertilization increases nutrient losses from soil to water that cause pollution and eutrophication. Moreover, an excess of N and P can also impair crops growth (Zhu et al. 2017). Therefore, knowledge of the optimal nutrient requirement of crops is fundamental to maintain good yields and fruit quality and to minimize nutrient waste and environmental impacts (Fandi et al. 2010).

Many experiments have previously linked the availability of nutrients in crops with fruit quality (sugar content or titratable acidity). However, the effects of N and P availability on tomato are still controversial. Hernández et al. (2020) reported that a decrease in the N dose from transplant onwards in the cultivation of tomato plants resulted in a decrease in sugar concentration and yield. However, two different studies showed that a moderate reduction in N supply does not affect yield and indeed improves fruit quality through an increased total soluble sugar (TSS)/titratable acidity (TA) ratio (Truffault et al. 2019; Bénard et al. 2009). Moreover, a reduction in N fertilization was shown to exert a positive effect on vitamin C and phenolic contents, although depending on the dose N deficiency can also negatively impact tomato yield (Erba et al. 2013; Wei et al. 2018). On the other hand, Fandi et al. (2010) showed that reduced P availability can lead to higher TSS, despite Zhu et al. (2017) observed that yield and postharvest qualities were not significantly affected by P rates in a two-year experiment in tomatoes. Overall, these studies indicate that various agricultural practices must be finely controlled to achieve an optimal cultivation in greenhouse tomatoes, showing significant effects for the cultivar, N dose in nutrient solution, treatments for plant disease control and fruit ripeness, among others (Erba et al. 2013). Thus, it is important not only to study in detail the impact of nutrient availability in crops but also the mechanisms underlying these effects considering that these effects may be strongly cultivar-dependent. The aim of the present study was to examine the influence of N and P availability on the fruit yield and quality of tomato plants (*Solanum lycopersicum L.* var. Meyity), with a particular emphasis on evaluating the associated changes in the hormonal profiling during fruit development.

Materials and Methods

Experimental Design and Samplings

Seeds from tomato plants (*Solanum lycopersicum* var. Meyity), a pear tomato variety that was chosen for the study because of its commercial and economical interest, were bought at the Agricultural Cooperative Vallès (Llerona, NE Spain) Seeds were sown on perlite, vermiculite, and peat substrate on February 5th, 2018 and grown under a long photoperiod (16 h light/ 8 h darkness regime) in a constant-environment chamber (90–110 µmol quanta m-2 s-1, air temperature between 21 and 23 °C, and relative humidity around 65%). Three weeks later, plants were transferred into multipots with the same substrate and kept under the same conditions in the growth chamber until March 12th, 2018. Then, plants were transferred into 4L pots (one plant per pot) with the same substrate and grown in a greenhouse at the Faculty of Biology of the University of Barcelona (Barcelona, NE Spain) until the end of the study period on June 21st, 2018. After transplanting, all plants were irrigated three times a week with Hoagland solution. Fourteen days later, plants were then divided into three groups on March 26th, 2018: (1) a control group, irrigated with Hoagland solution (Hoagland and Arnon 1938); (2) a group deficient in N, irrigated with modified Hoagland solution with 20% less of N; and (3) a group deficient in P, irrigated with modified Hoagland solution in which soluble P ($NH_4H_2PO_4$ at 115.08 g/L) was replaced by insoluble P (soft ground rock phosphate). The daily mean temperature in the greenhouse during the study was 25.9 °C and the daily mean relative humidity was 58.1%. During harvest (June 20th and 21st, 2018), plants were exposed to a long photoperiod (under a 16 h light/ 8 h darkness regime), and the daily mean temperature and relative humidity were 25 ºC and 55%, respectively (Suppl. Figure S1).

Fruits were sampled at six developmental, ripening stages (adapted from Takizawa et al. 2014, see Fig. 1): stage I, developing fruit with a peel that is still completely green; stage II, first color changes occur, but still less than 10% of the peel surface has started to change color; stage III, 10%–30% of the peel has changed color; stage IV overall break in color from green to yellow/pink; stage V, dark red coloration starts to appear, with 60%–90% of the surface is not green; and stage VI, mature fruit, commercial harvest (Fig. 1). For all treatments, one fruit per plant from six plants per stage and treatment were sampled at each developmental stage, dipped in liquid N_2 and stored at 80 ºC until hormone profiling analyses. Moreover, six additional fruits per plant were sampled at harvest (stage VI) to analyze fruit quality parameters. All samplings were performed at predawn (1 h before sunrise).

