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Photosynthetic characters of canopy and storage root yield of sweet potato (*Ipomoea batatas* L.) grow in different soil compaction

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Abstract

Soil compaction is a critical constraint that restricts the attainment of high and stable yields of sweet potato. Photosynthesis is a key factor in yield formation. But the mechanism of soil compaction affects the photosynthesis and storage root (SR) yield of sweet potato remains elusive. A field experiments were carried out with two varieties in control, loose, and compacted soil conditions, canopy apparent photosynthesis (CAP), gas exchange parameters and PIabs of the functional leaves, SR yield were measured, and the relationship between yield and photosynthetic characters was studied as well. Compared with the control, the SR yield was significantly increased in loose soil with an average increase of 27.03%~38.74%, but decreased in compacted soil with an average reduction of 17.87%~15.92%. Both loosening and compaction treatments increased the leaf area index (LAI), and the increase in the latter is significantly higher than that in the former. Canopy interception rate in loosening treatment was much higher than that of compaction soil. The CAP showed a similar change in yield, with a strong positive correlation to SR yield and single storage root weight. Loose soil also improved gas exchange parameters, PIabs, the reverse was found in compacted soil. Compared to the control, the loose treatment significantly improved economic coefficient and reduced leaf starch content, while the compaction treatment showed the opposite trend. Path analysis revealed that the net photosynthetic rate (*P*n) had the most total effect and higher direct effect on increasing CAP. Therefore, soil compaction primarily regulates SR yield through CAP, with Pn exerting a significant impact on CAP. Enhanced soil compaction led to reduced photosynthate output in functional leaves, resulting in decreased Pn and increased

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LAI. Consequently, an inappropriate canopy structure with low canopy interception is formed.

Keywords: canopy apparent photosynthesis, PIabs, gas exchange parameters, storage root yield, soil compaction, sweet potato.

1. Introduction

Sweet potato is a globally significant tuberous crop, with a total production of 8.64×10^7 tons on 7.25×10^6 hectares, and an average yield of 11.9 tons/hectare (FAOSTAT, 2023). It demonstrates remarkable adaptability and thrives in diverse terrains, including hilly, mountainous, and plains (Sun et al. 2022). There has been a substantial increase in soil compaction, which is widely recognized as one of the primary challenges to soil fertility, crop productivity, and food safety (Keller et al. 2019). Soil compaction led to a substantial decrease in SRs yield, with reductions ranging from 30% to 90% (Shi et al. 2019). This phenomenon is frequently observed not only in plains (Bogunovic et al. 2018), but also in hilly and mountainous regions (Xoconostlecázares et al. 2010). Hence, it is crucial to make clear the impact of soil compaction on sweet potato yield in order to maximize production potential.

The bulking rate and single weight of sweet potato SRs decreased with increasing soil compaction, while the root tip number and hypocotyl diameter of soybean showed a significant increase (Li et al., 2024). The soybean root system may change due to limited water and nutrient availability in the soil, caused by restricted gas diffusion between roots and the rhizosphere (Horák et al. 2022). The development of sweet potato SRs is mainly influenced by photosynthesis, as they store photosynthate. However, there are conflicting findings on the effect of soil compaction on photosynthesis. Some studies indicated that soil compaction reduces photosynthesis rates (Mariotti et al. 2020; Huntenburg et al. 2021), which was ascribed to a decrease in stomatal conductance, thus impeding CO_2 diffusion to the mesophyll (Philip and Azlin 2005). Net photosynthesis (*P*n), stomatal conductance (gs), and transpiration rates (E) of soybean were reduced up to 50% under compaction (Ferreira et al., 2023). While the study in potato showed that photosynthesis rates did not differ between compaction treatments after ground cover (Huntenburg et al., 2021). The response of photosynthesis to soil compaction may vary across studies, however, a consistent observation was the reduction in leaf size and plant carbon assimilation. But sweet potato leaves exhibited an increase in size rather than decrease under soil compaction. This indicated that the response mechanism of sweet potato to soil compaction differed from other crops. The CAP provides a more precise indication of the photosynthesis of field crops (González and Manavella, 2021), while chlorophyll fluorescence parameters have been widely employed to identify disruptions in the photosynthesis apparatus caused by abiotic stress (Grzesiak 2009). So our study aims to investigate the CAP variation at different development stages, gas exchange parameters, chlorophyll fluorescence parameters of functional leaves, and quantify how the CAP, and functional leaf photosynthesis of sweet potato respond to soil compaction and how they affect SR yield.

