



Sweetpotato storage root formation as affected by soil organic amendment applications

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Received: 28 March 2022 / Revised: 15 July 2022 / Accepted: 13 May 2023 / Published online: 27 May 2023
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Abstract

Organic amendments have been utilised as a source of nutrients to improve the growth and yield of many crops, including sweetpotato. However, none of the studies examined the relationship between organic amendments and the initiation of sweetpotato storage roots (SRs). A study was conducted in sweetpotato Orleans cultivar to investigate anatomical changes to roots during storage root formation aiming to elicit if organic amendment affects SR formation by changing soil available nitrogen (N) concentration. Two locally available organic amendments including poultry manure (PM) and sugarcane trash (SCT), were used in this experiment at different rates. Six treatments were included in the study: unamended soil (control), unamended soil with chemical fertiliser, PM 22 Mg/ha, PM 66 Mg/ha, SCT 10 Mg/ha and SCT 30 Mg/ha. Compared with unamended control, SCT application at both rates, 10 or 30 Mg ha⁻¹, significantly promoted the formation of SRs and reduced root lignification, while PM amendment from 22 to 66 Mg ha⁻¹ significantly inhibited SR initiation and enhanced the formation of lignified roots, which appear to be associated to high soil available N caused by PM addition. During the SR initiation, all amended treatments increased N accumulation in plants compared to the control. These results indicated that excessive soil available N introduced by PM amendment could inhibit the formation of SR of sweetpotato. Thus, when applying a lower rate of PM to sweetpotato, and planting should be delayed from 2 to 3 weeks after amending to avoid the detrimental effect on SR initiation. Excessively high rates of PM soil amendment (66 Mg ha⁻¹) should be avoided. A suitable rate of SCT may be applied (~10 Mg ha⁻¹ in this study) to promote SR formation of sweetpotato in soil with adequate available N level, but high rates could lead to immobilisation of N and suppress crop growth.

Keywords Sweetpotato · Root anatomy · Storage root formation · N acquisition · Anomalous cambium

Introduction

Organic soil amendments are commonly used in agriculture to improve soil organic matter content and other soil properties, which result in a better environment for root growth (Davis and Wilson 2000). In general, organic amendments have been proved to enhance root growth of crops (Donn

et al. 2014; Xiao et al. 2016) and result in increased nutrient uptake and yield (Backer et al. 2017; Mehdizadeh et al. 2013; Xiao et al. 2016). The application of soil organic amendments has been demonstrated to improve the yield of many crops such as vegetative, grain, root and tuber crops (Agyarko et al. 2013; Lin et al. 2016; Mehdizadeh et al. 2013; Xiao et al. 2016). The effect of organic amendments on root and tuber crops has received less research attention. Some studies examined the influence of these products on such crops. The application of poultry manure increased cassava yield by around 30% (Ojeniyi et al. 2012). The growth and yield of radish (*Raphanus sativus* L.) increased significantly when organic soil amendments was in use (Adekiya et al. 2019; Sandeep et al. 2014). In potato (*Solanum tuberosum* L.), manure and compost were recorded to improve tuber yield (El-Sayed et al. 2015; Ninh et al. 2015).

The number of SRs varies greatly between individual plants, leading to variation of yield up to 50% (Villordon

Communicated by F. Araniti.

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et al. 2009). Obviously, SR yield of the crop is determined by the plant density, SR number and SR size. The density is adjusted well by commercial practices (Meyers et al. 2014). As the initiation process of SRs determines the number as well as the size and shape of SRs, it is one of the key factors that affect crop yield and market value.

The application of organic amendments was investigated in some previous studies on sweetpotato. Some products such as wheat straw biochar, green leaf manure and poultry manure have been demonstrated to improve SR yield (Agyarko et al. 2013; Liu et al. 2014; Nedunchezhiyan et al. 2010). Applications of organic amendments could stimulate SR development (Isobe et al. 1996) or increase sugar content as well as SR appearance quality (Dou et al. 2012). However, none of these studies focused on the influence of these substances on the storage root formation.

Locally available organic amendments were chosen for this study to examine the effects of these products on sweetpotato SR initiation. Queensland is the biggest producer of sugarcane in Australia which accounts for around 95% of Australia's sugarcane (SRA 2019) and produces a large amount of trash (10–15 Mg/ha/year) (Zafar 2022). National poultry litter was estimated at around 1.2 million tons per year and expected to increase with industry expansions (McGahan et al. 2013). Obviously, organic amendments are a source of N and available N released into the soil after amending with these products may differ due to amendment properties and application rates. In the previous study, insufficient or excessive N supply inhibited the formation of SRs of 'Orleans' sweetpotato cultivar (Dong et al. 2022). Therefore, in this study, we focused on how N soil availability change caused by soil amendments affects SR formation. Accordingly, the study aims (1) to investigate the influence of organic amendments on sweetpotato during SR initiation (2) to determine the rate and type of amendments should be used for sweetpotato cropping.

Materials and methods

Plant materials and growth conditions

The experiment was conducted in a glasshouse at the Queensland Department of Agriculture and Fisheries Bundaberg Research Facility (lat. 24°50'54" S, long. 152°24'14" E) from 12 May to 1 July 2019. The average daily maximum and minimum temperature during the study period inside the glasshouse were 26.5 °C and 14.3 °C, respectively, and the average daily maximum and minimum relative humidity were 87.9% and 48.8%, respectively. The average photosynthetic photon flux density inside the glasshouse was 530 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at midday during the experimental period. Approximate day length is about 10 h 40 min. A sandy loam

soil (Dermosol) (Isbell 2016) was used for the experiment. Poultry manure blend (PM) (Fine farm organics, Victoria, Australia) and sugar cane trash (SCT) (ORECO Group, Queensland, Australia) were used as soil amendments in this study. Granular fertilisers including urea (Richgro, Jandakot, West Australia) (46% N as NH_4^+), Nitrocal (Campbells Fertiliser Australia, Laverton North, Victoria) (15.5% N as NO_3^-), Potash (Richgro, Jandakot, West Australia) (41.5% K) and superphosphate (Richgro, Jandakot, West Australia) (9.1% P) were added into the soil.

Healthy uniform cuttings of 'Orleans' with six fully opened leaves and at least 20 cm long were utilised to examine SR initiation. One cutting was planted horizontally in each pot with three nodes without leaves buried under the sand and three fully opened leaf staying above-ground.

Growth medium preparations

Black plastic pots of 20 cm in diameter and 27 cm in height were used in this experiment. 3.5 L of dermosol soil was mixed thoroughly with the respective amount of amendments and fertilizers (Table S1) to fill the pot. Characteristics of soil and organic amendments used for the experiment were analysed at Environmental Analysis Laboratory, Southern Cross University, Australia (Table S2). Available nutrients at the beginning of the experiment were adjusted to the same level in all pots except A0 as N 500 mg, P 1000 mg and K 1800 mg pot^{-1} . The treatment A0 contains N 113 mg, P 42 mg and K 282 mg pot^{-1} . The amount of P and K supplied for plants in this experiment is similar to the total P and K supplied for sweetpotato when using Hoagland's nutrient solution in previous studies (Dong 2021). N available for each plant was around 50% recommendation for basal N fertilisation of sweetpotato (Loader et al. 1999). Because a key purpose of soil amendment is to increase soil organic carbon ©, amendments were applied to achieve two levels of carbon concentrations in the mixture at 2.16% and 2.55% (from 1.97 of the original soil). Pots were settled in the glasshouse for 1 week before planting. Tap water was added in the pots to field capacity 3 days before transplanting to ensure sufficient and similar moisture in all pots.