Yield and Fruit Quality Parameters

Total production of fruits per plant was measured at first harvest (between June 20th and 21st, 2018). In addition, the fresh weight and dry weight of fruits were measured by weighing freshly harvested fruits. Tomato quality was determined by measuring total soluble sugars (TSS), titratable acidity (TA) and sugar/acid (TSS/TA) ratio. For fruit quality analysis, tomato juice was extracted. One mL of juice was used to determine TSS using a digital refractometer HI 96,801 (HANNA

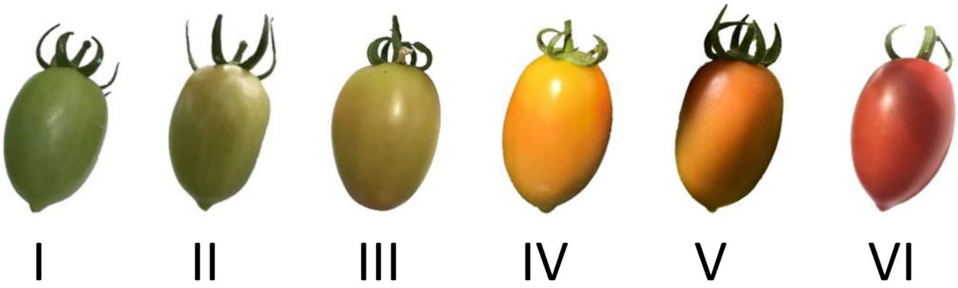

Fig. 1 Ripening stages of tomato fruits sampled during the study (from left to right, stages I–VI). Stage I, developing fruit with a peel that is still completely green; stage II, first color changes occur, but still less than 10% of the peel surface has started to change color; stage III, 10%–30% of the peel has changed color; stage IV overall break in color from green to yellow/pink; stage V, dark red coloration starts to appear, with 60%–90% of the surface is not green; and stage VI, mature fruit, commercial harvest (color figure online)

instruments, Woonsocket, USA). Moreover, 10 mL of juice were diluted with 100 mL of distilled water and this solution was used for the determination of TA with 0.1 N NaOH, using phenolphthalein (1%) as an indicator (Latimer 2016).

Hormone Profiling

Endogenous contents of phytohormones were determined by ultrahigh-performance liquid chromatography coupled to tandem mass spectrometry (UHPLC–MS/MS), as described by Müller and Munné-Bosch (2011). In short, 100 mg of liquid N_2-grounded fruit samples were extracted with 250 mL of solvent (methanol:isopropanol:acetic acid) using ultrasonication for 30 min and vortexing. Next, the pellet was re-extracted again using ultrasonication for 30 min and vortexing and the collected supernatants were filtered through a 0.22 mm PTFE filter before analyses. Phytohormone contents were analyzed by UHPLC–MS/MS as described (Müller and Munné-Bosch 2011). Internal standards, including d_5-*trans*-zeatin, d_5-*trans*-zeatin riboside, d_6-isopentenyl adenosine, d_4-1-aminocyclopropane-1-carboxylic acid, d_4-salicylic acid, d_6-abscisic acid, d_5-jasmonic acid, d_4-melatonin, d_5-indole-3-acetic acid and d_2-gibberellin$_4$ were used for quantification.

Statistical Analyses

Results were analyzed by one-way factorial analysis of variance (ANOVA), followed by Tukey HSD post hoc tests or by two-way ANOVAs followed by Student's *t*-tests, using IBM® SPSS® Statistics 19 (Armonk, NY). Differences were considered significant at a probability level of $P < 0.05$.

Results

Impact of N and P Availability on Yield and Fruit Quality

Total crop yield (kg tomato/plant) was not negatively affected either by reduced N or P availability (Fig. 2a). The fresh or dry weight of fruits was neither affected by treatments (Figs. 2b, c). Therefore, reduced nutrient availability applied in this study did not result in significant reductions in yield. In contrast, reduced N and P availability impacted on the fruit quality parameters analyzed: total soluble sugars (TSS), titratable acidity (TA) and sugar/acid ratio (TSS/TA). TSS were affected in different ways in plants treated with low N supply or plants treated with low soluble P. TSS was reduced by 11.8% when N availability was reduced, while it increased by 7.4% when the availability of soluble P was reduced (Fig. 3a). TA was not influenced by N deficiency, but it decreased by 12.5% under reduced P availability (Fig. 3b). Finally, changes in TSS/TA paralleled those of TSS, but with even higher differences due to the reductions in TA under P deficiency. In plants with a reduced N availability, the sugar/acid ratio decreased by 12.5%, while this ratio increased by 17.8% with reduced P (Fig. 3c).