2 Materials and Methods

2.1 Materials and test design

The field experiment was conducted at the Agricultural Test Station of Shandong Agricultural University in Taishan District, Tai'an City, Shandong Province (360°09′N，117°09′E； 128 m asl) during 2017 and 2018. The sweet potato cultivars used were Shangshu 19 (SS19) and Jixu 23 (JX23). The tested soil was sandy loam. Three compaction levels were used: (1) compaction (C), where the 0–20-cm soil layer of the treatment was compacted by a vibrating tamper (HS-75R, HANSA, Germany), with a bulk density of 1.40–1.50 g cm^{-3} and a compaction of > 0.6 MPa and < 1.2 MPa; (2) control (no compaction, CK), where the bulk density of the 0–20-cm soil layer was 1.30–1.40 g cm^{-3} and the compaction was approximately 0.3–0.4 MPa; and (3) loosening (L), the bulk density in the 0–20-cm soil layer was 1.20–1.30 g cm^{-3}, and the compaction was approximately 0.1–0.2 MPa. The soil in this treatment was mixed with organic fertilizer, sand, and common loamy soil. After mixing, the organic matter content of the soil in the loosening was consistent with the other treatments. The nitrogen, phosphorus, and potassium contents in the three treatments were adjusted to similar levels using potassium sulfate and urea. In 2017, the available nitrogen, phosphorus, potassium, and organic matter in the 0–20-cm soil layers were 79.47 mg kg^{-1}, 42.47 mg kg^{-1}, 112.33 mg kg^{-1}, and 1.30 %, respectively, and in 2018, it was 88.73 mg kg^{-1}, 35.22 mg kg^{-1}, 90.51 mg kg^{-1}, and 1.13 %, respectively. The physical properties of the soil under the three treatments are shown in Table 1. The field experiment employed a two-factor split-plot experimental design with five replications, using cultivars as the primary plots and compaction as the subplots. Each plot covered an area of 20 m^2, with row spacing-80 cm and plant spacing-25 cm. Sweet potato was planted on May 10 and May 9, harvested on October 22 and October 20 in 2017 and 2018, respectively.

Table 1. Physical characteristics of the soil (1 day before planting).

Year	Soil Layer (cm)	Treatments	Soil Compactness (kpa)	Soil Soil bulk density (g/cm^3)	Soil Specific Gravity (g/cm^3)	Total Porosity (%)	Capillary porosity (%)	Non-capillary Porosity (%)
2017	5-10	L	126.49 c	1.26 c	2.58 a	51.35 a	24.86 b	26.49 a
		CK	301.16 b	1.33 b	2.64 a	49.81a	24.15 b	25.66 a
		C	541.63 a	1.46 a	2.73 a	46.38 b	31.78 a	14.60 b
	10-15	L	224.23 c	1.30 c	2.57 b	49.35 a	25.50 c	23.85 a
		CK	464.12 b	1.39 b	2.73 a	49.19 a	31.68 b	17.51 b
		C	927.74 a	1.49 a	2.75 a	45.71 b	38.30 a	7.41 c
2018	5-10	L	143.17 c	1.25 c	2.57 a	50.69 a	24.62 b	26.07 a
		CK	267.91 b	1.33 b	2.65 a	48.92 a	25.30 b	23.62 b
		C	826.07 a	1.47 a	2.74 c	46.66 b	31.21 a	15.45 c
	10-15	L	174.17 c	1.29 c	2.58 b	49.62 a	25.46 c	24.16 a
		CK	508.06 b	1.38 b	2.73 a	48.65 a	30.14 b	18.51 b
		C	1230.6 a	1.49 a	2.75 a	45.83 b	36.91 a	8.92 c

Note: Values followed by different lowercase letters within a column in the same year of the same varieties are significantly different among different treatments ($P < 0.05$). The same as below.

Soil compaction was measured using a soil compaction metre (CP40 Ⅱ, Cinstral Exports Pty Ltd T/A Rimik, Australia) at the seedling stage, early, middle and late stage of SR bulking. The soil volumetric moisture content in the 0–20 cm and 20–40 cm layers was measured every five days after transplanting to canopy cover. The moisture content per cubic metre (m^3) = H × 1 m^2 × soil volumetric water content (%), where H is the soil depth. The plot with the highest water content served as the standard for adjusting the water content in the remaining plots. From transplanting to canopy cover, irrigated all treatments 1~2 times to ensure the soil relative humidity of the control treatment was above 60%; the irrigation amount was consistent across all treatments. The other management is similiar to that of general field crops, with the climate for two growing seasons detailed in Fig. 1.