Experiment design

The experiment consisted of six treatments including unamended, synthesis fertilisers, PM 22t/ha, PM 66 Mg/ha, SCT 30 Mg/ha and SCT 10 Mg/ha (hereafter A0, AF, PM22, PM66, SCT10 and SCT30, respectively) with multiple harvests over the study period. The pots were arranged in a complete randomized design (CRD). During each harvest, six plants for each treatment were harvested for measurements. Three plants were used for anatomical observations and morphological analysis of the roots, and the other three

were used for CN analysis. In total, 4 harvests were conducted over the experiment period including 144 plants (6 treatments \times 4 harvests \times 6 plants per harvest). Eight additional plants per treatment (48 plants in total) were grown for backup purposes in case death or abnormal growth occurred.

Sampling date

Plants were sampled at 10, 21, 35 and 49 DAT. Six uniform plants divided into two sets were sampled for each treatment on a sampling date. Plants were dug out carefully to minimise root damage and washed in tap water to remove all soil.

Measurements and data collections

Available NH_4^+ , NO_3^- and total C, N in soil samples

Soil samples were taken from three harvested pots for each treatment at planting, 10, 21, 35 and 49 DAT. They were dried in an oven at 40 °C to a constant weight. Then, all samples were stored in the -80 °C freezer until analysis. A solution of 0.1 M MgSO_4 was used to extract NH_4^+ and NO_3^- in soil samples (Choosang et al. 2018). The concentration of NH_4^+ and NO_3^- were determined by Ammonium and Nitrate Ion Selective Electrodes (ISEs) (Van London Co., Houston, Texas, USA). Total C and N concentration in soil samples were analysed using TruMac® Carbon/Nitrogen Analyser (LECO Corporation, Michigan, USA). C:N ratio was calculated based on their concentration in dried mass basis.

Anatomical changes in ARs

Sampling for root anatomy was performed at 10, 21, 35 and 49 DAT. Three plants from each treatment were dug out carefully and washed in tap water to remove all growth substrates. All adventitious roots (ARs) from an individual plant were harvested and sectioned using sharp razor blades (Villordon et al. 2009). Only very thin sections not cut obliquely were used. Anatomical observations were recorded from sections at around 3–4 cm from the proximal end of roots (Villordon et al. 2009). Transverse sections of all ARs were stained by Toluidine Blue O 0.05% to observe the anatomy under a microscope (Eguchi and Yoshinaga 2008). After staining, they were rinsed in water until there was no stain left on the sections (O'Brien and McCully 1981). Images for each section were taken under a microscope to determine anatomical feature development (Figure S1). Some main anatomical characteristics of ARs were investigated via those images. Other characteristics, including initial development of regular vascular cambium (IRVC), completed regular vascular cambium (RVC), appearance of anomalous cambium (AC) and lignification

of more than 50% of the stele cells (LC) were characterised throughout the sampling dates.

Classifying AR development

ARs were classified into storage roots (SRs), pencil roots (PRs) and lignified roots as described by Wilson and Lowe (1973). ARs with anomalous cambium (AC) encircling the primary and secondary xylem elements and/or central metaxylems were considered as SRs (Belehu et al. 2004; Villordon et al. 2009; Wilson and Lowe 1973). Those roots with at least one of the protoxylem elements connected to the central metaxylems by a strand of lignified cells and some meristematic activities were around the central metaxylem developed into PRs. When more than 50% of stele cells was lignified, these roots would be lignified roots. Sections were observed under an Olympus CX31 microscope (Olympus corporation, Tokyo, Japan) and images were taken by a Nikon DS-L2 camera (Nikon corporation, Tokyo, Japan).

Carbon and nitrogen analysis in sweetpotato plants

Three plants from each treatment were harvested at 10, 21, 35 and 49 days after transplanting (DAT). Shoots and roots from each plant were dried separately in an oven at 70 °C to a constant weight. Then, samples were stored in a -80 °C freezer until analysis. Total N and C in plant samples were analysed using TruMac® Carbon/Nitrogen Analyser (LECO Corporation, Michigan, USA).

Statistical data analysis

All statistical analysis was conducted using IBM® SPSS® software (version 25; IBM, New York, United States) statistical package. Percentage data were transformed using arcsine, whereas measurement data were square root transformed in SPSS for analysis. One-way ANOVA was used to test how plants reacted to different organic soil amendments for each harvest. As different plants were sampled in each harvest, two-way ANOVA (rather than repeated measure ANOVA) was used to analyse the global effects of organic amendments, time and interactive effect of amendment and time on anatomical root features, N acquisition, and the number of initiated SRs. The means were compared using Turkey HSD. *P* value of less than 0.05 was regarded as statistically significant. Graphs were produced using SigmaPlot® software package (version 14; SYSTAT Software, Inc, California, United States) and Microsoft® Excel® for Office 365 MSO (Microsoft Corporation, Washington, USA).

Results

Effects of soil amendments on N concentration in soil samples

Available N and total N in soil were examined over the study period. Results showed that the effects of soil amendments were statistically different in the concentration of soil available N after planting (Fig. 1). As no N fertilisation was added in A0 treatment, the lowest N availability was recorded in this treatment. Although initial soil available nutrients were modified to the same level in all amended pots, there were significant differences in

the concentration of available NO_3^- and NH_4^+ among amended treatments due to the different decomposition rate and soil amendment interaction, especially related to NH_4^+ . In the treatments with PM, uric acid in the amendment metabolised rapidly to NH_4^+ , so a higher concentration of NH_4^+ was recorded in those treatments. In contrast, the immobilisation effect in SCT treatments reduced the available N in soil. Therefore, the highest and lowest available N was observed in the PM66 and SCT30 treatment, respectively. In all observations, both PM treatments had significantly higher available NO_3^- and NH_4^+ than treatments with SCT.