Impact of N and P Availability on the Hormonal Profiling of Maturing Fruits

The endogenous content of hormones was analyzed at six ripening stages of tomatoes development (as described in

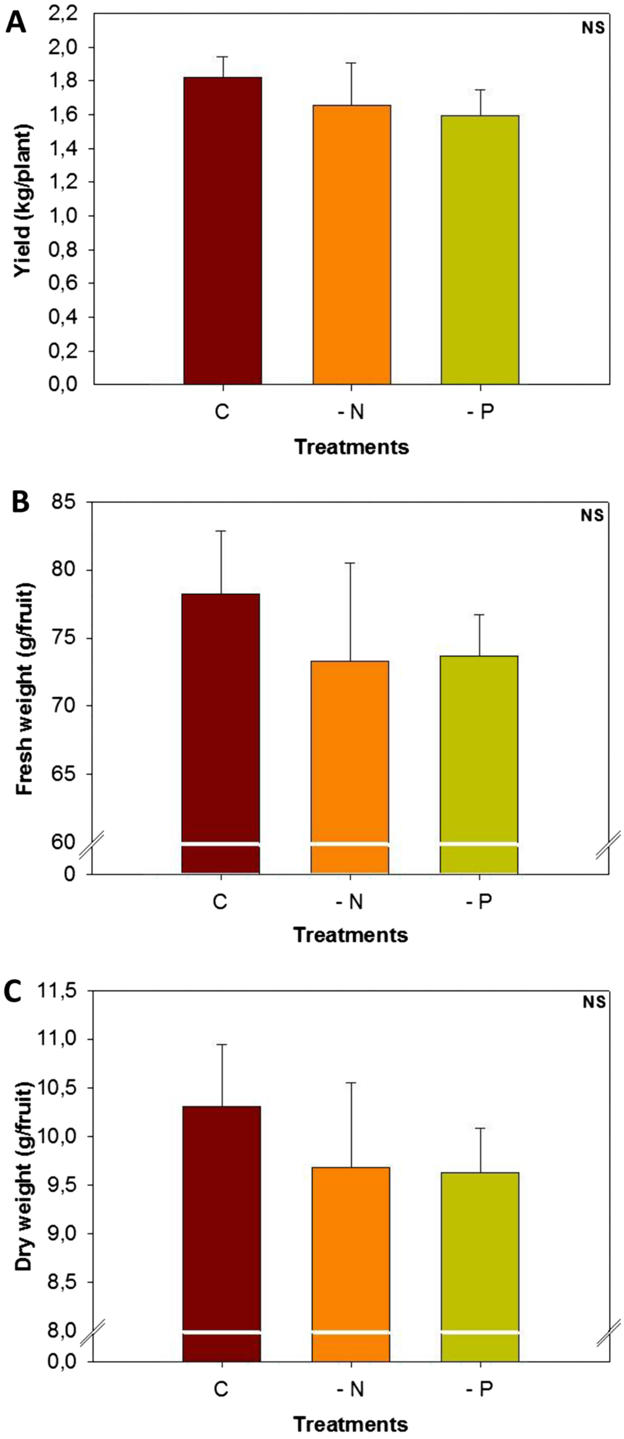

Fig. 2 Yield of greenhouse-grown tomato plants grown in the greenhouse subject to changes in nutrient availability (see materials and methods for details). **a** Yield; **b** Fruit fresh weight; **c** Fruit dry weight. For yield estimation, data represent the mean ± standard error of $n=6$ plants, with all fruits being analyzed from each plant. For fresh and dry weights, data represent the mean ± standard error of $n=6$ plants, with six fruits being analyzed for each plant. Differences between treatments were analyzed using a one-way ANOVA with Tukey post hoc tests. *NS* not significant (color figure online)

