Impacts of Woody Residue Amendments and Compost on 'Beauregard' Orange Fleshed Sweet Potato (Ipomoea batatas L.)

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Abstract

Orange-fleshed sweet potatoes (OFSP) are valued for their bioactive compounds and ability to thrive in nutrient-poor soils. This study investigated the short-term effects of woody residues and compost on OFSP, focusing on plant growth, storage root production, and bioactive compounds. Conducted in a commercial orchard, the experiment compared different organic fertilization treatments with a control. Four treatments were established: Treatment 1 (T1) received compost fertilization; Treatment 2, control, (T2) had no fertilization; and Treatments 3 (T3) and 4 (T4) were fertilized with high (150 t ha^{-1}) and low (75 t ha^{-1}) doses of woody plant residues,

respectively. Although woody residue application initially hampered plant growth, it ultimately enhanced biological nitrogen fixation, phosphorus availability, and reduced stress and senescence. Agronomic production did not differ between the compost and woody residue treatments but was increased at the high woody residue dose compared to control. At late growth stages, ascorbic acid decreased in all treatments. At this time, the total phenolic content in storage roots remained high in the woody residue treatments. Conversely, compost reduced the bioactive compounds, without affecting growth, potentially due to oxidative stress in late growth stages. The lower crop senescence index and comparable agronomic production to the compost treatment suggest that woody residues were beneficial for OFSP growth and bioactive composition. The superior quality of the crop produced with woody residues indicates that this is an effective organic fertilization method for sweet potato production that can contribute to its resilience to environmental variations.

Keywords: *Ipomoea batatas*, Organic agriculture, Antioxidant activity, Carotenoids, Woody residues, Healthy food

1. Introduction

Sweet potato, *Ipomoea batatas* (L.) Lam., is a root vegetable crop of the *Convolvulaceae* family, ranking seventh in the world in terms of production. In 2022, global production amounted to 86.4 million tons, harvested from 7.2 million hectares (FAOSTAT, 2022). Sweet potatoes are grown in various tropical regions of the world, mainly in Asia and Africa (Mello et al., 2022; Rosero et al., 2022). In temperate areas, their production is restricted by temperature, and in Europe they are considered a minor crop (Galvao et al., 2021). Specifically, production in Spain reached 62,302 tons in 2017, with 45 thousand tons exported in 2022 (FAOSTAT, 2017). Different genotypes express varying flesh colors (i.e., white, purple, yellow, and orange) and bioactive compound profiles, which are related to nutritional quality (de Albuquerque et al., 2019;

Hernández Suárez et al., 2016; Makori et al., 2020). As sweet potatoes are a source of vitamin A and other bioactive compounds with antioxidant properties (Neela and Fanta, 2019), their consumption has been associated with health benefits, including cognitive and memory improvement, cancer chemoprevention, anti-obesity effects, and protection against cardiovascular diseases (Laveriano-Santos et al., 2022).

Orange-fleshed sweet potatoes (OFSP) do not require large amounts of nitrogen (N) for good yields. In fact, the addition of mineral N to manure fertilization did not increase storage root production in an Eutric Fluvisol in Mozambique (Conz et al., 2021). As sweet potatoes can thrive in less fertile soils with minimal fertilization and irrigation, they have been proposed as a crop that can improve human nutrition and quality of life (Tedesco et al., 2023). Some studies have shown that the growing location influences the antioxidant activity of different sweet potato varieties, including OFSP (Pazos et al., 2022a). Conz et al. (2021) also found that the use of legume residue and animal manure had a negative impact on the production of sweet potato storage roots in sandy clay loam soils under tropical climatic conditions. Darko et al. (2020) reported that mineral fertilization did not have a positive effect in OFSP growing in a tropical savanna sandy loam soil. In contrast, other studies indicate that cultivating sweet potatoes with legumes, when accompanied by the application of mineral N, improves the yield and quality of the storage roots (Fernandes et al., 2021; Navarro et al., 2020a). In the Mediterranean region, it is considered that the nutrient requirements of sweet potatoes can be met without fertilization or with limited additions of mineral or organic fertilizers (Baixauli and Maroto Borrego, 2016; Kakabouki et al., 2021). Moreover, fertilization may increase the green biomass and reduce storage root production (Duan et al., 2018). On the other hand, some studies have demonstrated the endophytic nitrogen-fixing capacity of sweet potatoes (Terakado-Tonooka et al., 2013; Yoneyama et al., 2017), which may enable them to thrive in nutrient-poor soils.

Woody residues are carbon (C)-rich materials that can rapidly increase organic matter and biological activity in agricultural soils, although they may temporarily reduce nutrient availability (Barthès et al., 2010). While lower nutrient levels can prime the decomposition of soil organic matter and nutrient cycling (Joan et al., 2017; Li et al., 2022), increased biological activity may

improve soil physical conditions (Xu et al., 2022). Key benefits of C-rich amendments include increased water retention, reduced soil compaction as well as N, P and Mg crop uptake (Fontana et al., 2023). Other organic amendments include N-rich composts that can increase stabilized soil organic matter along with nutrient availability, although this might reduce soil microbial activity (Molina-Herrera and Romanyà, 2015).

The application of C-rich soil amendments constitutes a sustainable farming strategy that can maintain crop yields while simultaneously improving the quality of vegetables (González-Coria et al., 2022). Recent research suggests that C-rich amendments can influence the bioactive makeup of vegetables, which could be attributed to an increase in microbial abundance and reduced availability of free nutrients in the soil. Consequently, plants may shift their nutrient acquisition mechanisms from directly absorbing nutrients from the soil solution to pathways involving interactions with microbes.

We hypothesize that applying large amounts of woody residues will reduce the availability of nutrients, thereby increasing the content of bioactive compounds in sweet potato storage roots due to nutritional stress. In this context, this study aimed to examine the effects of different organic fertilization practices, including the incorporation of woody residues (*i.e.* C-rich amendments), on plant growth, storage root production, and bioactive compound content of orange-fleshed sweet potato (OFSP).

2. Materials and methods

2.1 Experimental design

The field trial was carried out at the Cal Notari farm located in Sant Boi del Lobregat (41° 19' 10.5204" N, 2° 2' 57.9768" E) in a peri-urban area of Barcelona, Spain, and involved the collaboration of local organic farmers. The study was performed with orange-fleshed *Ipomoea batatas* cv. *Beauregard*, with vine cuttings transplanted at the end of May 2021 (spring season). There were two harvests: one on 17 September 2021 (107 days after planting) and the other on 8 October 2021 (128 days after planting), hereafter referred to as the early and late harvests, respectively. The experimental design consisted of a control treatment without fertilizer application (T2), which was compared with (i) the addition of 12.5 t ha^{-1} of compost derived from