There were significant differences in total N in the soil between treatments (Table 1). PM applications increased

Fig. 1 Effects of soil amendments on available N in soil (mg/g dwt) at various sampling times. **A** available NO_3^- ; **B** available NH_4^+ ; **C** total N ($\text{NO}_3^- + \text{NH}_4^+$). Values are indicated as mean \pm SE ($n = 3$). ANOVA results are based on square root transformed data. Two-way ANOVA results including the effect of treatment, time, and treatment by time on SRs and PRs are shown. Different letters are significantly different among treatments on single sampling dates (Turkey's HSD, $P < 0.05$). Abbreviations: A0 Unamended, AF Amended with synthesis fertilisers, PM22 22 Mg ha⁻¹ poultry manure, PM66 66 Mg ha⁻¹ poultry manure,, SCT10 10 Mg ha⁻¹ sugarcane trash and SCT30 30 Mg ha⁻¹ sugarcane trash

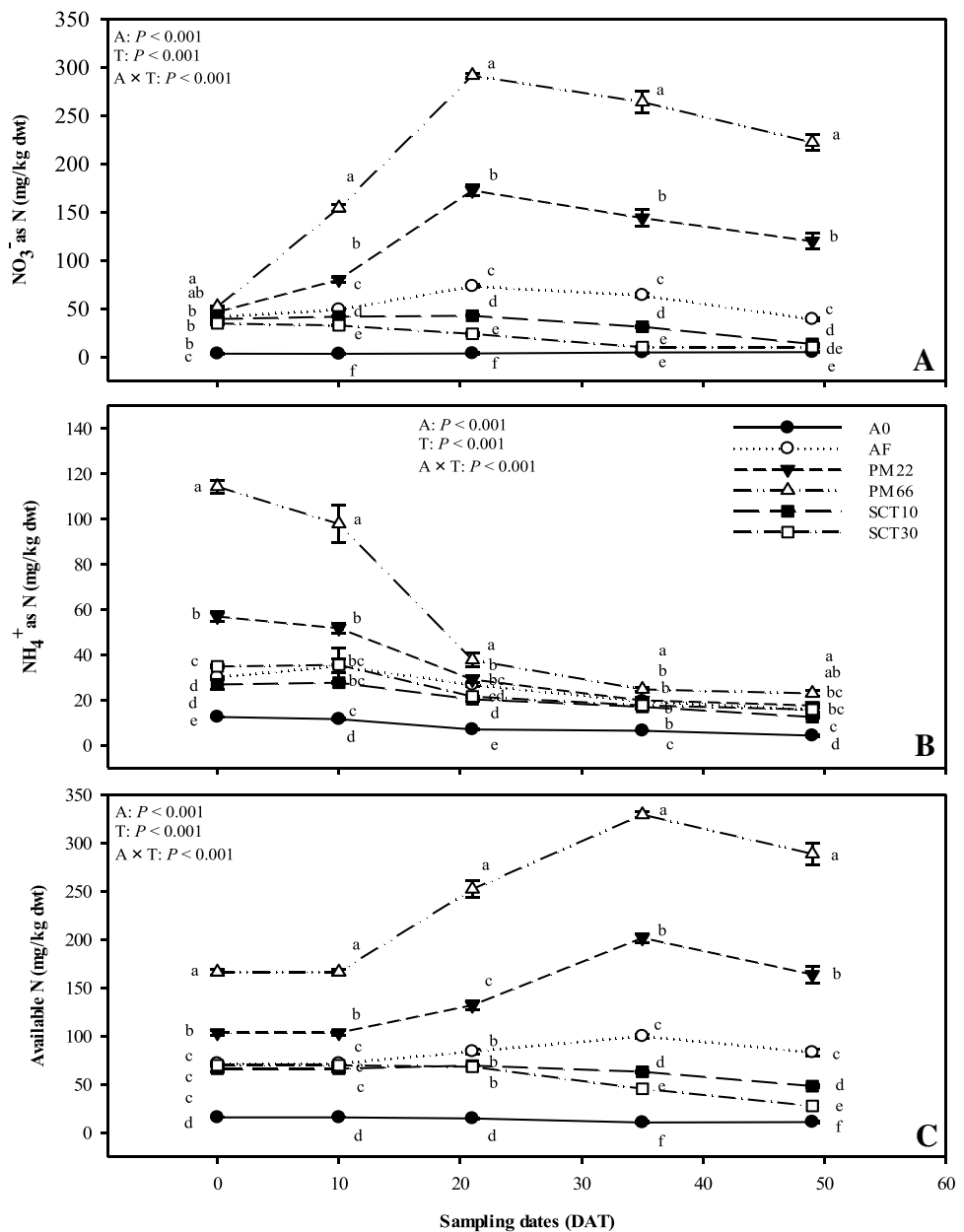


Table 1 Effects of soil amendments on total N (%) in soil at various sampling times

| Treatment | Planting | 10 DAT | 21 DAT | 35 DAT | 49 DAT | ANOVA |
|----------------|---------------------|---------------------|---------------------|--------------------|--------------------|-------------------|
| A0 | 0.088 ^c | 0.087 ^c | 0.084 ^c | 0.081 ^b | 0.079 ^b | A: $P < 0.001$ |
| AF | 0.097 ^c | 0.094 ^c | 0.091 ^c | 0.088 ^b | 0.082 ^b | T: $P < 0.001$ |
| PM22 | 0.118 ^b | 0.114 ^b | 0.113 ^b | 0.105 ^b | 0.096 ^b | A × T: $P = 0.08$ |
| PM66 | 0.173 ^a | 0.159 ^a | 0.154 ^a | 0.135 ^a | 0.130 ^a | |
| SCT10 | 0.097 ^c | 0.097 ^{bc} | 0.097 ^{bc} | 0.088 ^b | 0.087 ^b | |
| SCT30 | 0.099 ^{bc} | 0.094 ^c | 0.096 ^{bc} | 0.089 ^b | 0.088 ^b | |
| <i>P</i> value | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | |

The table presents the mean values followed by standard errors (SE) ($n=3$). ANOVA results are based on square root transformed data. Means followed by different letters are significantly different (Turkey's HSD, $P < 0.05$) within columns using one-way ANOVA. Two-way ANOVA results, including the effect of treatments, time and treatments by time are shown in the last column

A Amendment treatment, T time, A0 Unamended, AF Amended with synthesis fertilisers, PM22 22 Mg ha⁻¹ poultry manure, PM66 66 Mg ha⁻¹ poultry manure, SCT10=10 Mg ha⁻¹ sugarcane trash and SCT30=30 Mg ha⁻¹ sugarcane trash

total N in soil while SCT treatment had trivial effect on the total N due to the low N concentration. Treatment PM66 had significantly higher total N than other treatments on all sampling dates, and reduced C/N ratio in soil, whereas SCT increased this rate (Table 2). The two-way ANOVA results showed that the main effects of amendment treatment and sampling time were significant on the total N and C/N ratio in soil while the interactive effect of treatment by time was not significant. Overall, soil total N reduced over time and C:N ratio increased in all treatments.

Effects of soil amendments on root anatomy of sweetpotato

In the early stage of root development, there was a significant effect of soil amendments on cambium formation. Both treatments with PM increased the rate of roots with NC compared to other treatments at 10 DAT (Table 3). As the activity of primary cambium resulted in the development of IRVC and gradually formed RVC, IRVC reduced

over time and could not be found in roots at 49 DAT. Meanwhile, RVC increased during 10 and 21 DAT before decreasing until 49 DAT (Table 3). The appearance of AC was observed in all treatments from day 21 (Table 3). The formation of this characteristic increased until 49 DAT. The treatment PM66 had a significantly lower rate of roots with this feature compared to the control (A0), SCT10 and SCT30 treatments had the highest percentage of root developed AC than other treatments. The development of LC increased over time in all treatments and there was no significant difference among treatments at 21 DAT. After that, the treatment PM66 promoted LC formation with the highest rate observed at both 35 and 49 DAT (Table 3). However, both SCT10 and SCT30 treatments had the lowest rate of lignified roots varying from around 10 to 28%.