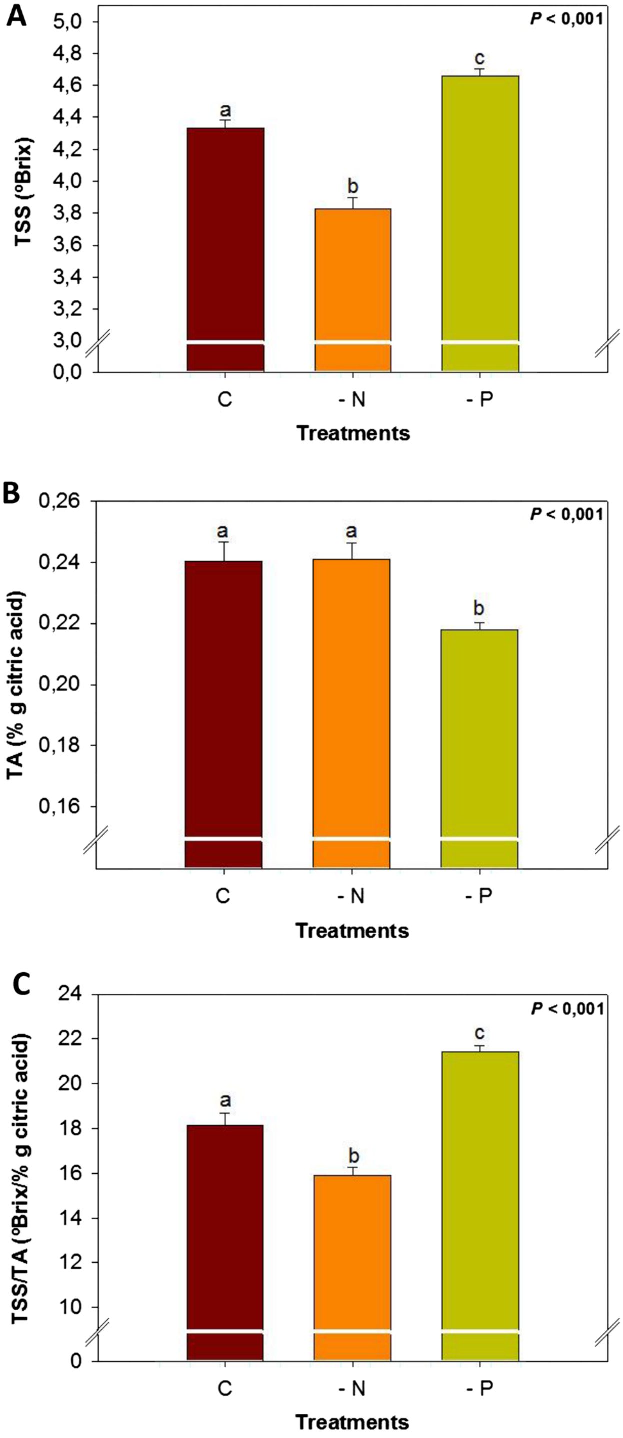

Fig. 3 Fruit quality of greenhouse-grown tomato plants grown in the greenhouse subject to changes in nutrient availability (see materials and methods for details). **a** Total soluble sugars; **b** Titratable acidity; **c** Total soluble sugars/ titratable acidity ratio. Data represent the mean ± standard error of $n=6$ plants, with six fruits being analyzed for each plant. Differences between treatments were analyzed using a one-way ANOVA with Tukey post hoc tests. Different letters show significant differences between treatments (color figure online)