112 woody plant residues with an N richness of 2.2 % and a C/N ratio of 13 (T1) and (ii) two doses
113 of fresh woody plant residues: treatments T3 (150 t ha^{-1}) and T4 (75 t ha^{-1}) with an N richness of
114 1.2% and a C/N ratio of 39.5. The fresh woody residues were obtained from pruning residues
115 from local municipal sources and were chipped to a size of < 8 cm before being used as
116 amendments. The compost dose was calculated based on the maximum amount of N allowed in
117 composts according to EU fertilizer regulation 2019/1009. The amounts of wood plant residues
118 were applied following the recommendations of (Lemieux and Germain, 2000) and was applied
119 just before planting the OFSP. These wood plant residues were expected to increase soil
120 microbial activity and reduce nutrient availability in the short term (Barthès et al., 2010).
121 The treatments were replicated four times and distributed in sixteen plots of 7.5 x 1.5 m,
122 arranged in two lanes separated by one meter (Fig. 1). A 1.5 m buffer zone separated each plot
123 from the next. Before OFSP planting, the soil was cultivated to a depth of 20 cm using a rotary
124 tiller to incorporate the compost and woody residues.
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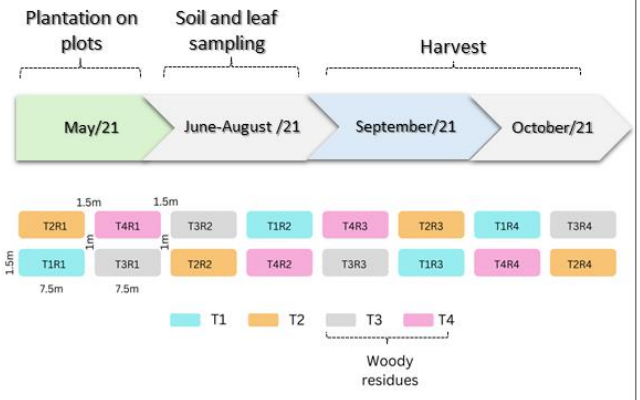


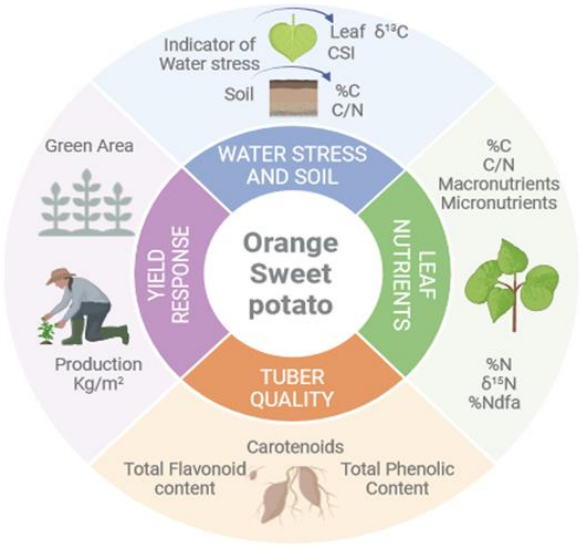


Fig. 1. Experimental design in randomized blocks. The experiment begun in May 2021 with the incorporation of the different fertilization treatments: T1, compost treatment; T2, control (no fertilizer added); T3, 15 kg/m^2 of woody residues; T4, 7.5 kg/m^2 of woody residues. Treatments were allocated into four blocks, where one replicate (R) of each treatment was present in each block. After the application of the treatments, orange-fleshed sweet potato vine cuttings were transplanted. The growing period comprised from May 2021 to August 2021. In September 2021, a first early harvest was performed and then in October 2021 a second late harvest was carried out.

2.2. Leaf and soil analyses

Leaf samples were collected in August 2021 from eight plants in each plot at the late flowering stage and they were bulked into a single sample per plot. Each sample was then oven–dried to dryness at 60 °C and finely ground using an automatic pestle and mortar (RM 200, RETSCH, Haan, Germany). Carbon and nitrogen contents and isotope ratios $\delta^{13}C$ and $\delta^{15}N$ in leaves were determined using an isotope-ratio mass spectrometer (CF IRMS, Flash 2000 HT, Thermo Fisher Scientific, Bremen, Germany). The percentage of N derived from the atmosphere (% N_{dfa}) was calculated using the ^{15}N natural abundance method (Boddey et al., 2001), with weeds collected in each plot serving as a reference. Leaf $\delta^{13}C$ was used as an indicator of water stress. Leaf mineral nutrients other than N were analyzed using inductively coupled plasma optical emission spectrometry (ICP-OES) after a wet digestion with concentrated HNO_3 and $HClO_4$ (Zasoski, 1977).

Soil samples were collected during crop growth in July 2021. In each plot, two 5x5 volumetric samples were drilled to a depth of 20 cm and bulked into a single sample. After 2 mm sieving, all soil samples were ground in an agate mortar and analyzed for total N by isotope ratio mass spectrometry and organic C by wet oxidation (Soon and Abboud, 1991). Sieved soil samples were also used to determine water holding capacity by measuring the weight difference between water-saturated and air-dried soil samples.

2.3 Sweet potato plant growth and storage root production

The green area (GA) and crop senescence index (CSI) were measured by analyzing zenithal images taken with conventional cameras five times during sweet potato growth using Image J software (Casadesús and Villegas, 2014; Gracia-Romero et al., 2017; Sancho-Adamson et al., 2019). The images were analyzed using Breedpix 0.2 software adapted to JAVA8 and integrated as a plugin in FIJI. Four images were taken around noon on each sampling day. The GA was calculated as the percentage of green pixels in a given image, defining green as $60^\circ <$ Hue $< 180^\circ$, and was used to estimate plant growth. GA and the greener area index (GGA), which defines green more strictly as $80^\circ <$ Hue $< 180^\circ$, excluding pixels with a yellowish-green hue, were used to determine the CSI. The CSI was calculated as the difference between GA and GGA divided by GA times 100.

The storage roots were harvested at days 107 and 128 after planting, corresponding to the early and late harvests, respectively. The total production of both commercial and non-commercial storage roots was assessed. Storage roots were considered marketable if they weighed between 150 g and 800 g. Sweet potato roots that were damaged or lacked a uniform shape, as determined by visual inspection, were discarded.

2.4 Sweet potato analyses

To identify bioactive compounds, commercial storage roots within the caliber range of 150-300 g were selected for analysis. After harvesting, the storage roots were cured for 15 days at room temperature. Subsequently, the fresh storage roots were weighed, washed, peeled, cut into 2 cm^3 slices, and crushed with a hand-held mixer until a paste was obtained. The sweet potato paste was stored at -20 °C until analyses.

2.4.1 Reagents

Methanol (LC-MS grade) was procured from Merck (Darmstadt, Germany). were obtained from Sigma-Aldrich (Darmstadt, Germany). Sodium carbonate, sodium nitrite, aluminum chloride, sodium hydroxide and sulfuric acid were all obtained from Panreac Química S.A.U. (Barcelona, Spain). DTT and *meta*-Phosphoric acid were obtained from Sigma and Fluka (Seelze, Germany), respectively. Methyl tert-butyl ether (MTBE), Folin-Ciocalteu reagent, gallic

acid, ascorbic acid, all-*E*-α-carotene, all-*E*-β-carotene, all-*E*-lycopene, all *E*-lutein, fucoxanthin, β-cryptoxanthin, and astaxanthin were purchased from Sigma-Aldrich (Darmstadt, Germany).