Therefore, the formation and development of cambium were all inhibited in both PM22 and PM66 treatments, and lignification was promoted from day 35. In contrast, SCT applications (SCT10 and SCT30 treatments) stimulated

Table 2 Effects of soil amendments on C/N ratio in soil at various sampling times

| Treatment | Planting | 10 DAT | 21 DAT | 35 DAT | 49 DAT | ANOVA |
|----------------|--------------------|---------------------|--------------------|--------------------|---------------------|-------------------|
| A0 | 22.5 ^{ab} | 22.6 ^{ab} | 22.9 ^{ab} | 23.9 ^{ab} | 24.2 ^{abc} | A: $P < 0.001$ |
| AF | 20.5 ^{bc} | 21.3 ^{abc} | 21.5 ^b | 22.1 ^b | 23.6 ^{bc} | T: $P < 0.001$ |
| PM22 | 18.7 ^c | 18.7 ^{bc} | 19.3 ^{bc} | 20.0 ^b | 21.3 ^{bc} | A × T: $P = 0.99$ |
| PM66 | 14.9 ^d | 16.3 ^c | 16.7 ^c | 19.1 ^b | 19.4 ^c | |
| SCT10 | 22.5 ^{ab} | 22.9 ^{ab} | 23.0 ^{ab} | 24.4 ^{ab} | 26.2 ^{ab} | |
| SCT30 | 25.7 ^a | 27.1 ^a | 26.8 ^a | 28.8 ^a | 28.9 ^a | |
| <i>P</i> value | <0.001 | 0.001 | <0.001 | 0.004 | 0.001 | |

The table presents the mean values followed by standard errors (SE) ($n=3$). ANOVA results are based on square root transformed data. Two-way ANOVA results are shown in the last column. Means followed by different letters are significantly different (Tukey's HSD, $P < 0.05$) within columns using one-way ANOVA

A Amendment treatment, T time, A0 Unamended, AF Amended with synthesis fertilisers, PM22 22 Mg ha⁻¹ poultry manure, PM66 66 Mg ha⁻¹ poultry manure, SCT10=10 Mg ha⁻¹ sugarcane trash and SCT30=30 Mg ha⁻¹ sugarcane trash

Table 3 Effects of organic soil amendments on the development of anatomical features of roots in different sampling times

| Cambium | Treatment | 10 DAT | 21 DAT | 35 DAT | 49 DAT | ANOVA |
|----------|----------------|--------------------|--------------------|--------------------|---------------------|--------------------|
| NC (%) | A0 | 24.1 ^{ab} | 0.0 | | | A: $P < 0.001$ |
| | AF | 23.8 ^{ab} | 2.2 ^{ab} | | | T: $P < 0.001$ |
| | PM22 | 31.0 ^a | 4.4 ^{ab} | | | A × T: $P = 0.06$ |
| | PM66 | 38.3 ^a | 9.4 ^a | | | |
| | SCT10 | 24.4 ^b | 0.0 | | | |
| | SCT30 | 12.4 ^{ab} | 0.0 | | | |
| | <i>P</i> value | | 0.004 | 0.006 | | |
| IRVC (%) | A0 | 72.6 ^{ab} | 38.2 ^a | 14.4 ^c | | A: $P < 0.001$ |
| | AF | 57.6 ^b | 19.9 ^b | 8.8 ^{bc} | | T: $P < 0.001$ |
| | PM22 | 57.8 ^b | 21.4 ^b | 2.8 ^{ab} | | A × T: $P = 0.001$ |
| | PM66 | 61.7 ^{ab} | 19.3 ^b | 8.6 ^{bc} | | |
| | SCT10 | 60.7 ^{ab} | 16.1 ^b | 0.0 | | |
| | SCT30 | 74.8 ^a | 19.6 ^b | 0.0 | | |
| | <i>P</i> value | | 0.006 | 0.005 | < 0.001 | |
| RVC (%) | A0 | 3.3 ^{ab} | 18.2 ^b | 14.1 ^{ab} | 11.6 | A: $P < 0.001$ |
| | AF | 18.5 ^b | 28.0 ^{ab} | 14.6 ^{ab} | 10.9 | T: $P < 0.001$ |
| | PM22 | 11.2 ^{ab} | 30.3 ^{ab} | 27.7 ^a | 13.7 | A × T: $P < 0.001$ |
| | PM66 | 0.0 | 38.1 ^a | 28.3 ^a | 3.0 | |
| | SCT10 | 14.9 ^{ab} | 27.1 ^{ab} | 14.1 ^{ab} | 5.8 | |
| | SCT30 | 12.7 ^{ab} | 19.6 ^b | 11.6 ^b | 2.8 | |
| | <i>P</i> value | | 0.016 | 0.003 | 0.007 | 0.058 |
| AC (%) | A0 | | 33.3 ^b | 48.7 ^b | 50.0 ^{cd} | A: $P < 0.001$ |
| | AF | | 40.0 ^{ab} | 55.8 ^b | 59.4 ^{bc} | T: $P < 0.001$ |
| | PM22 | | 34.7 ^b | 44.4 ^b | 44.4 ^{de} | A × T: $P = 0.02$ |
| | PM66 | | 19.1 ^c | 28.8 ^c | 34.1 ^e | |
| | SCT10 | | 45.5 ^a | 68.7 ^a | 71.5 ^a | |
| | SCT30 | | 48.7 ^a | 67.7 ^a | 68.7 ^{ab} | |
| | <i>P</i> value | | < 0.001 | < 0.001 | < 0.001 | |
| LC (%) | A0 | | 10.3 | 22.7 ^b | 38.4 ^{bc} | A: $P < 0.001$ |
| | AF | | 9.8 | 20.7 ^b | 29.7 ^{bcd} | T: $P < 0.001$ |
| | PM22 | | 9.2 | 25.1 ^{ab} | 41.9 ^b | A × T: $P < 0.001$ |
| | PM66 | | 14.2 | 34.3 ^a | 62.9 ^a | |
| | SCT10 | | 11.3 | 17.2 ^b | 22.7 ^d | |
| | SCT30 | | 12.1 | 20.7 ^b | 28.5 ^{cd} | |
| | <i>P</i> value | | | 0.751 | 0.002 | < 0.001 |

The table presents the mean values followed by standard errors (SE) ($n=3$). Means followed by different letters are significantly different ($P < 0.05$) within columns. ANOVA results are based on arcsine-transformed data. Original data is given in the table

NC No cambium, IRVC Initial regular vascular cambium, RVC Complete regular vascular cambium, AC Anomalous cambium, LC lignified cells, A0 Unamended, AF Amended with synthesis fertilisers, PM22 22 Mg ha⁻¹ poultry manure, PM66 66 Mg ha⁻¹ poultry manure, SCT10 10 Mg ha⁻¹ sugarcane trash and SCT30 30 Mg ha⁻¹ sugarcane trash