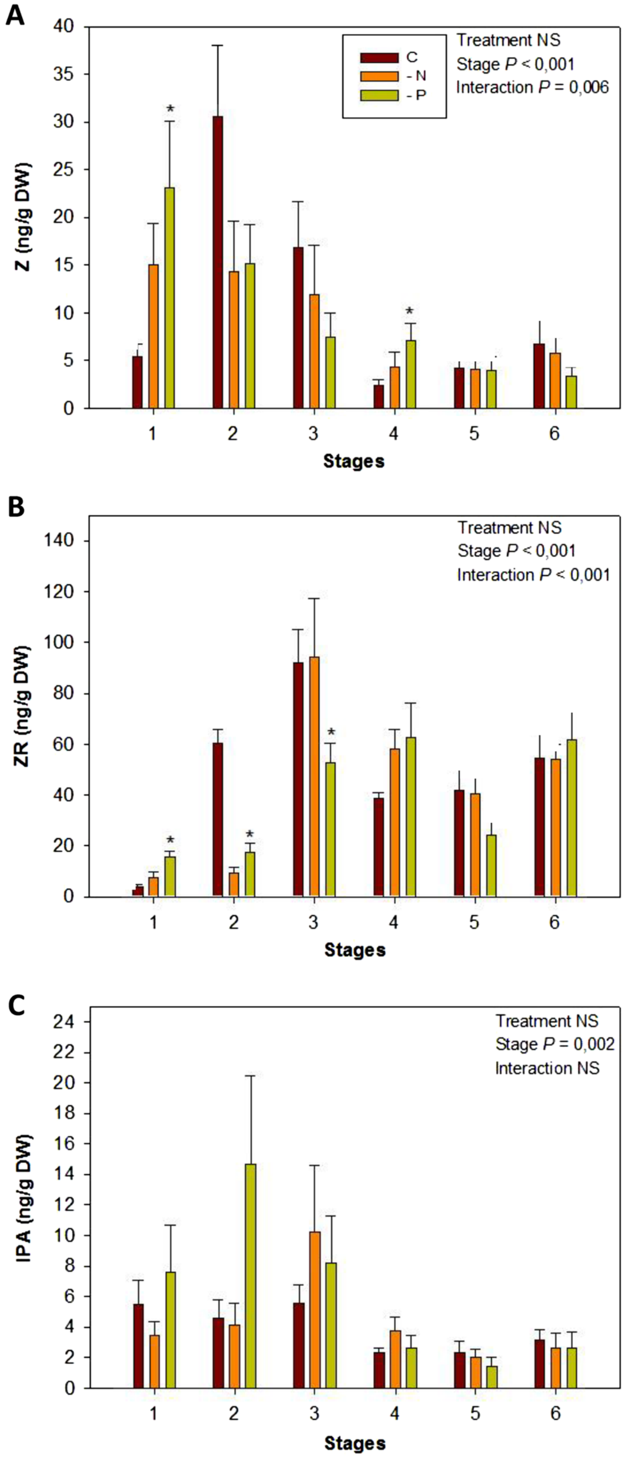

Fig. 4 Variations in the endogenous contents of **a** the bioactive cytokinin *trans*-zeatin (Z), **b** its immediate precursor *trans*-zeatin riboside (ZR) and **c** isopentenyl adenosine (IPA) during tomato fruit development in plants subject to changes in nutrient availability (see materials and methods for details). A description of fruit developmental stages is shown in Fig. 1. Data represent the mean ± standard error of $n=6$ plants, with one fruit being analyzed for each plant. Differences between treatments and stages were analyzed using a two-way ANOVA. When differences between treatments or the interaction was significant, a Student's t-test was applied to examine differences between any given treatment and the control. Results of ANOVA (with P values) are shown in the inlets, while results of Student's *t*-tests (when $P \leq 0.05$) are shown by an asterisk. *NS* not significant (color figure online) ▶

Fig. 1) for each treatment, to evaluate the differences in the hormonal regulation of the ripening process depending on the availability of N and P. Results showed that P availability has a major impact on the hormonal regulation of tomato ripening, not only during the first fruit developmental stages (stages I and II) but also during color break (stage IV).

The contents of the bioactive cytokinin, *trans*-zeatin (Z) increased significantly under reduced P availability compared to controls not only at early stages of development (stage I) but also during color break (at stage IV, Fig. 4a). Interestingly, while *trans*-zeatin riboside (ZR) content was higher in fruits with reduced P availability that those of control plants at stage I, this trend reversed at stages II and III, so that developing fruits at these stages in plants with reduced P availability showed lower ZR contents than controls (Fig. 4b). Treatment-related changes in ZR, the immediate precursor of Z contents, disappeared at later stages of fruit development. Furthermore, contents of isopentenyl adenosine (IPA) were not significantly modified by nutrient availability in any ripening stage (Fig. 4c). Despite reduced N availability negatively impacted on TSS content (Fig. 3a), the endogenous contents of cytokinins in maturing fruits were not influenced by a deficiency in N.

Aside from nutrient treatment effects on cytokinin contents, the impact of reduced P availability was observed in the contents of 1-aminocyclopropane-1-carboxylic acid (ACC, the immediate precursor of ethylene), salicylic acid (SA) and jasmonic acid (JA), while ABA content was not significantly affected (Fig. 5). While SA content increased at stage I, contents of SA, JA and ACC increased at stage II under reduced P availability compared to controls. The endogenous contents of ACC, SA, ABA and JA in maturing fruits were not influenced by a deficiency in N.

The contents of the auxin indole-3-acetic acid (IAA), melatonin (MEL) and gibberellin 4 (GA_4) were not influenced by N and P availability (Fig. 6). Interestingly, MEL accumulated at relative high levels in tomato fruits attaining maximum values at initial stages of ripening and decreasing later during development. Despite these decreases, MEL contents ranged between 0.4 and 0.6 mg/g DW in ripen