2.4.2 Extraction and determination of total phenolic content and total flavonoid content

The extraction for the antioxidant analyses was performed following the method of Hsu et al., (2003). with some modifications. In a 10 mL test tube, 0.5 g of OFSP paste was mixed with 5 mL of methanol. The mixture was homogenized for 1 min and samples were immediately sonicated for 15 min. After centrifugation at 4000 rpm for 10 minutes at 4 °C, the supernatant was carefully transferred to a glass tube. The samples were subjected to a second extraction under the same conditions. The pooled supernatants were evaporated with a vacuum evaporator (miVac DNA concentrator, Genevac LTD, Warminster, England). The dry extracts were reconstituted with 1 mL of methanol, transferred to a 2 mL Eppendorf tube, and stored at −80°C until analyses.

Total phenolic content (TPC) was determined as described previously (Pérez et al., 2023; Vallverdú-Queralt et al., 2011). The Folin-Ciocalteu (F-C) reagent reacts with water-soluble antioxidants in foods and human samples and is based on a redox reaction measured as gallic acid equivalents (GAE) (Vallverdú-Queralt et al., 2011). Thirty microliters of the OFSP methanolic extracts were mixed with 150 µL of F-C reagent (1:10 dilution v/v) and 120 µL of 7.5% (w/v) Na_2CO_3 solution in a 96-well microplate. The microplate was incubated at 45°C for 15 min, followed by cooling for 30 min at room temperature in the dark. Absorbance was read at 765 nm using a UV Vis Spectrophotometer (Thermo Scientific-Varioskan lux 3020). Samples were evaluated in triplicate. A stock solution of gallic acid 1000 ppm was used for preparing standard solutions (linearity 5-100 ppm) to plot the calibration curve. The results were expressed as µg of GAE/g of fresh weight (FW).

Total flavonoid content (TFC) was measured using a colorimetric assay based on the formation of flavonoid-aluminium compounds, following a previously described method with minor modifications (Pinto et al., 2017). Briefly, 30 µL of the extracts was mixed with 75 µL of distilled water and 45 µL $NaNO_2$ solution 1% (v/v) in a 96-well microplate. This mixture was incubated for 5 min at room temperature and then 45 µL of 5% $AlCl_3$ solution was added. After 1 min, 60 µL NaOH 1M and 45 µL of distilled water were added. The absorbance was read at

510 nm using a UV-Vis Spectrophotometer (Thermo Scientific-Varioskan lux 3020). Catechin was used as a standard to prepare a calibration curve (linearity 5-300 ppm). The results were expressed as µg of catechin equivalents /g of FW.

2.4.3 Extraction and determination of carotenoids

Carotenoids were extracted as previously described (de Alvarenga et al., 2019). OFSP paste (0.5 g) was weighed in a 10 mL test tube and diluted with 5 mL of ethanol and *n*-hexane (4:3 v/v), after which the mixture was vortexed. The samples were sonicated for 10 min in an ice bath to lyse the plant cell walls and then centrifuged at 4000 rpm for 20 min at 4°C. The phases were separated, and the polar phase was used for a second extraction. For this, after adding 5 mL of ethanol:hexane solution, 0.5 mL of water was added to force phase separation. The rest of the extraction was carried out under the same conditions as detailed above. The two non-polar fractions were pooled and evaporated using a nitrogen curtain. The residue was reconstituted in 1 mL of TBME, vortexed, and then filtered with a 0.22 µm PTFE filter into a 2 mL amber vial for HPLC analysis.

A QTRAP4000 triple quadrupole mass spectrometer (Sciex, Foster City, CA, USA) equipped with an APCI ionization source operating in positive–ion and multiple reaction monitoring mode was used for the identification of carotenoids. The mass spectrophotometer conditions were optimized according to Rinaldi de Alvarenga et al. (2019). The separation was carried out using an ACQUITY TM UPLC (Waters; Milford, MA, USA), with a YMC C_{30} 250 x 4.6 mm, 5µm column (Waters Co., Milford, MA, USA), at a flow rate of 0.6 mL/min at 25 °C. The injection volume was 5µL. The mobile phase consisted of 100% methanol (A) and MTBE: methanol (8:2 v/v) (B). A gradient was used to separate the carotenoid compounds under the following conditions: 0 min, 90% A; 10 min, 75% A; 20 min, 50% A; 25 min, 30% A; 35 min, 10% A; 43 min, 6% A; 48 min, 6% A; 50 min, 90% A; and 57 min, 90% A. Commercially available carotenoid standards were used to identify carotenoids: lutein (Chengdu Biopurify Phytochemicals), lycopene, α-carotene, β-carotene fucoxanthin, astaxanthin, β-cryptoxanthin, and zeaxanthin (Extrasynthese).

For the quantification of carotenoids, the chromatographic analysis was carried out using the same conditions as for the identification, as described by Rinaldi de Alvarenga et al. (2019). Analyses were performed using an ACQUITY UPLC coupled to a photodiode array (PDA) detector (Waters Corporation ®, Milford, MA, USA). The PDA detector was applied in the range of 200-700 nm and the chromatograms were acquired at 450 nm. The quantification was achieved using external calibration curves in triplicate.

2.4.4. Extraction and determination of ascorbic acid

Ascorbic acid was extracted and determined based on the methodology by (Vallverdú-Queralt et al., 2012) with some modifications. Briefly, 0.1 g of OFSP paste was mixed with 0.5 mL of a solution containing 45 g of metaphosphoric acid and 7.5 g of DTT per liter. The mixture was vortexed and sonicated for 10 min and then centrifuged at 4000 rpm for 10 min at 4ºC. The supernatant was transferred into another flask and the extraction was repeated. Both supernatants were pooled and filtered through a 0.22 μm hydrophilic filter into an amber vial for UPLC analyses.

For the chromatographic separation, an ACQUITY UPLC H-Class system equipped with a diode-array detector and an automatic sample injector was used (Waters Corporation ®, Milford, MA, USA). The mobile phase was a 0.01% sulfuric acid solution adjusted to pH 2.6 and used in isocratic mode. The separation was carried out with an ACQUITY UPLC BEH C18 column (1.7 μm, 2.1 mm x 50 mm, Waters). The flow rate was 0.7 ml/min, and all UV spectra were recorded at 245 nm. Ascorbic acid in the samples was identified and quantified using a pure ascorbic acid standard for identification and a standard curve for quantification.