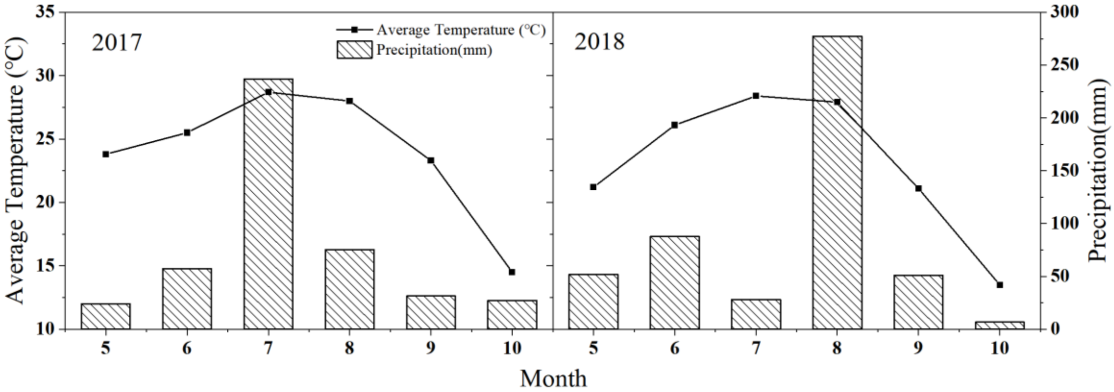

Fig. 1 Climate data for the two growing seasons of sweet potato.

2.2 Sampling and measurement method

2.2.1 Canopy apparent photosynthesis

The CAP was measured in a modified closed gas exchange system using an infrared gas analyser (GXH-305, China) (Hay and Porter, 2006), which was portable and easy to move in the field. The aluminum-framed chamber measured 0.80 × 0.90 m in area and 0.70 m in height, with the outer cover sealed using a high light transmittance mylene film (about 95% light transmittance). A 25 cm fan was placed at the top to mix the gas and balance the temperature. The CO_2 concentrations decreased linearly, usually measured within 60 seconds of the chamber closing. Two rows of sweet potatoes were chosen in the chamber, and measurements were taken every 20 days from 60 to 140 days after planting (DAP), between 9:00 and 11:00 A.M. Three sampling site with consistent growth were selected to mearsure for each treatment, and the respiration rates of soil were measured in the open spaces of the adjacent area. The CAP was calculated as follows:

$$\text{CAP} = \text{slope} \times \text{n} / A \qquad (1)$$

Where the slope presents the reduce in the CO_2 concentration per unit time (μmol mol^{-1} s^{-1}), n is moles number of air in the chamber, and A standing for the ground area. The value of n equal to PV/RT, where P is the pressure in kPa, V is the chamber volume in L, T is the temperature in K, and R is the gas constant (8.314 k Pa L mol^{-1} K^{-1}).

2.2.2 Gas exchange measurements

Gas exchange measurements were conducted at 20-day intervals from 60 to 140 days post-planting. In sunny, windless conditions, the photosynthetic rate of the fifth fully opened leaf (with the highest photosynthetic rate) at the top of the stem was measured between 9:30 and 11:30 A.M. Fifteen leaves with similar growth were selected for each treatment across three replications. The Portable Photosynthesis System (CIRAS-3, PP Systems International, Inc. Amesbury, USA) was used. The measuring head was subject to the following conditions: leaf temperature, 28 °C; reference CO_2 content, 380 ppm, and ambient air humidity. The PPFD during the measurements was set to 1000 μmol (photon) m^{-2} s^{-1} throughout the experiments. The *P*n, E, gs, and Ci in the intercellular spaces were automatically recorded.

2.2.3 Chlorophyll fluorescence parameters of the functional leaves

The parameters were measured every 20 days from 60 to 140 DAP. The MPEA chlorophyll fluorescence meter (Hansatech Instruments Ltd., King's Lynn, UK) was connected to a computer for precise value determination. Prior to fluorescence signal measurements, the plants were dark-adapted for at least 30 minutes. The fifth unfolded leaf at the top of the stem was measured. 15 leaves with similar growth characteristics were selected for each condition.

The following parameters were considered:

PIabs = RC/ABS • [φ Po /(1-φ Po)] • [ψ_O /(1-ψ_O)], the performance index of the absorbance basis.

2.2.4 Canopy interception rate

From 60 to 140 DAP, the canopy interception rate of sweet potato was assessed using a SunScan plant canopy analyzer (Delta-T Devices, UK). Measurements were carried out on clear and calm days between 12:00 and 14:00. Incident and reflectance radiation were measured above the canopy (15 cm above) and below the canopy (5 cm above the ground), with each treatment replicated five times.