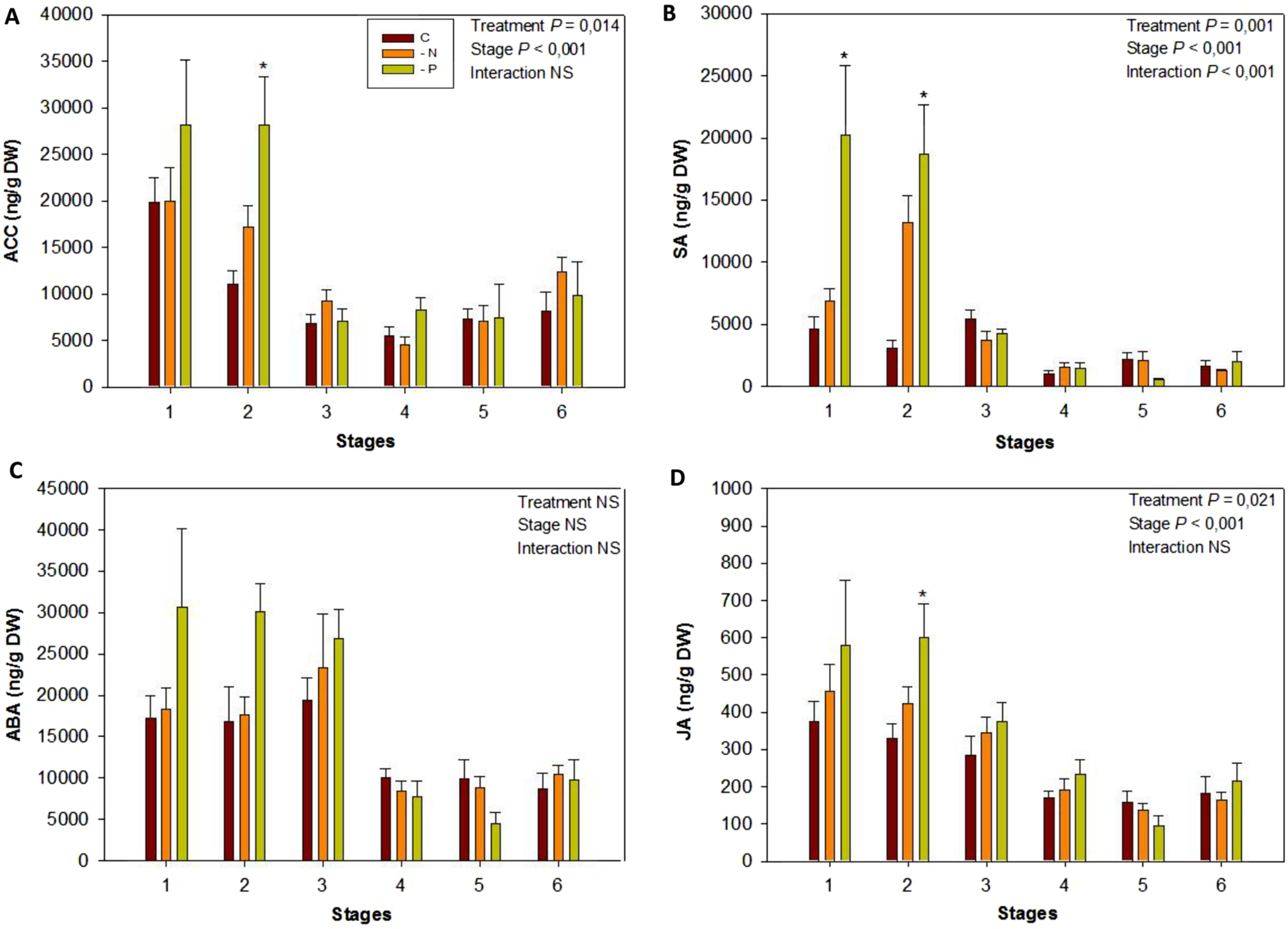

Fig. 5 Variations in the endogenous contents of **a** the 1-aminocyclopropane-1-carboxylic acid (the immediate ethylene precursor), **b** salicylic acid (SA), **c** abscisic acid (ABA), and **d** jasmonic acid (JA) during tomato fruit development in plants subject to changes in nutrient availability (see materials and methods for details). A description of fruit developmental stages is shown in Fig. 1. Data represent the mean ± standard error of $n = 6$ plants, with one fruit being analyzed for each plant. Differences between treatments and stages were analyzed using a two-way ANOVA. When differences between treatments or the interaction was significant, a Student's t-test was applied to examine differences between any given treatment and the control. Results of ANOVA (with *P* values) are shown in the inlets, while results of Student's *t*-tests (when $P \leq 0.05$) are shown by an asterisk. *NS* not significant (color figure online)

tomato fruits at harvest, showing no significant differences between treatments (Fig. 6).

Discussion

A proper nutrient management is essential to optimize growth and production in the cultivation of tomato plants. Although the effect of nutrient deficiencies on yield has been extensively studied in several tomato varieties, their influence of fruit quality is still not fully understood. Of special interest is the case of P, an element of phosphate, which strengthens roots and helps them to mature early, so that P availability is essential for plant growth and for attaining optimal tomato yields. Rock phosphate is recommended in organic farming as a source of P for plants since is more environmentally friendly than inorganic phosphate (Zapata and Roy 2004). On the one hand, results of the present study have shown that insoluble P from soft ground rock phosphate can be used for the growth of tomato plants to improve fruit quality without negatively impacting on yield, an effect that may be associated with changes in the endogenous contents of hormones in developing fruits. On the other hand, it is also shown that N deficiency negatively impacts on fruit quality by reducing the sugar content of fruits.

When the availability of soluble P was reduced in Meyity, an increase in TSS together with a reduction in TA were observed, which resulted in an increase in the TSS/TA ratio. This improvement in fruit quality was achieved without negatively impacting fruit yield. A similar effect was observed by another study that reported that decreasing inorganic P availability in tomato plants increased TSS in fruits (Fandi