2.5 Statistical analyses

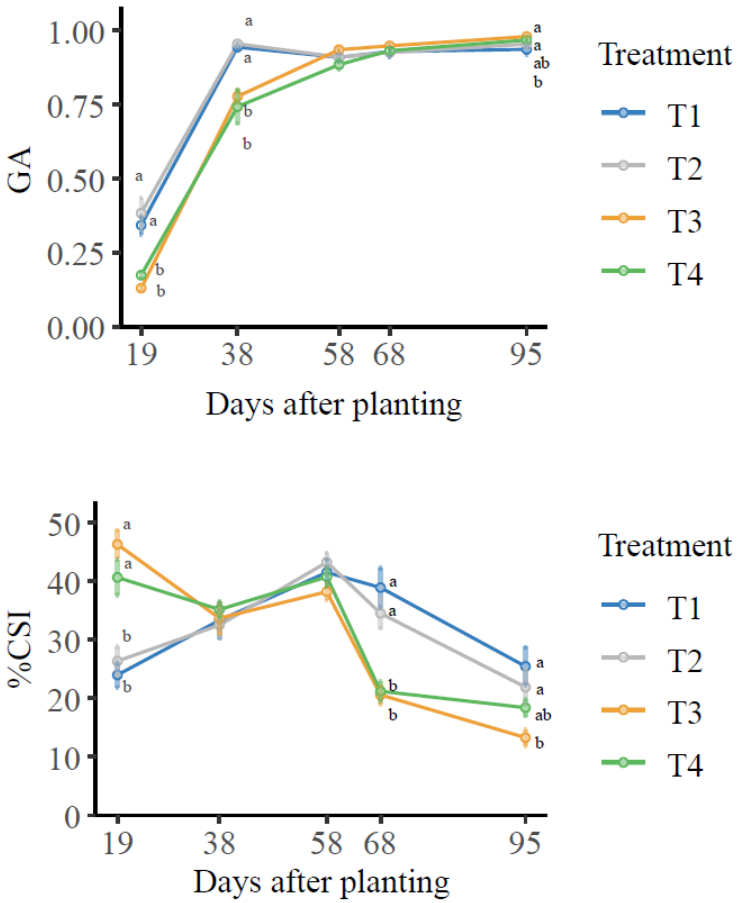
Statistical analyses were performed using SPSS 21.0 (SPSS Science, Chicago, USA), Metaboanalyst 5.0, and R-studio (R foundation for statistical Computing, Vienna, Austria). All data were subjected to one-way analysis of variance (ANOVA) to evaluate the statistical differences among fertilization treatments. Additionally, a UNIANOVA with “Treatment” and “Harvest” as factors considering the “Block” was fitted to test for differences between harvests and to determine interactions between treatment and harvest. When significant effects were

observed in the one-way ANOVA, post-hoc multiple comparisons were conducted using the Duncan test. For all analyses, results were considered statistically significant at a *p*-value <0.05. Pearson correlations were used to examine the relationships between soil organic C and N, plant stress variables, and bioactive compound content.

3. Results

3.1. Crop growth and water stress

Crop growth was assessed by measuring crop cover (*i.e.*, the GA). Twenty days after planting, both the compost and control treatments (T1 and T2, respectively) exhibited a greater GA compared to the woody residue amendments (T3 and T4) (Fig. 2). However, two months after planting, this difference disappeared. With time, all treatments resulted in an equal crop cover, with a GA close to 1. Water stress was evaluated by determining the CSI, soil water holding capacity (WHC), and $\delta^{13}C$ enrichment. The CSI followed a similar trend to the GA, with T3 and T4 initially showing higher values than T1 and T2 before decreasing. Subsequently, the lowest CSI was obtained with T3 at day 90 after planting (Fig. 2). The WHC was higher in the woody residue treatments compared to the compost treatment (Table S1), the maximum value (84.7 L/m^2) being achieved in T3. The addition of woody residues at both application rates resulted in lower $\delta^{13}C$ enrichments compared to the compost and control treatments (Fig. 3).



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302 **Fig. 2.** Crop Senescence index (CSI) and Green Area (GA) after 90 days of planting in the four fertilization

303 treatments. Data points and standard errors represent the mean of four replicates. Different letters indicate

304 statistical differences among treatments (Duncan, $p \leq 0.05$). T1, compost treatment; T2, control treatment

305 (no fertilizer added); T3, 15 kg/m^2 of woody residues; T4, 7.5 kg/m^2 of woody residues.

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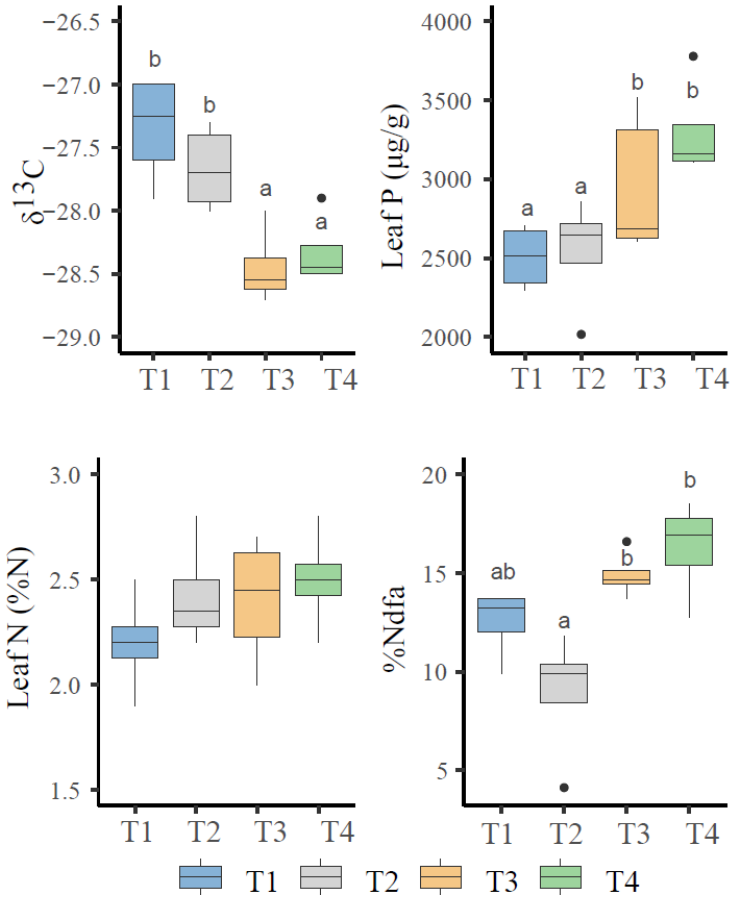


Fig. 3. Leaf composition and mineral nutrients in sweet potato leaves in the four fertilization treatments. Boxplots represent the quantitative distribution of four replicates. Different letters indicate statistical differences among treatments (Duncan, $p \leq 0.05$). T1, compost treatment; T2, control treatment (no fertilizer added); T3, 15 kg/m^2 of woody residues; T4, 7.5 kg/m^2 of woody residues. $\delta^{13}C$, Carbon isotope composition; N, nitrogen; P, phosphorous; N_{dfa}, Nitrogen derived from the atmosphere.

3.2. Nutrient availability and biological nitrogen fixation

Leaf N and phosphorous (P) as well as leaf soluble nutrients were evaluated in OFSP at late flowering (Fig. 3, Table S2). Whereas the N content did not vary among treatments, P levels were 22% higher in the woody residue treatments compared to T1 and T2 (Fig. 3). The rest of the macro and micronutrients did not change among treatments with the exception of Mg, the contents of which were a 18% lower in T3 compared to T1 (Table S2). The $\%N_{dfa}$ was also higher after fertilization with woody residues compared to the control, with values of 15 and 17% for

the high and low doses, respectively. In the control, the N_{dfa} values showed a significant variability, ranging from 4 to 12% (Fig. 3).