Canopy transmittance (%)= (PAR - PAR_0)/PAR×100 % (2)

Canopy reflectance (%)= PAR'/PAR×100% (3)

Canopy interception (%)= 100-Canopy transmittance (%)-Canopy reflectance(%) (4)

Where, PAR is the PAR above the canopy, PAR_0 is the PAR at the base of the ridges, and PAR' is the reflected light above the canopy.

2.3 Statistical analysis

Statistical analysis was conducted with IBM SPSS Statistics 25 (IBM Inc., Chicago, IL, USA). The statistical significance were assessed using ANOVA, followed by Duncan's multiple range test. Figures were generated using SigmaPlot software (SigmaPlot 12.0, Systat Software, San Jose, CA, USA).

3 Results

3.1 Effects of soil compaction on SR yield of sweet potato

Compared with the control, the SR yield was significantly increased in loosening treatment, and the average increase of two years was 27.03%~38.74%, while they were decreased in compaction treatment, and the average reduction was 17.87%~15.92%. The single storage root weight changed similiar to the yield. The change of single SR weight and economic coefficient was similiar to that of yield (Table 2). The result of statistical analysis indicated that treatment, the interaction between year and treatment had significant effect on yield. There were significant differences in the number of SRs, single SR weight and economic coefficients between treatments as well. That is, the soil compaction led to changes in SR yield, primarily through the regulation of individual SR weight.

Table 2. Effect of soil compaction on SR yield, its economic coefficient of sweet potato.

Year	Varieties	Treatment	Number of storage root (lump plant^{-1})	Fresh weight (g lump^{-1})	Storage root yield (t ha^{-1})	Economic coefficient (%)
2017	SS19	L	4.6 b	244.3 a	55.7 a	70.8 a
		CK	4.4 b	214.5 b	47.8 b	65.9 b
		C	5.7 a	141.5 c	40.2 c	61.8 c
	JX23	L	3.6 b	315.1 a	55.9 a	79.6 a
		CK	3.5 b	274.8 b	46.9 b	75.3 b
		C	4.4 a	188.9 c	41.1 c	63.7 c
2018	SS19	L	4.0 b	296.3 a	59.1 a	80.1 a
		CK	3.9 b	223.3 b	43.4 b	67.6 b
		C	4.6 a	148.9 c	34.4 c	56.4 c
	JX23	L	3.0 b	363.2 a	54.2 a	89.7 a
		CK	2.9 b	243.3 b	34.2 b	83.4 b
		C	3.6 a	154.8 c	27.6 c	71.2 c

Analysis of variance (*p* value)				
A (Year)	0.004	0.17	0.0023	0.018
B (Variety)	<0.001	<0.001	0.094	<0.001
C (Treatment)	<0.001	<0.001	<0.001	<0.001
A×B	0.60	0.0077	0.075	<0.001
A×C	0.23	0.0015	<0.001	<0.001
B×C	0.14	0.053	0.36	0.0023
A×B×C	0.39	0.42	0.57	<0.001

Note: Values followed by different lowercase letters within a column are significantly different among different treatments ($P < 0.05$). The same as below.

3.2 Effects of soil compaction on the photosynthetic area and canopy interception rate

3.2.1 LAI

During SRs bulking, the LAI first increased and then decreased, the peak values were observed at 120 and 100 DAP for SS19 and JX23, respectively. Compared to the control, the LAI was significantly increased in loosening and compaction treatments,with the average increase of 37.54% and 63.81. The highest LAI was obtained in the compaction treatment at 120 and 100 DAP for JX23 and SS19. Subsequently, the LAI in the compaction treatment exhibited a more rapid decline compared to the other treatments after reaching its peak (Fig. 2). In summary, the group structure of loosening treatment appeared to be suitable; however, the group is excessively large within the compact soil.

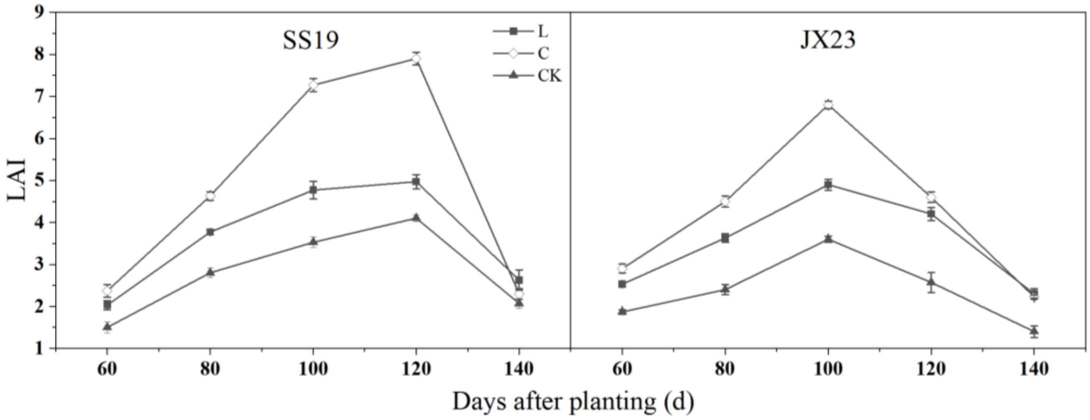

Fig. 2 Effect of soil compaction on LAI (2018).