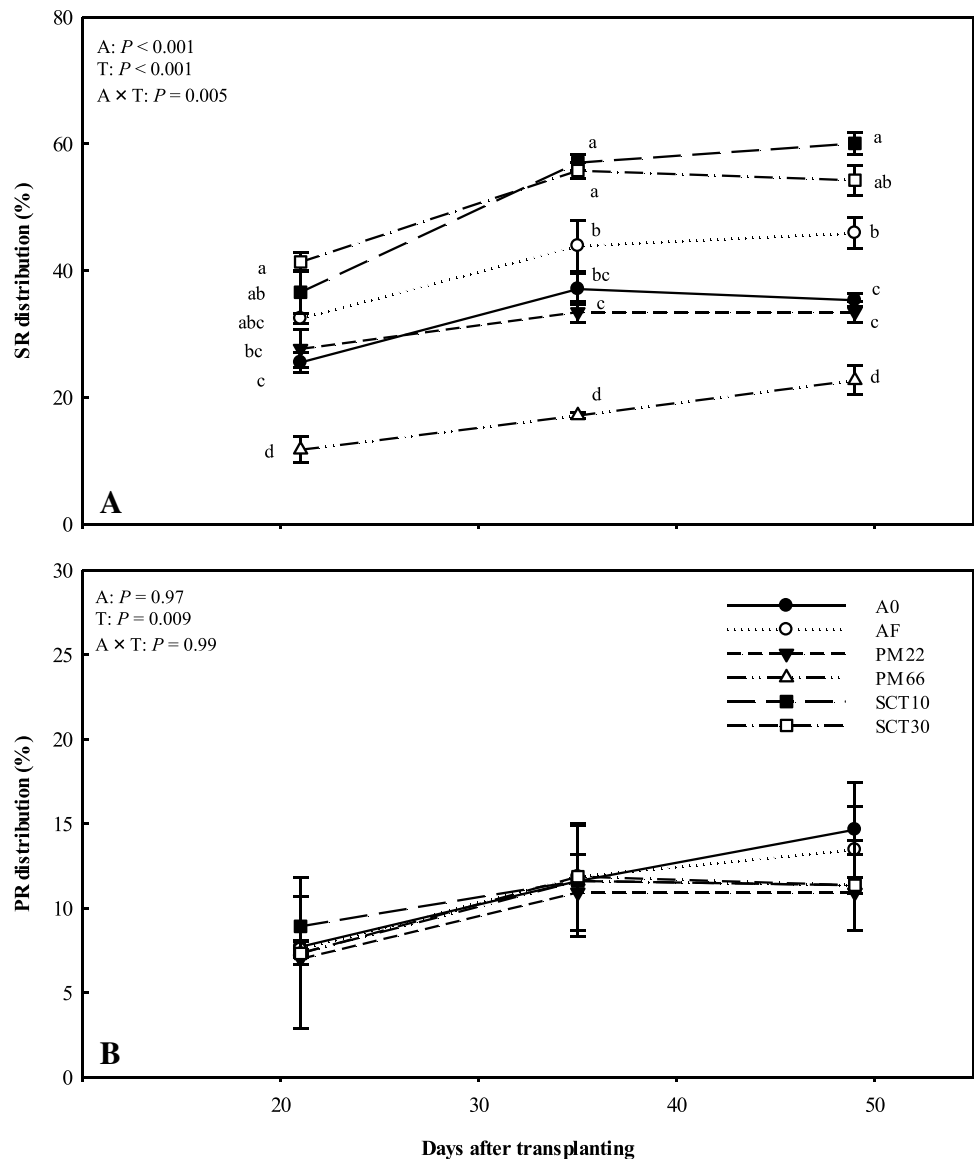
the initiation of the vascular cambium and anomalous cambium throughout the SR formation.

Results from this experiment showed that there were significant effects of soil amendment applications on the SR initiation (Fig. 2A). All amended treatments had higher rates of SRs compared to A0. The SCT10 and SCT30 treatments had a similar rate of SRs, which were significantly higher than those of all other treatments. Although

AF treatment had a higher distribution of SRs than A0, PM22 and PM66, it was still lower than SCT10 and SCT30 treatments.

In this experiment, there was no statistical difference in the distribution of PRs (Fig. 2B). The percentage of PRs increased over time and reached the highest rate at the final sampling. The main effect of time was significant at different sampling times ($P = 0.009$).

Fig. 2 Effects of organic soil amendments on the formation of SRs and PRs over time. **A** Distribution of SRs; **B** Distribution of PRs. Values are indicated as mean \pm SE ($n=3$). ANOVA results are based on arcsine-transformed data. Two-way ANOVA results, including the effect of treatment, time, and treatment by time, on SRs and PRs are shown. Different letters indicate significant differences among treatments on single sampling dates using one-way ANOVA (Tukey's HSD, $P < 0.05$). Abbreviations: *SRs* Storage roots, *A0* Unamended, *AF* Amended with synthesis fertilisers, *PM22* 22 Mg ha⁻¹ poultry manure, *PM66* 66 Mg ha⁻¹ poultry manure, *SCT10* 10 Mg ha⁻¹ sugarcane trash and *SCT30* 30 Mg ha⁻¹ sugarcane trash



Effects of soil amendments on plant performances and storage root weight of sweetpotato

Results from this experiment showed that all amended treatments had significantly higher growth parameters (above-ground dry weight and root dry weight) compared to A0 (Table 4). PM treatments (PM22 and PM66) increased the above-ground weight of plants but reduced the weight of roots which was mainly due to the reduction in number of SRs. However, SCT application (SCT10 and SCT30 treatments) maintained moderate shoot growth and promoted root weight. Although there was no significant difference among treatments on SR diameter at 49 DAT, a significantly lower value for root length was found in the PM66 treatment. As a result, the lowest SR weight was observed in PM66 treatment, which was similar to that of A0. Treatments

SCT10 and SCT30 had the greatest SR weight compared to other treatments.

Effects of soil amendments on N acquisition in plants

Soil amendments had significant effects on N acquisition in plant tissues (Fig. 3A, B). Overall, the concentration of N in vines and roots decreased over time due to the growth of the plants. Higher N concentration in both vines and roots was observed in treatment amended with soil amendments. PM treatments had significantly higher N concentration in both vines and roots and PM66 treatment had the highest concentration of N on all sampling dates. SCT treatments had lower N accumulation in plants and the higher rate SCT application had a lower N concentration in plants.