3.3. Agronomic production of OFSP

Agronomic production of OFSP was assessed in two harvests: the early harvest in September 2021 and the late harvest in October 2021. The early harvest was performed 107 days after planting while the late harvest 128 days after planting. The addition to the soil of 15 kg/m^2 of woody residues significantly increased the production of commercial OFSP in the early harvest compared to the control treatment (Table 1). Moreover, T3 agronomic production was higher compared to T4 in the early harvest. Agronomic production of OFSP was higher in the late harvest (Table S3). The yields of commercial sweet potatoes ranged from 2.4 to 3.7 kg/m^2 in the early harvest versus 3.4 to 4.8 kg/m^2 in the second. The higher dose of woody residues resulted in a production of 3.74 kg/m^2 in the early harvest and 4.78 kg/m^2 in the late whereas the lower dose yielded 2.69 kg/m^2 and 4.11 kg/m^2 in the early and late harvest, respectively (Table 1). The compost treatment had a yield of 2.7 kg/m^2 and 4.5 kg/m^2 in the early and late harvest, respectively.

Table 1 Agronomic production (kg/m^2) of commercial storage roots and non-commercial storage roots of OFSP in the September and October harvests in the four fertilization treatments. T1, compost treatment; T2, control treatment (no fertilizer added); T3, 15 kg/m^2 of woody residues; T4, 7.5 kg/m^2 of woody residues.

	September		October	
Treatment	Commercial	Non-commercial	Commercial	Non-commercial
T1	2.86 ± 0.21 ^{ab}	0.75 ± 0.13	4.52 ± 0.20	1.17 ± 0.18
T2	2.45 ± 017 ^{a}	0.66 ± 0.07	3.37 ± 0.29	1.67 ± 0.35
T3	3.74 ± 0.23 ^{b}	0.39 ± 0.15	4.78 ± 0.22	0.81 ± 0.13
T4	2.69 ± 0.45 ^{a}	0.61 ± 0.31	4.11 ± 0.72	1.84 ± 0.40

Values are the mean ± standard error of four replicates. When present, letters indicate statistical differences among treatments within harvest (Duncan, $p \leq 0.05$).

3.4. Antioxidant capacity, carotenoids and ascorbic acid in storage roots of OFSP

Antioxidant capacity was assessed by evaluating the total phenolic and flavonoid contents of the OFSP. Overall, the TPC was higher in the late harvest in October (Fig. 4, Table S3), with

344 the exception of T4, which resulted in a higher TPC in the early harvest in September. The
345 application of woody residues increased the TPC, which conversely was reduced by the compost
346 treatment (Fig. 4). In the late harvest, the highest TPC values were found in T3 (296 GAE/g FW)
347 and T4 (288 µg GAE/g FW), whereas the lowest were obtained in T1 (Fig. 4).

348 On the other hand, the TFC was higher in the early harvest (Fig. 4, Table S3), and there
349 were not significant differences among treatments, unlike in the late harvest, when the differences
350 were significant. The lowest TFC (148 µg catechin/g FW) was observed in T4 (Fig. 4).

351 Carotenoids were identified and quantified in OFSP by UPLC-MS/MS and UPLC-PDA,
352 respectively. The main carotenoids found were β-carotene (26.6 to 29.9 µg/g FW) (Fig. 4) and
353 its hydroxylation product β-cryptoxanthin (1.9 to 2.3 µg/g FW). The highest values of β-
354 cryptoxanthin in the early harvest (2.3 µg/g FW) were obtained with T3 and in the late harvest
355 with T4 (2.29 µg/g FW) (Fig. 4, Table S3). The highest levels of β-carotene were found in T3,
356 which were statistically different from those of T1 (Fig. 4).

357 Ascorbic acid was quantified by UPLC-PDA. Its contents were higher at the early harvest
358 compared to the late harvest (Table S3 and S4). While the concentration of ascorbic acid in
359 September was of 38.5 µg/g FW, the levels in October dropped by an 80%, ranging from 4.8 to
360 8.4 µg/g FW (Table S4). No differences among treatments were found at the early harvest while
361 T4 had the lowest ascorbic acid levels at the late harvest (Table S4).

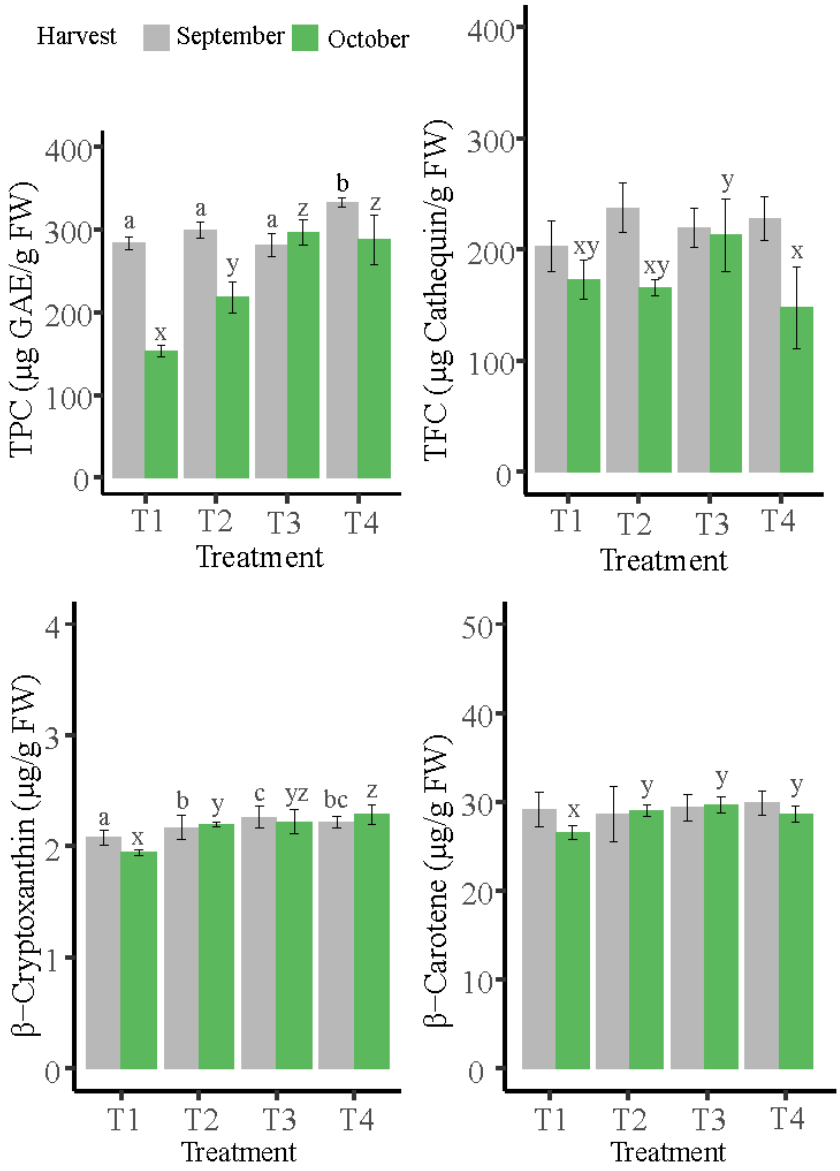
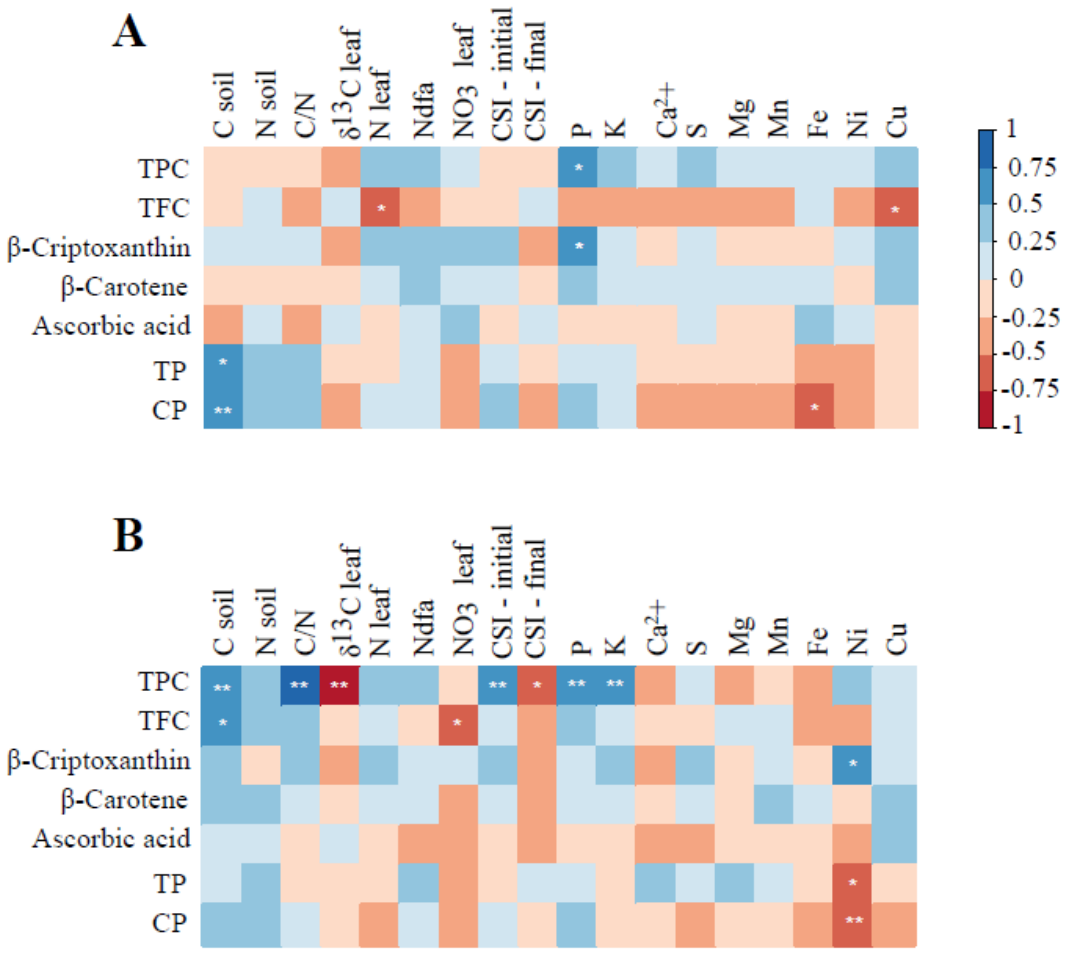