3.2.2 Canopy interception rate

Compared to the control, the loosening treatment had the highest canopy interception rate, while the compaction treatment showed the lowest despite having a higher LAI. This could be attributed to frequent leaf turnover in the compaction treatment, resulting in numerous small leaves that may potentially cause localized light leakage (Fig 3).

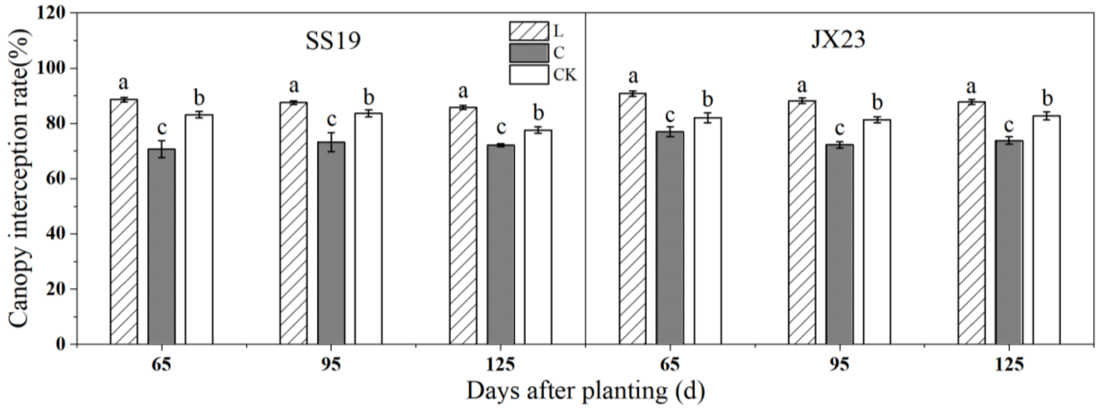

Fig. 3 Effect of soil compaction on canopy interception rate (2018).

3.2 Effects of soil compaction on the CAP rate

The CAP of sweet potatoes follows a bimodal curve, with peak values at 80 and 120 DAP and a trough at 100 DAP. The occurrence of the trough coincides with the rainy season, during which there was an increase in soil compaction due to sustained precipitation.

Compared with the control, the loosening treatment increased the CAP rate significantly with an average increase of 29.46% and 38.76%, for the SS19 and JX23, respectively, the greater significant increase appeared at 80 DAP and 140 DAP. And the compaction treatment decreased the CAP rate significantly with the average reduction of 17.31% and 20.21%, the most significant reduction appeared at 60 DAP and 80~100 DAP (Fig. 4). That is, soil compaction affected the CAP greatly in the early and middle growth stages, when the soil compaction was reduced the CAP was increased greatly during the late growth stage.

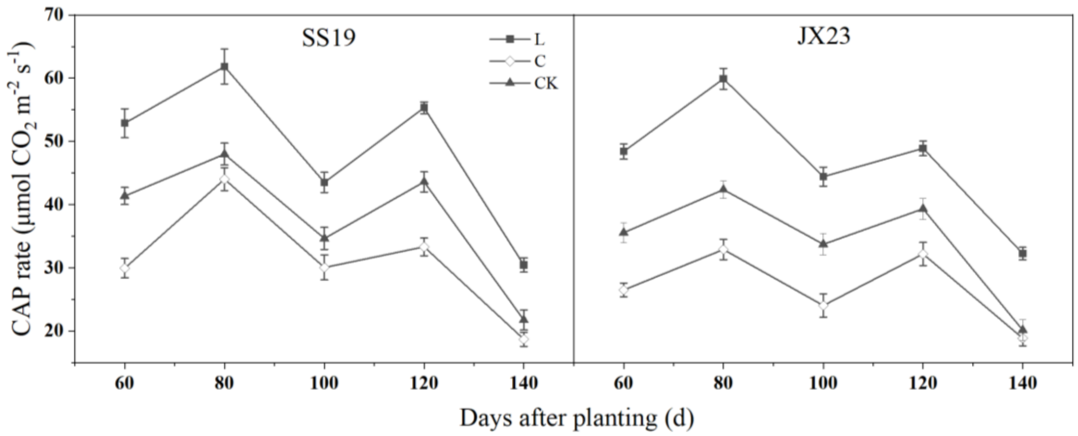

Fig. 4 Effect of soil compaction on canopy apparent photosynthesis rate (2018).