Table 4 Effects of soil amendments on biomass weight, SR length, SR diameter and SR yield at 49 DAT

| Treatment | ADW (g) | RDW (G) | SRL (mm) | SRD (mm) | FSRW (g) | AFWSR |
|----------------|-------------------|------------------|--------------------|----------|--------------------|--------------------|
| A0 | 1.8 ^e | 1.6 ^d | 81.1 ^a | 7.7 | 7.4 ^c | 2.3 ^c |
| AF | 4.7 ^b | 4.2 ^b | 73.9 ^{ab} | 7.8 | 19.4 ^{ab} | 3.9 ^{ab} |
| PM22 | 5.0 ^{bc} | 2.8 ^c | 74.1 ^{ab} | 9.6 | 13.3 ^b | 4.4 ^a |
| PM66 | 6.0 ^a | 1.8 ^d | 50.4 ^b | 8.3 | 7.0 ^c | 2.7 ^{bc} |
| SCT10 | 4.2 ^c | 4.6 ^a | 69.5 ^{ab} | 9.0 | 23.6 ^a | 3.8 ^{abc} |
| SCT30 | 3.4 ^d | 4.2 ^b | 74.3 ^{ab} | 9.3 | 22.5 ^a | 4.0 ^{ab} |
| <i>P</i> value | <0.001 | <0.001 | 0.02 | 0.64 | <0.001 | 0.04 |

The table presents the mean values followed by standard errors (SE) ($n=3$). ANOVA results are based on square root transformed data. Means followed by different letters are significantly different ($P<0.05$) within columns (Turkey's HSD)

ADW Above-ground dry weight, *RDW* Root dry weight, *SRL* Storage root length, *SRD* Storage root diameter, *FSRW* Fresh storage root weight, *AFWSR* Average fresh weight of each storage root, *A0* Unamended, *AF* Amended with synthesis fertilisers, *PM22* 22 Mg ha⁻¹ poultry manure; *PM66* 66 Mg ha⁻¹ poultry manure; *SCT10* 10 Mg ha⁻¹ sugarcane trash and *SCT30* 30 Mg ha⁻¹ sugarcane trash

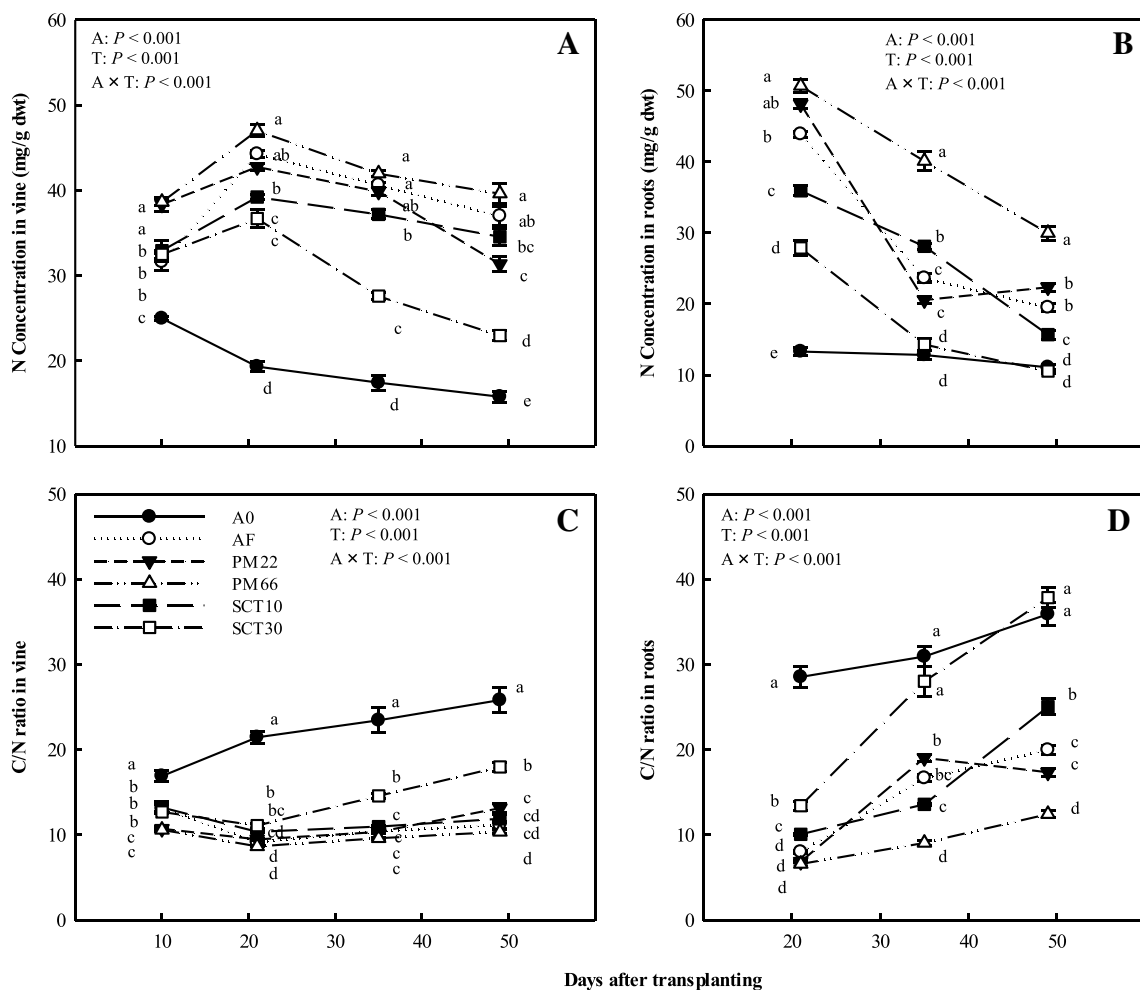


Fig. 3 N concentration in sweetpotato and C/N ratio as affected by soil amendments. **A** N concentration in vines; **B** N concentration in roots; **C** C/N ratio in vines and **D** C/N ratio in roots. Values are indicated as mean \pm SE ($n=3$). ANOVA results for N concentration for both vines and roots are based on square root transformed data. Two-way ANOVA results, including effects of amendments, harvesting date, and amendment by time are shown. Different let-

ters indicate significant differences among treatments on the same harvesting date (Tukey's HSD, $P<0.05$) using one-way ANOVA. Abbreviations: *A0* Unamended, *AF* Amended with synthesis fertilisers, *PM22* 22 Mg ha⁻¹ poultry manure, *PM66* 66 Mg ha⁻¹ poultry manure; *SCT10* 10 Mg ha⁻¹ sugarcane trash and *SCT30* 30 Mg ha⁻¹ sugarcane trash

There was an increasing trend on the C/N ratio in vines and roots (Fig. 3C, D). All treatments with soil amendments had a significantly lower value than unamended treatment (A0). Among amended treatments, the higher ratio was recorded in treatments with SCT, while lower rate was recorded in treatments with PM.

The total N acquisition in plants increased over time in all treatments (Fig. 4). The significantly lower N was observed in treatment A0 on all sampling dates and the highest was found in the PM66 treatment in all observations except 21 DAT. In general, more N was allocated to vines rather than roots, especially for PM66.