Fig. 4. Antioxidant capacity and carotenoids (α-cryptoxanthin and β-carotene) in OFSP in in the September and October harvests in the four fertilization treatments. Bars represent the mean and standard error of four replicates. Different letters indicate statistical differences among treatments within harvest (Duncan, $p \leq 0.05$). Statistical differences in September are represented by "abc" while in October by "xyz". TPC, total phenolic content; TFC, total flavonoid content; GAE, gallic acid equivalents. T1, compost treatment; T2, control treatment (no fertilizer added); T3, 15 kg/m^2 of woody residues; T4, 7.5 kg/m^2 of woody residues.

3.5. The relationships of plant stress and nutritional status with antioxidant activity and total sweet potato production

Pearson´s correlation analyses were used to investigate the relationships of soil quality (C and N content, and C/N ratio), leaf nutritional status, and stress parameters (isotope ratio $\delta^{13}C$, CSI) with production and antioxidant activity and contents of sweet potatoes (Fig. 5). Testing these relationships implies evaluating the quality and quantity of OFSP in these soils and its adaptation to the different fertilization conditions. The data of soil quality parameters are shown in Table S5, and the initial and final CSI were included in the analyses to account for differences in plant development (see Fig. 2). In the early harvest (September), TPC and β-cryptoxanthin showed significant positive correlations with leaf P, whereas TFC correlated negatively with leaf N (Fig. 5A). No significant correlations with plant nutrition and stress parameters or with soil parameters were observed at this time. In contrast, in the second harvest (October), soil C and C/N ratio showed strong positive correlations with TPC (Fig. 5B). Moreover, somewhat surprisingly, TPC correlated negatively with plant stress indicators (isotope ratio $\delta^{13}C$, CSI), indicating that at two months of planting, the higher the TPC, the lower the plant stress. TPC was strongly and positively correlated with leaf P and K. In the late harvest, the other antioxidant products measured did not show any relationship with soil and plant stress parameters except for a positive relationship between leaf N and β-cryptoxanthin. There was no correlation between ascorbic acid and soil or leaf parameters at any harvest. (Fig. 5B). Storage root production only showed a positive relationship with soil organic C at the early harvest and a negative relationship with leaf N at the second harvest.



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399 **Fig. 5**. Heatmap of Pearson´s correlation coefficient (r) between antioxidants compounds and plant

400 nutritional and soil statuses. September data (early harvest) are shown in heatmap **A** whereas October

401 data (late harvest) are shown in the heatmap **B**. Blue indicates a positive correlation whereas red, a

402 negative correlation. TPC, total phenolic content; TFC, total flavonoid content; TP, total production; CP:

403 commercial production; Ndfa, N derived from the atmosphere; CSI, crop senescence index. Significant

404 results are indicated by and asterisk: $p < 0.05$*, $p < 0.01$**.

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4. Discussion

Orange-fleshed sweet potato (OFSP) is a low-input crop and a source of bioactive compounds, especially carotenoids (Conz et al., 2021a; de Albuquerque et al., 2019), which makes it a good option for nutrient poor soils under the current food and land crisis. In this study, we tested different organic and sustainable management practices to grow OFSP in low nutrient soils, with a focus on the use of high doses of woody residues in order to increase soil nutrient cycling. Given the little evidence on the nutritional quality of organically-grown sweet potatoes, our study provides valuable insights into how organic amendments can impact not only soil health but also the nutrient composition and agronomic performance of OFSP, promoting sustainable agricultural practices in challenging environments.