3.4 Effects of soil compaction on the Gas exchange parameters of the functional leaves

At 80, 100 and 120 DAP, the loosening treatment significantly improved the *P*n, *Ci*, *gs* and *E* of the functional leaves, whereas the compaction treatment had opposite effects, which was consistent with the 2-year data. In 2017, the gas exchange parameters exhibited significant variation at the trough of CAP rate (100 DAP), whereas in 2018, a noticeable alteration was observed in the second peak of CAP rate (120 DAP) (Fig. 5). The occurrence of periods characterized by significant inter-annual variability is primarily linked to the temporal distribution of intense precipitation.

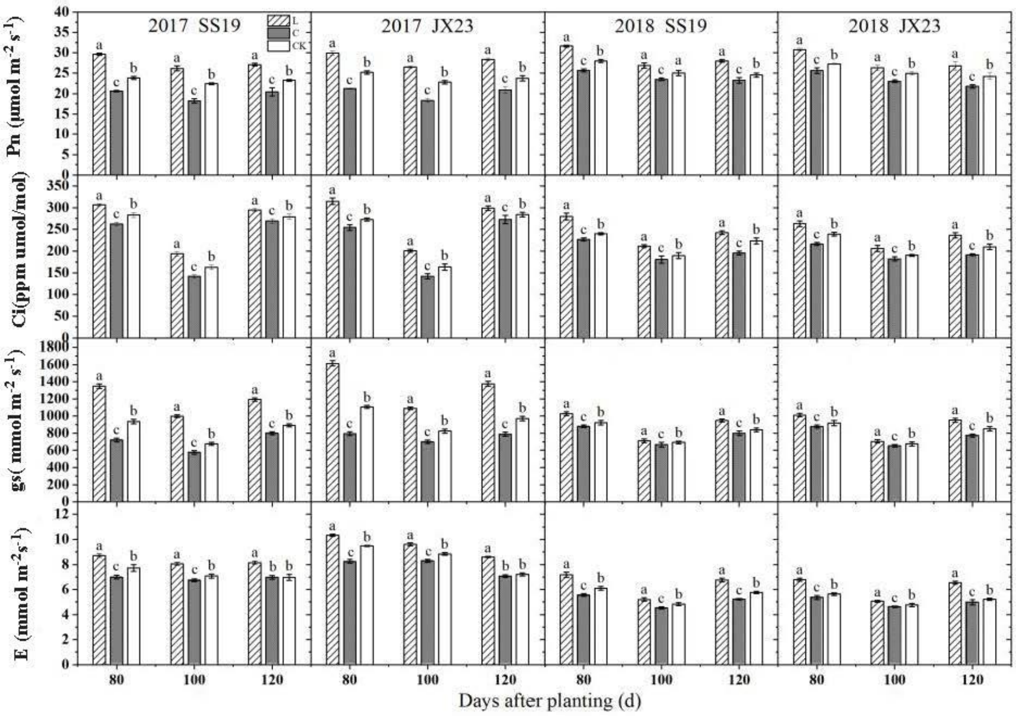

Fig. 5 The effect of soil compaction on gas exchange parameters in leaves of sweet potato.

3.5 Effect of soil compaction on PIabs

PIabs is the performance index of the PS Ⅱ reaction centre, which reflects the overall performance of PS Ⅱ. The loosening treatment significantly increased the PIabs of the functional leaves by 55.63% and 38.50% in SS19 and JX23, respectively, compared to the control treatment. In contrast, the compaction treatment led to a significant decrease in PIabs by 28.33% and 22.29%, respectively (Fig. 6). Hence, loose treatment is benefit to improvement of the overall performance of PS Ⅱ.