Discussion

Effect of soil amendment on available N concentration in soil samples

The two types of soil amendments in our study strongly affected soil available N. Although all treatments except A0 were adjusted to the same soil available N level before the experiment, the application of PM increased the total content of N and the higher rate of PM application led to the higher available N content in soil due to the rapid decomposition of PM. The N soil availability in the PM

treatments was mainly NH_4^+ , with a high rate observed right after application until 6 weeks and the availability decreasing with time (Hue and Silva 2000). In line with our results, the use of PM as soil amendments have been recorded to improve N available in soil in previous studies (Agyarko et al. 2013; Hirzel et al. 2007; Ojeniyi et al. 2012). In contrast, SCT applications lowered these parameters compared to PM treatments and AF treatments (unamended with the same level of fertilisation addition). Although SCT amendment slightly increased the total N in soil, it decreased the available N. In line with this result, SCT application at the rate of 3 Mg carbon ha^{-1} reduced the available NO_3^- , NH_4^+ in soil compared to the unamended treatment (Muhammad et al. 2011). It has been suggested that plant residues with C:N ratio higher than 30 are expected to result in immobilisation, while those with C:N ratios less than 30 cause N mineralisation (Alexander 1977). This explains why the concentration of available NO_3^- , NH_4^+ in soil responded differently to different type of organic amendments in our experiment. As the available N in the SCT treatments decreased over the study period and the crop required more N for their development, plants in the SCT30 treatments developed some N deficiency symptom after 35 days from the planting. Therefore, addition of N for sweetpotato grown in amended soil needs to be considered to achieve optimum N concentration for SR initiation.

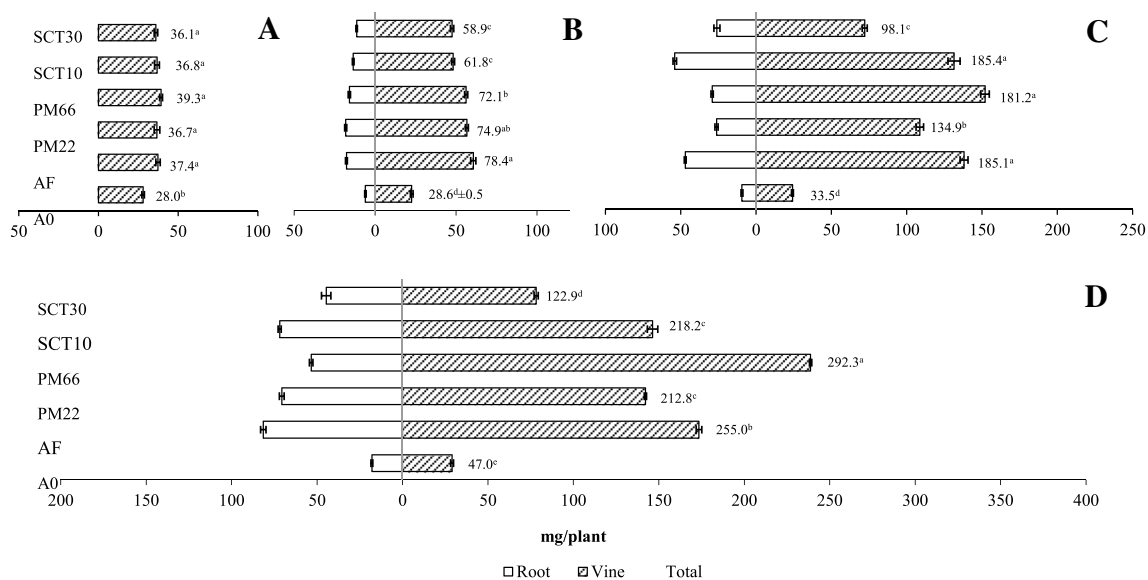


Fig. 4 Effects of soil amendments on the acquisition of N (mg/plant) in vines and roots on 10 (A), 21 (B), 35 (C) and 49 (D) DAT. The x-axis represents the N acquisition and the y-axis represents the treatments. Numbers are mean values of total N acquisition of the whole plant (vines + roots) ($n=3$). ANOVA results are based on root transformed data. Means followed by different letters indicate significant differences among treatments using one-way ANOVA (Tukey's HSD, $P<0.05$).

Abbreviations: A0 Unamended, AF Amended with synthesis fertilisers, PM22 22 Mg ha^{-1} poultry manure, PM66 66 Mg ha^{-1} poultry manure, SCT10 10 Mg ha^{-1} sugarcane trash and SCT30 30 Mg ha^{-1} sugarcane trash

Effect of organic soil amendment on root anatomy of sweetpotato

In this experiment, soil amendments had a significant effect on the formation of sweetpotato SRs, which is likely to be mediated by soil N level. SCT10 treatment promoted the initiation of IRVC and RVC in the early stage of root development as indicated by higher rates of roots with these features at 10 DAT and lowest percentage of roots without cambium development during this period. After that, this treatment continued to promote the formation of AC, and resulted in the highest rate of SR. The treatment SCT30 showed a similar pattern but weaker effect as SCT10. This may be due to a stronger N immobilisation effect, which led to some degree of N deficiency. Similarly, crop residue additions have been recorded to increase the number of tuber in potato (Verma et al. 2011). PM application at either rate (PM22 and PM66 treatments) inhibited the formation of cambium as indicated by the highest rate of NC development in roots. In the later stages, those PM treatments promoted the lignification in roots and reduced the rate of SR in plants. This might be due to the high concentration of N in soil. Overall, the effect of soil organic amendments on the initiation of SR in this study is consistent with SR formation pattern in response to N fertilisation rates (Dong 2021). The optimal available N level stimulating SR formation in the N rate experiment was 320 mg/pot and 640 mg/pot showed inhibition. This work used 500 mg/pot, which may lead to inhibition effect. When SCT N immobilisation brings it down, it shows good stimulation, while decomposition of PM increases the level and lead to inhibition. Therefore, the effect of soil amendments on SR formation is at least partially mediated by the change of soil available N due to soil organic amendment. The results suggested that using organic soil amendments could lead to positive or negative effects on SR initiation of sweetpotato depending on the product's properties.

According to the results from this study, possible mechanisms related to the formation and development of vascular cambium would associate with the nutrients in the organic amendments added into soil. PM usually contains high amounts of N especially in the form of uric acid (60–70%) (Hue and Silva 2000; Nahm 2003) and the aerobic decomposition of uric acid after amending leads to the high concentration of NH_4^+ in soil (Nahm 2003; Vogels and Van der Drift 1976). Therefore, application of PM may result in increasing the concentration of available N in soil, which, if accumulated to excessive level, was demonstrated to adversely affect the initiation of SRs in previous studies (Gifford et al. 2008; Togari 1950). Although, nutrients in all pots were adjusted to the same level during amending, SCT pots may have lower N concentrations due to the immobilisation of N in conjunction with the decomposition of this amendment. This could result in the optimal soil available N

concentration for SR initiation as indicated by higher rate of initiated SRs compared to other treatments (initial N level was higher than the optimal level for SR formation observed in our previous studies). Another possible reason for the increase of SR formation in SCT treatments would be due to its effect on the bulk density of the soil. It has been suggested that high soil bulk density which is often related to soil compaction, reduced the initiation of SRs (Chua and Kays 1982).

Effects of organic soil amendments on plant performance and yield of Orleans during SR formation stage

Both treatments PM22 and PM66 had significantly higher above-ground biomass but lower root biomass at 49 DAT compared to A0 and AF treatments. This means that those treatments promoted shoot growth but inhibited root growth, leading to reduced SR yield. The growth of vines in sweetpotato is positively related to N fertilisation supply (Knavel 1971) and higher plant biomass is also due to the high nutrient content in soil (Brouwer 1962; Grechi et al. 2007). PM used for the current study had ammoniacal N at a rate of 1880 mg kg^{-1} and the total N was 3.99%. Therefore, high N content in PM resulted in the promotion of shoot growth in this experiment.