Crop performance, evaluated here through agronomic production, crop cover (i.e. GA), senescence (i.e. CSI) and acclimation to stress (i.e. $\delta^{13}C$ enrichment), seemed to be better in OFSP grown with woody residues. Agronomic production was higher in T3 compared to the control treatment at the early harvest, GA did not vary among treatments and both T3 and T4 had lower CSI and $\delta^{13}C$ values (Table 1, Fig. 2 and Fig. 3). While the control treatment and the low dose of woody residues did not reach the levels of T3, the compost treatment had a comparable yield to the high dose of woody residues (Table 1). In a slightly alkaline soil such as the one in our experiment, (Navarro et al., 2020b) observed an agronomic production of 0.45 kg/m^2 in 'Beauregard' sweet potato fertilized with compost at 92 days after planting, which is more than six times lower than our early harvest yield. In a recent study in Brazil using woody residues as an organic amendment, the yield of orange sweet potato cv. *Beauregard* was 3 kg/m^2 at 150 days after planting (Toroco et al., 2023). In contrast, we obtained similar yields as early as 107 days after planting. Our productivity is in line with Spanish marketable yields, which range from 2.2 kg/m^2 to 3 kg/m^2 in coastal areas (Ministry of agricultural Fisheries and Food, 2022). Specifically, for an organically grown *Beauregard* sweet potatoes, (Treadwell et al., 2008) obtained an agronomic production of 2.9 kg/m^2, which is similar to our yield in the early harvest, despite our slightly alkaline soils, which are not the preferred growth conditions for sweet potato (Constantin

et al., 1975). On the other hand, our marketable yield of 4.2 kg/m^2 in the second harvest, significantly exceeds both benchmarks. Sweet potato production in Spain has been reported to increase from 75-90 days after planting to 140-160 days after planting (Miguel & Marsal, 2008), which would be in line with our higher yields at the late harvest, which was performed at day 128 days after planting. The fact that the differences among treatments disappeared from the early harvest to the second could be attributed to the occurrence of plant stress at that moment.

Carbon isotope composition ($\delta\ ^{13}C$) is a long-term integrator of ecophysiological processes such as stomatal conductance, photosynthetic capacity, and water-use-efficiency (Ehleringer and Vogel, 1993; Farquhar et al., 1989). Higher $\delta^{13}C$ values have been found in sweet potato plants under water stress compared to irrigated plants (Gouveia et al., 2019). Hence, the lower $\delta^{13}C$ enrichments obtained with T3 and T4 compared to T1 and T2, together with a higher WHC and lower CSI, suggests that the sweet potatoes fertilized with woody residues at both application rates were better acclimated to summer water scarcity than those grown with compost or in control conditions. Wood mulches are known to promote water retention by reducing temperature fluctuations and water evaporation (Gruda, 2008; Soumare et al., 2002). The incorporation of woody residues into soil therefore holds promise for mitigating water stress in horticultural systems. A higher soil WHC has been linked to improved soil organic matter and soil structure, facilitating better water infiltration and root penetration, and thereby reducing the risk of water stress for plants (Baveye, 2023; Vogel et al., 2022).

P and Mg were the only two leaf nutrients that showed significant differences among treatments (Fig. 3, Table S2). Few studies have assessed the effect of woody residues on leaf crop nutrients and the available reports show contrasting results. For instance, Arlotta et al. (2023) found no differences in nutrients in sweet potatoes grown in bare soil or with wood mulch. In contrast, Fontana et al. (2023) observed higher P and Mg contents in winter wheat fertilized with ramial wood chips. Our findings are in partial agreement with their results, as leaf P in T3 was higher compared to the compost treatment, but leaf Mg was lower (see Table S2). It has been reported several times that wood decomposition promotes microbial activity which, in turn, leads

to increased P concentrations (Hallman et al., 2023; Ji et al., 2023; Stefani et al., 2023). A higher leaf P content after woody residue application suggests that the increase in labile C induced by this treatment could have enhanced P mobilization (Fujisaki et al., 2015). In fact, C and P have been shown to interact in urban park green spaces where changes in labile C can influence nutrient dynamics (Huang et al., 2021). The abundance of labile C may stimulate microbial activity, enhancing the breakdown of organic matter and leading to greater P availability in the soil. As P availability increases, it may, in turn, support further microbial growth, creating a positive feedback loop that accelerates nutrient cycling. This together with the fact that sweet potato has been reported to have a high P use efficiency (Minemba et al., 2019) could have contributed to a greater plant nutrient uptake, leading to the recovery of plant growth and the good agronomic performance of the woody residue treatments. Given the ongoing P losses from soil erosion in the Mediterranean region and the fact that organic farming practices exclude inorganic fertilizers – currently the primary source of P inputs (Panagos et al., 2022) - - the integration of sweet potato cultivation with woody residue amendments represents a promising organic strategy, as it not only adds P to the system but also enhances P mobilization. Future research on the mechanisms by which woody residues increase P availability and uptake could help preserve soil P stocks and improve P mobilization in agricultural soils, particularly in the context of climate change, where sustainable nutrient management is increasingly critical.

The absence of differences in leaf N between treatments is striking considering that the compost fertilizer had a lower C/N ratio than the woody residues (see Materials & Methods). Moreover, the application of woody mulches is known to reduce N availability in the first crop after the amendment, as the soil microbiota may temporarily compete with plants for nutrients (Lalande et al., 1998). However, from the second crop onwards, N remobilization can occur due to microbial activity (Lalande et al., 1998; Soumare et al., 2002). The fact that the woody residue amendments did not reduce leaf N suggests that sweet potato can compensate for N deficiency in soil. This compensation may occur through endophytic N_2 fixation, as evidenced by the increased N_{dfa} (Terakado-Tonooka et al., 2013; Yoneyama et al., 2017, 1997), as well as through symbiotic associations with arbuscular mycorrhizal fungi, which could further enhance nutrient acquisition

(Negeve and Roncadori, 1985; Oapos;Keefe and Sylvia, 1992) . Understanding the specific microbial interactions that enhance nutrient cycling could provide deeper insights into optimizing soil health and plant nutrition in organic systems.

Storage roots' quality of OFSP was assessed through TPC, TFC, carotenoid and ascorbic acid contents. Our TPC values fall within the range of phenolics reported for sweet potato (Laveriano-Santos et al., 2022), while our total flavonoid content (TFC) values exceed the average of 121 µg/g dry weight reported in the same review. Notably, we report 150–230 µg of flavonoids on a fresh weight basis, indicating a higher flavonoid concentration compared to the average values discussed and suggesting a positive effect of organic amendments on OFSP nutritional quality. In terms of carotenoids, β-carotene and β-cryptoxanthin were the primary carotenoids found in our OFSP storage roots, which is in line with previous reports (Alam et al., 2020, 2016; Kim et al., 2015, 2012). Our values are also in the range of those reviewed by Laveriano-Santos et al., (2022). A difference in carotenoid levels was only found in the compost treatment, where β-cryptoxanthin levels were lower at the late harvest (Fig. 4, Table S3).

Maturity and size are also reported to influence the content of bioactive compounds in sweet potato. Typically, larger and more mature sweet potatoes have lower TPC and antioxidant capacity while having higher β-carotene contents (Pazos et al., 2022a; Setoguchi et al., 2023). This explains why the TPC was higher at the early harvest (ca. 300 µg GAE/g FW) compared to the late harvest (239 µg GAE/g FW) (Table S5). However, it is worth noting that the highest TPC values in the late harvest were observed in sweet potatoes grown with T3 and T4 (Fig. 4), which may be linked to environmental factors rather than maturity alone.