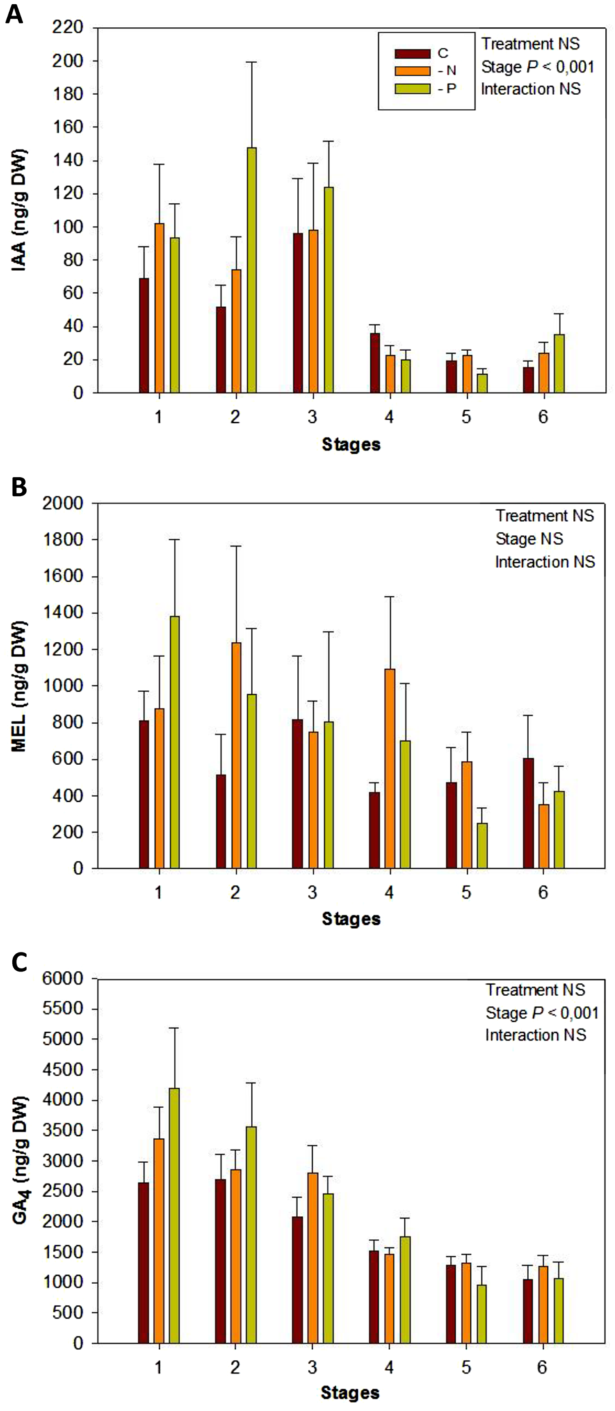

Fig. 6 Variations in the endogenous contents of **a** the auxin indole-3-acetic acid (IAA), **b** melatonin (MEL) and **c** the bioactive gibberellin GA_4 during tomato fruit development in plants subject to changes in nutrient availability (see materials and methods for details). A description of fruit developmental stages is shown in Fig. 1. Data represent the mean ± standard error of $n=6$ plants, with one fruit being analyzed for each plant. Differences between treatments and stages were analyzed using a two-way ANOVA. When differences between treatments or the interaction was significant, a Student's *t*-test was applied to examine differences between any given treatment and the control. Results of ANOVA (with *P* values) are shown in the inlets, while results of Student's t-tests (when $P \leq 0.05$) are shown by an asterisk. *NS* not significant (color figure online)

et al. 2010). Moreover, Sung et al. (2015) observed that there are also changes in sugars in xylem sap of tomato plants under P deficiency. Contrarily, two experiments reported that changes in P availability did not significantly vary soluble sugars or acidity of tomatoes (Abu-Alrub et al. 2019; Liu et al. 2011). Importantly, none of these previous studies used insoluble P from soft ground rock phosphate, so our results show for the first time to our knowledge that this agricultural practice can be used for organic cultivation of tomatoes to achieve tomatoes with higher sugar contents while yield is not negatively impacted. The present study opens new avenues for a more sustainable production of greenhouse tomatoes, but further research will be needed to prove the significance of these results in other tomato varieties cultivated using other agricultural practices. In contrast, reduced N availability results in lower sugar contents in the fruit, thus indicating that the deficiency of this nutrient must be prevented to achieve an optimal fruit quality and yield.

Interestingly, the improvement in fruit quality in tomato plants treated with insoluble P from soft ground rock phosphate seemed to be mediated by changes in the endogenous contents of hormones in developing fruits. Enhanced TSS and TSS/TA ratio together with reduced TA in fruits under low P availability might be explained by significant changes in the endogenous contents of hormones in developing fruits, particularly by an increase in the content of bioactive cytokinin *trans*-zeatin at early stages of development (stage I) and during color break (stage IV), which might be associated with an increased sink activity (Roitsch and Ehneß 2000). While *trans*-zeatin riboside content increased in developing fruits at stage I, it decreased at stages II and III compared to the control plants, thus suggesting a transient downregulation of the enzymatic release of the riboside moiety of the cytokinin (conversion of *trans*-zeatin riboside to *trans*-zeatin) at these stages, while *trans*-zeatin production increased again during color break in tomatoes. Aside from a prominent role in the regulation of sink strength be upregulating apoplastic investases, cytokinins are phytohormones implied in cell division acting as the main regulators of cell cycle progression (Schaller et al. 2014). Also, cytokinins have been related with abiotic stress response (Sharma et al. 2019). In this sense, Keshishian et al. (2018) reported that salt stress in tomato seedlings caused as well as an increase in endogenous cytokinin content. In our study, enhanced Z contents under low P availability paralleled an increase in tomato quality, which fits well with the role of cytokinins in increasing sugar contents and could alleviate the potential negative effects of low P availability on growth.