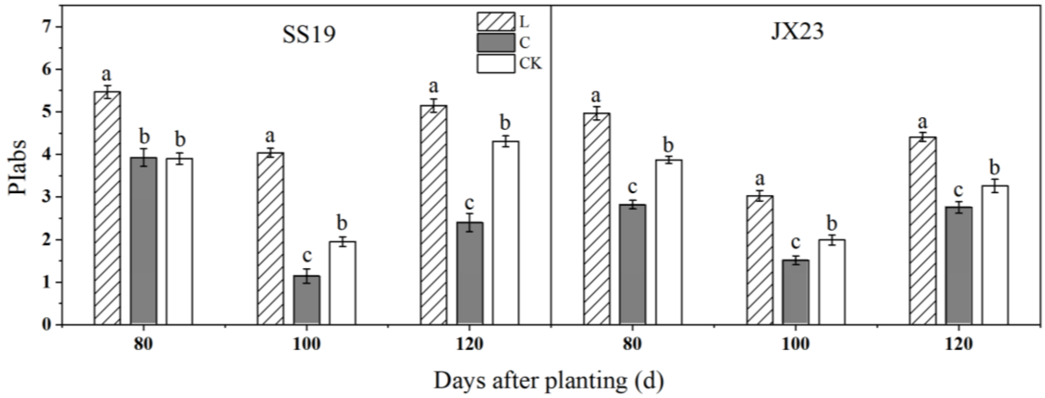

Fig. 6 The effect of compaction on PIabs of leaves of sweet potato (2018).

3.6 Determining the main influencing factors of the canopy apparent photosynthesis

The regression equation Y= 38.38 + 4.67X1 + 1.61X2 + 0.15X3 - 0.34X4-0.029 X5 + 2.03X6 - 18.00X7 - 115.61X8 + 2.24X10 (F = 29.58, R^2 = 0.938, *P=0.0001*) was obtained by stepwise regression using the CAP rate as the dependent variable and, LAI (X1), canopy interception (X2), *P*n (X3), *Ci* (X4), *gs* (X5), *E* (X6), Vj (X7), Wk (X8), ψo (X9), and PIabs (X10) as the independent variables. The correlation analysis revealed a significant positive correlation between *P*n, canopy interception, Ci, gs, E, Ψo and PIabs with the CAP. Path analysis revealed that gas exchange parameters and PIabs were the primary contributors to increased CAP. Gas exchange parameters, particularly *P*n and Ci, had the most significant direct effects, and the overall impact of *P*n was mainly driven by its direct effects, while most other factors were primarily influenced by the indirect effects of *P*n (Fig. 7).

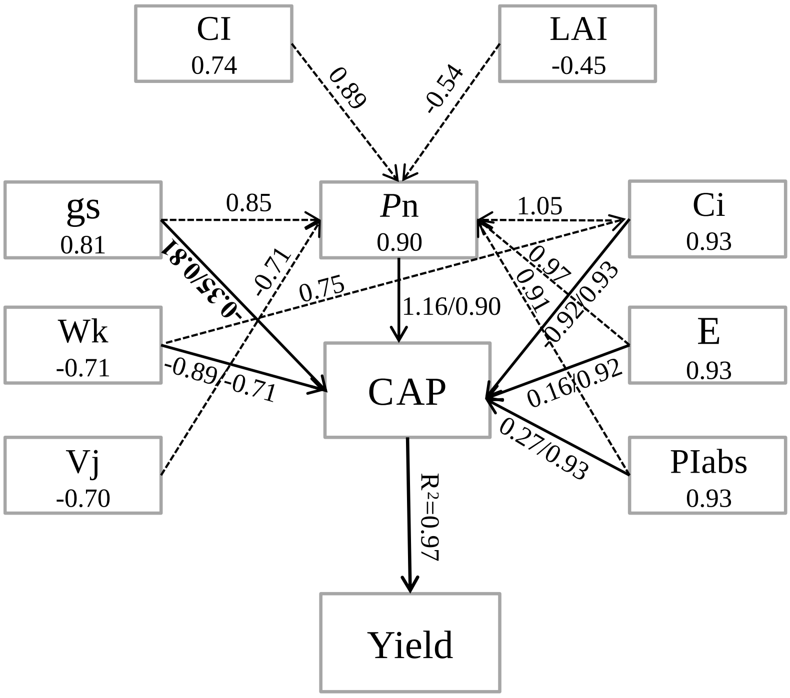

Fig. 7 The path analysis among functional leaf photosynthesis, canopy apparent photosynthesis and storage root yield. **Note:** Dashed and solid lines indicate indirect and direct impacts, respectively. The number above or below the arrow line indicates the direct effects / total effects. R^2 represents the correlation coefficient. The number in the box indicates the correlation coefficient between the item in box with the CAP.

4 Discussion

4.1 Effects on SR yield of sweet potato

This study found a significant increase in SR yield when soil compaction was reduced (Table 2), consistent with previous research (Shi et al. 2019). Improving photosynthesis can increase crop yields (Dong et al. 1993), as more than 90% of crop outputs are directly related to photosynthesis (González and Manavella, 2021; Chen et al. 2022). Within the realm of field crops, the CAP exerts a pronounced impact on yield formation. However, limited research has been conducted on the effect of soil compaction on sweet potato photosynthesis and its correlation with SR yield. This study revealed that variations in single SR weight were the primary contributing factor to differences in SR yields (Table 2). A significant positive correlation was obtained between the CAP and SR yield (*r= 0.99, P<0.05*), as well as the single SR weight (*r= 0.90, P<0.05*). Our previous research has revealed that reducing soil compaction resulted in higher single SR weight by increasing dry matter accumulation in the SRs (Shi et al. 2019). Consequently, soil compaction mainly affects the accumulation of photosynthates in SRs by regulating the CAP, thus impacting single SR weight and leading to variations in SR yield.