Treatments SCT10 and SCT30 maintained shoot growth and promoted root growth in this pot experiment and thereby moderate above-ground dried biomass and higher root dried biomass were observed in treatments with SCT. The result could be associated with a very high C:N ratio in the SCT amendment. The activity of soil microorganisms to decompose the material added into soil would slowly release N for plants (Hue and Silva 2000). Thus, the available N in soil in the SCT treatments was lower in those treatments compared to PM treatments. In addition, SCT10 had higher available N concentration in soil compared to SCT30, which also resulted in greater growth of both roots and vines.

The SCT applications in this study increased the SR weight of sweetpotato at 49 DAT. Both SCT treatments, SCT10 and SCT30, had significantly higher SR weight compared to all other amendment treatments including AF treatment. This could be due to the improvement of soil properties. A significantly higher C:N ratio in soil was observed in the treatments with SCT in this pot experiment. Soil C:N ratio is important as it affects soil microbial communities, which are a critical soil functional component. Generally, their alteration could affect the nutrient cycle and soil fertility. Plant residue applications have been reported to reduce the bulk density of soil (Zebarth et al. 1999), which was considered to affect SR initiation and development (Chua and Kays 1982; Togari 1950). The application of crop straw at a rate of 7.5 Mg ha^{-1} has been reported to

improve sweetpotato yield in a previous study (Pan et al. 2019). Hence, our result confirmed the positive effects of plant residues on the yield of sweetpotato.

Effects of organic soil amendments application on N accumulation in plants during SR formation stage

By the end of our experiment, the plant tissue N concentration was the highest in PM66 while lowest in SCT30. A possible reason for this would be the N availability in soil and N uptake. It was concluded that the concentration of N in plants is determined by N uptake and depends on the available N in soil (Pederson et al. 2002). Poultry manure amendment has been recorded to increase N uptake in sweetpotato (Siose et al. 2018), and we see a positive correlation between tissue N concentration and soil available N.

On the final harvesting, the accumulation of N in plant of PM 66 treatment was significantly higher than other treatments and allocated mainly in vines. The SCT30 treatment had lower N accumulated in the whole plant compared to others except for the A0 treatment. Statically significant higher N accumulation in potato was observed in treatment amended with PM at rates of 300–600 kg total N ha⁻¹ (Lynch et al. 2008). Similarly, PM application for cassava also resulted in higher N accumulation in plants compared to the control and NPK fertiliser treatments (Ojeniyi et al. 2012). In addition, organic amendments have been reported to affect N uptake of plants. For example, crop residue application at a rate of 10 Mg ha⁻¹ significantly reduced N uptake in corn plants (Nguyen et al. 2016). Therefore, different organic amendments differentially affected N accumulation in plants dependent on the types and application rates.

The accumulation of N in plants is related to N levels supplied in soil. In the PM66 treatment, uric acid in the amendment metabolised rapidly to NH₄⁺ and so higher concentration of NH₄⁺ was found in soil. As a result, higher N accumulation was observed in this treatment as increasing N supply led to higher N accumulation in plants (Pederson et al. 2002). Nitrogen stimulated leaf growth through the synthesis of proteins involved in cell expansion and cytoskeleton synthesis (Bassi et al. 2018). The content of N in leaf affected photosynthesis (Allison et al. 1997) as it is partly related to photosynthetic enzymes, pigment content and the size, number and composition of chloroplast. Sufficient N supply leads to easy assimilation which need to be balance by more carbon (Lawlor 2002). Nitrogen is assimilated in roots but the larger part is translocated to leaves which are a sink for N during vegetative stage (Xu et al. 2012). It is also related to allocation. In general, when soil N level is high, plants do not need many roots to absorb resources from soil. In this case, biomass mainly allocate to shoots, leading to high shoot to root ratio, as well as a balance between photosynthates produced by leaves and nutrients absorbed by root.

Moreover, some plant hormones such as cytokinin, auxin are associated to N levels (Kiba et al. 2011; Matsumoto-Kitano et al. 2008; Samuelson et al. 1992). These phytohormones stimulate cell growth and plant growth. Therefore, the accumulation and allocation of N were also related to the plant physiological processes such as photosynthesis and plant hormone functions.

Conclusions

Results from this study indicated that the application of soil amendments had significant effects on SR initiation of sweetpotato due to their effects on N availability in soil. Both PM treatments increased N availability in soil, which resulted in suppression of SR formation and promotion of lignified roots. PM66 treatment promoted shoot growth but inhibited root growth, resulting in the highest N accumulation in vines, but the lowest N accumulation in roots. Overdosage of PM negatively impacted FSRW mainly by reducing SR number but the growth of individual SR was not impacted. However, SCT application reduced available N in soil, which is associated with increasing vascular cambium development and SR initiation. Generally, both low and high rates of SCT treatments promoted the formation of SR as indicated by a significantly higher rate of SR at all sampling times compared to other treatments. In addition, those treatments maintained shoot growth and enhanced the growth of roots as suggested by the moderate N accumulation in plants. Our results suggested that only a low rate of PM could be applied to sweetpotato and planting should be delayed from 2–3 weeks after amending to avoid the detrimental effect on SR initiation. A low rate of SCT could be used to promote SR initiation but a high rate of this carbon-rich amendment could lead N deficiency, probably due to N immobilisation.

Author contributions statement Manuscript title: Sweetpotato storage root initiation as affected by soil organic amendment applications. All persons who meet authorship criteria are listed as authors and all authors certify that we have participated in the study with different roles as below. Hong Tham Dong: conceptualisation, methodology, investigation, formal analysis, writing original draft. Yujuan Li: conceptualisation, review and editing, resources. Philip Brown: conceptualisation, review and editing. Cheng-Yuan Xu: conceptualisation, supervision, methodology, visualization.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11738-023-03570-3>.

Acknowledgements The research was funded through CQUniversity's Research Higher Degree Candidature Budget and Australian Research Training Program Scholarship. The authors are grateful to Professor

Arthur Villordon from the LSU AgCenter Sweet Potato Research Station, USA, for significant contributions and professional advice in the root anatomy study of this project. Thanks are expressed to Queensland Department of Agriculture and Fisheries Bundaberg Research Facility and its staffs for their assistance during the experiment.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions. The authors declare that the study was funded through CQUniversity's Research Higher Degree Candidature Budget and Australian Research Training Program Scholarship. The research has received support from Professor Arthur Villordon from the LSU AgCenter Sweetpotato Research Station in term of professional advice in the root anatomy. This work was supported by Queensland Department of Agriculture and Fisheries Bundaberg Research Facility and its staffs for the glasshouse operations.

Data availability Authors confirm that all data supporting the findings of the study are included in the manuscript. Raw data that support the findings of the current study are available from the corresponding author on reasonable request.

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