Environmental stress conditions can result in the accumulation of reactive oxygen species, which if excessive, may lead to oxidative stress and cellular membrane damage (Mittler et al., 2011; Noctor et al., 2014). To counteract this, plants activate defense mechanisms, including the synthesis of polyphenols (Lattanzio et al., 2006; Šamec et al., 2021) and vitamin C (Akram et al., 2017). Unexpectedly, our research revealed that the plants experiencing the highest levels of stress – indicated by elevated values of $\delta^{13}C$ and CSI in T1 and T2 treatments – did not

exhibit higher phenolic contents (Fig. 4). In contrast, the woody residue treatments, which were under less stress, showed the highest TPC, particularly at the late harvest.

While the accumulation of phenolic compounds or flavonoids in response to abiotic stress is well documented in sweet potato leaves (Jung et al., 2011; Krochmal-Marczak et al., 2020), the literature regarding stress effects on storage roots is limited and inconsistent. Some studies have reported an increase of antioxidants in sweet potato storage roots under drought and extreme temperatures (Franková et al., 2022; Musilová et al., 2024; Padda and Picha, 2008; Rautenbach et al., 2010). However, other research has shown that harsh environmental conditions can decrease the levels of phenolics and carotenoids (Pazos et al., 2022). Motsa et al., (2015) suggested that this reduction in antioxidant defenses may occur because storage roots expend their secondary metabolite pool to cope with stress. This could explain why T1 and T2 plants had already used their antioxidant defenses to mitigate oxidative stress, resulting in lower TPC. It is plausible that under more severe stress – such as at the late harvest – the demand for antioxidants outpaced their biosynthesis in the compost and control treatments (Hasanuzzaman et al., 2020). Alternatively, the stress response in sweet potato storage roots might involve other antioxidant systems, such as vitamin C and carotenoids.

Ascorbic acid, the most active form of vitamin C in foods (Davey et al., 2000), decreased at the second harvest in OFSP (Table S3 and Table S4). While OFSP is known for its high vitamin C and β-carotene content, phenolic compounds are typically present at higher concentration (Pazos et al., 2022b; Rautenbach et al., 2010). Our ascorbic acid levels were slightly lower than those reported by (Grace et al., 2014), although they examined a different OFSP cultivar. The lack of significant differences between treatments suggests that ascorbic acid accumulation was not stress-induced but rather constitutive. However, the reduction observed at the late harvest implies that there may have been a redistribution of resources towards other defense mechanisms. Indeed, phenolics have been reported to exhibit higher antioxidant activity compared to other antioxidants in sweet potato (Lebot et al., 2016) suggesting that phenolic compounds are the primary antioxidants that act upon oxidative stress in sweet potato storage roots. Additionally, higher phenolic content has been observed in delayed harvests of OFSP (Simões et al., 2020) .

In the case of T1 and T2, it is possible that phenolics had accumulated earlier and acted as scavengers during stress, leading to the observed decrease in TPC. Therefore, given the reduced contents of ascorbic acid in all treatments, OFSP could be experiencing a trade-off between the synthesis and accumulation of vitamin C and phenolic compounds. Moreover, the fact that the woody residue treatments maintained their TPC levels, suggests that these treatments might have a greater capacity to constitutively produce polyphenols and better tolerate stress.

The decrease in carotenoids with compost between the two harvests may be the result of T1 plants being more stressed, given that carotenoid accumulation in sweet potatoes has been shown to be highly responsive to stress signals (Zhang et al., 2023, 2022). A carotenoid biosynthetic gene particularly reactive to stress is the *chyB* gene, which encodes β-carotene hydroxylase, the enzyme that catalyzes the conversion of β-carotene to β-cryptoxanthin and ultimately to zeaxanthin (Davison et al., 2002; Du et al., 2010). The silencing of this gene has been reported to increase the accumulation of β-carotene and β-cryptoxanthin under salt stress in sweet potato (Kim et al., 2012). Hence, the lower contents of carotenoids in T1 in OFSP could be related to a stress-enhanced activity of β-carotene hydroxylase, resulting in the hydroxylation of β-carotene and β-cryptoxanthin.

We found a negative correlation between TFC and leaf N, suggesting a possible reaction to nutritional stress caused by the lack of N. Although reduced N levels can activate flavonoid biosynthetic pathways as a response to environmental stress (Treutter, 2006), it is well established that phenolic accumulation in storage roots is critically dependent on the root developmental stage. During early growth, storage roots exhibit elevated levels of phenolic compounds and enhanced antioxidant activities. However, as root growth progresses, these levels tend to decrease (Padda and Picha, 2007; Setoguchi et al., 2023). Furthermore, the impact of abiotic stress on sweet potato storage roots may diverge from conventional patterns. Pazos et al. (2022) observed adverse effects of water stress on TPC, anthocyanins, and antioxidant activities, which aligns with our findings in T1 and T2 treatments. Consequently, the developmental stage and abiotic stress could be responsible for the reduced TPC in the compost and control treatments. In turn, the higher TPC in the woody residue treatments at the late harvest could be attributed not only to the absence of

stress but also to the supposed enhancement of soil microbial activity by the incorporation of woody residues. Indeed, C-rich fertilizers have been reported to increase phenolic compounds in tomato (González-Coria et al., 2022) and tight relationships have been found between crop rotations (in our organic farm), polyphenols, and soil microbiota (Fan et al., 2022; McGivern et al., 2021). The fact that plants cultivated with woody residues experienced lower abiotic stress and displayed an increased phenolic content in their storage roots suggests a heightened adaptability to environmental conditions. This adaptation is noteworthy for maintaining good storage root quality, especially during the later stages of root development.

Our results show that using high doses of woody residues can slightly increase or maintain high commercial sweet potato production. The incorporation of woody residues into agricultural systems has been recognized for its potential to positively influence soil quality through various mechanisms. As woody residues undergo decomposition, they release organic matter into the soil, contributing to an improved soil structure (Horn et al., 1994; Li et al., 2018; N. C. Brady and R. R. Weil, 2008) .This fact, coupled with increased water retention capacity, provides a favorable environment for plant growth, particularly in regions susceptible to water stress (Lal, 2015). Moreover, woody residue application increased the availability of P and endophytic biological N fixation (*i.e.*, N_{dfa}). These improvements have the potential to positively impact crop yield and quality, with implications for sustainable agriculture practices (Schipanski et al., 2010).

5. Conclusions

The application of woody residues increased the bioactive compounds in late-harvested storage roots of OFSP. This was concomitant with reduced plant stress in later growth stages when the nitrogen fixing capacity and P availability increased. In contrast, compost application significantly reduced both TPC and carotenoids in the storage roots, despite plant growth and stress indicators being similar to those of the control treatment, and it appeared to increase oxidative stress at the late growth stages. The woody residue amendment at a high dose slightly increased or maintained a high production of commercial sweet potatoes, allaying concerns about yield reduction with woody residue-based organic practices for this crop. Sweet potato has proved

to be a low nutrient-demanding crop with a capacity for biological nitrogen fixation that could help overcome potential nutrient limitations arising from the application of woody residues. The possible increase in soil microbial activity induced by these amendments may have positively influenced secondary metabolism in orange-fleshed sweet potato. Consequently, sweet potatoes grown with woody residues, harvested at their optimal size and maturity might be of superior quality compared to sweet potatoes fertilized with compost.

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Declaration of interests

The authors declare that they have no conflicts of interest.

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