4.2 Effects on the photosynthetic characteristics of sweet potato

CAP is closely linked to the canopy architecture and positively correlated with light interception (Bhusal, et al., 2017). The LAI is an important index of canopy architecture. But the correlation between CAP rate and LAI varies among different crop species. The CAP was closely associated with changes in green leaf area in maize (Liu et al. 2015), whereas, the LAI was similar among varieties with distinct CAP rate in wheat (Tang et al. 2017). Moreover, an appropriate LAI can enhance the group's light distribution and interception ability (Maddonni et al 2001). The increase of soil compaction reduced ground cover expansion, decreased plant leaf area, shortened canopy cover duration, and restricted light interception (Assaeed et al. 2008). This study revealed that the loosening treatment appeared the highest CAP rate (Fig. 3), the greater LAI (Fig. 2) and the most canopy interception rate (Fig. 4), compared with the control treatment. The compaction treatment got the highest LAI but the lower canopy interception rate (Fig. 2, 4). This may be because compaction treatment led to excessive growth of stems and leaves, resulting in frequent alternation of new and old leaves. The CAP rate in the compaction treatment was reduced as well (Fig. 3). The previous study has improved that a suitable canopy structure, high chlorophyll content, and prolonged leaf duration can enhance CAP and biomass yield (Tang et al., 2017). Therefore, reducing soil compaction promotes appropriate canopy architecture, improves light penetration, and enhances the CAP.

Reducing soil compaction has been shown to enhance the net photosynthetic rate of leaves in various crops such as cucumber, strawberry, peanut, ginger, soybean, and potato (Du et al. 2010), while its increase has demonstrated an opposite effect. These findings were consistent with previous research on the physiological and agronomic response of soybean cultivars to soil compaction in the Brazilian Cerrado (Maddonni et al. 2001; Ferreira et al., 2023). While the other study in potato showed that *P*n did not differ between compaction treatments after ground cover (Huntenburg et al., 2021). In this study, we found *P*n, Ci, E and gs wers increased in the loosening treatment but decreased in the compation treatment (Fig. 4). The significant fluctuations were most pronounced during and after the rainy season (at 80 and 120 DAP). The variation in *P*n for loosening and compaction treatments was less than that of the CAP rate. Furthermore, the PIabs were enhanced in the loosening treatment (Fig. 6), other chlorophyll fluorescence parameters showed relatively small changes (Supplementary Table 1,). And Photosynthesis critically depends on the electron flow through PSII (Hussain et al. 2019), which functions as a fundamental photosynthetic unit within the thylakoid membrane of a chloroplast. The accumulation of starch within chloroplasts may result in the perturbation of thylakoid membranes, leading to a reduction in the photosynthetic efficiency of leaves. When soil compaction was intensified, leaves accumulate a lot of starch, while the loosening treatment leaves have high sucrose and low starch content (Supplementary Table 2). Meanwhile, the economic coefficient of compaction treatment was reduced (Table 2). So the excessive accumulation of starch in functional leaves was the primary factor contributing to the reduction in *P*n. The emphasis of the next research step should be on the output of leaf photosynthetic products.

Linear regression, correlation analysis, and path analysis were employed to identify the key factors influencing the CAP rate due to soil compaction. The results indicated a highly significant positive correlation between gas exchange measurements (*P*n, Ci, E and gs) and the CAP rate. Gas exchange measurements (*P*n, Ci, and E) had the most significant overall impact on enhancing the CAP. The total effects of *P*n were derived primarily from direct effects, which were the most substantial among the items, while the most items were derived mainly from indirect effects of *P*n (Fig. 7). Overal, the primary determinant of SR yield under soil compaction was the CAP rate. When modulating the CAP rate, it was crucial to consider gas exchange parameters, particularly in controlling the *P*n.

5. Conclusions

Soil compaction primarily influenced sweet potato SRs yield by modulating their CAP rate. Pn and canopy architecture were the primary determinant of CAP rate. As soil compaction increased, the reducing photosynthate output of leaves leads to starch accumulation, resulting in a marked reduction in photosynthetic rate and a substantial increase in LAI.

Acknowledgments

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