Furthermore, enhanced contents of bioactive cytokinin coincided with increased JA, SA and ACC (the ethylene precursor) concentrations at early stages of development, thus suggesting a complex hormonal crosstalk induced by low P availability. While ACC and JA increased at stage II, SA increased at stages I and II. SA is a phytohormone that has been associated to stress tolerance. Its role in tolerance to biotic stress is well established (Raskin 1992). Furthermore, there is increasing evidence of its relationship with tolerance to abiotic stress. For example, Senaratna et al. (2000) demonstrated that application of exogenous SA protected tomato and bean plants against stress due to drought or temperature (cold and heat). Moreover, Wasti et al. (2012) reported that adverse effects of salt stress in tomato plants were alleviated by exogenous application of SA. Also, the study of Guo et al. (2018) indicated that exogenous application of SA could alleviate Cd toxicity in tomato plants. In this regard, it has been shown a signaling role for SA triggering a cascade of events that would confer tolerance to abiotic stress (Shakirova 2007). Furthermore, the application of exogenous SA in tomato increases soluble sugars in leaves (Javaheri et al. 2012), an effect that is thought to be mediated by an increase in ABA (Klessig and Malamy 1994). In our study, developing fruits of plants exposed to low P availability seemed therefore to trigger a defense response mediated by enhanced SA contents, which could play a dual role: (i) a role in protecting fruits from biotic and abiotic stress (associated with low P availability), and (ii) help cytokinins in promoting sink strength and therefore sugar accumulation at early stages of development.

Moreover, ACC and JA contents increased significantly at stage II of fruit ripening in plants with low P availability compared with control plants. ACC is the immediate precursor of ethylene, which plays an important role in growth, development, and responses of plants to biotic and abiotic stresses, as well as in the ripening of climacteric fruits, such as tomatoes (Poel and Straeten 2014). JA may also be involved in the ripening of climacteric fruits and has a prominent role in biotic stress tolerance (Fan et al. 1998; Santino et al. 2013). The increase in ACC and JA contents observed in our study suggest that they may be more associated with a stress response, characterized by a higher accumulation of sugars at early stages of fruit development mediated by an hormonal crosstalk together with salicylic acid and cytokinins, than with changes in ripening, as differences in ACC and JA were only observed at stage I and not later in development.

On the other hand, a reduction in N availability in tomato crop caused a decrease in soluble sugars (Fig. 3a), which led to a reduction in the TSS/TA ratio (Fig. 3c). These results are in agreement with those of Hernández et al. (2020) and Ya-dan et al. (2017), who observed a decrease in soluble sugars in tomato plants with a lower dose of N availability. However, this reduction in quality seems to be caused through a mechanism independent from hormones, at least those measured in our study, since the content of hormones analyzed in the present study did not reveal any significant changes between plants with reduced N supply and control plants. It should be noted, however, that in some cases hormonal signaling can be affected without alterations in endogenous hormone contents; therefore, the possible link between N deficiency, hormonal (e.g., cytokinin) signaling and reduced sugar accumulation in fruits requires further investigation.

Conclusions

In conclusion, results show that a reduction of P may be used to increase tomato fruit sugar contents and modulate fruit quality while yield being not negatively impacted on tomatoes of the variety Meyity. These results may have important implications to reduce the depletion of natural P reserves to arrive at a more sustainable horticulture in the current frame of global change. The availability of nutrients during fruit growth and development (including ripening) has an important impact on fruit quality, and a better understanding of the nutrient requirement in tomato plants may be very helpful to improve crop yield and fruit quality, while reducing the impact of current agricultural practices in the environment. Reducing the availability of soluble P is therefore recommended for a more sustainable agriculture in the cultivation of tomato plants of the variety Meyity. Furthermore, it was shown here that several hormones may be involved in the modulation of fruit quality. Aside from cytokinins, which appeared to have the more prominent role in the increased accumulation of sugar contents observed in fruits of plants exposed to low P; SA, JA, ACC might also help plants to withstand stress and compensate for potential yield losses. Indeed, the hormonal response observed here in tomato fruits may simply reflect a defense response triggered by low P availability to ensure fruit and seed production by the plant. Moreover, according to the results obtained in tomato plants exposed to N deficiency, it may be concluded that the availability of N should be tightly controlled in tomato cultivation to prevent a reduction in the quality of tomatoes, here reflected by a reduction of sugar content in the fruit.

Author Contributions SMB was the supervisor of this project, planning all stages of this research. MN conducted the experiments, collected and interpreted the data, and wrote a first draft of the manuscript. SMB contributed to interpretation of the data and wrote the final version of the manuscript.

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Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflicts of interest.

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