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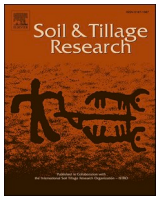

Oxygenation promotes vegetable growth by enhancing P nutrient availability and facilitating a stable soil bacterial community in compacted soil

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ABSTRACT

Soil compaction is a widespread phenomenon in intensive agriculture and can severely hamper root growth and crop yield. Hydrogen peroxide urea (UHP) has been employed as an effective measure for oxygenation in dryland systems. However, whether oxygenation via UHP could alleviate negative effects on vegetable growth induced by soil compaction is unknown. A pot experiment involving different soil bulk densities (1.2, 1.5, and 1.7 g cm^{-3}) with oxygenation at different stages of development (seedling stage, mid-growth stage) was conducted in amaranth (*A. mangostanus*), with non-oxygenation at different soil bulk densities as a control. Increased soil compaction affected vegetative growth of both the shoot and root system of amaranth and caused yield reduction. Oxygenation in topdressing significantly improved soil O_2 supply until the harvest period, imparted 17.9–20.4 % additional O_2 to soils. Increased O_2 supply alleviated soil compaction stress, and amaranth yield increased by 5.50–16.1 % at the same soil bulk density compared with control, respectively. Oxygenation during the mid-growth stage had a superior effect on vegetable growth compared to oxygenation at the seedling stage, coincident with the higher oxygen demand during mid-growth in amaranth. Oxygenation promoted root growth in compacted soil, and increased root length by 76.3 % at a soil bulk density of 1.5 g cm^{-3} and 74.7 % at a bulk density of 1.7 g cm^{-3} compared with control. The alleviatory effect on the root system can be linked to increased root catalase activity and decreased malondialdehyde content. Oxygenation furthermore increased phosphorus (P) bioavailability by increasing both phosphatase activity and the relative abundance of phosphate-solubilizing bacteria (*Firmicutes* and *Proteobacteria*), with an increase in DGT-P by 10.5–23.6 % compared to control. The soil bacterial co-occurrence network at a soil bulk density of 1.5 g cm^{-3} with oxygenation was more similar to 1.2 g cm^{-3} soil compaction with oxygenation, which possessed most complex and the proportion of connectors, but was dissimilar from 1.7 g cm^{-3} soil compaction with oxygenation, which was less stable microbial network structure. Improvement of O_2 content could build a healthy and stable rhizosphere bacterial community, and increased the proportion of important nodes in the network, which was conducive to the collaborative development of microorganisms to face compaction stress. And bacterial community structure with oxygenation in compacted soil could recovery to near normal microbiology community structure. The research provides a theoretical and technical framework for the development of strategies that can maximize crop yield in compacted soil.

1. Introduction

Soil compaction brought about by the use of agricultural machinery occurs widely in modern agriculture (Keller and Or, 2022; Batey and Mckenzie, 2006; Czy, 2004; Pagliai et al., 2003). It is recognized as one of the main factors that can lower crop yields and, thus, has been a serious agricultural problem around the world (Tomasz, 2014). Reportedly, approximately 68 million ha of land worldwide have issues

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due to soil compaction, and 14.7% of that land lies in Asia (Shaheb et al., 2021). In compacted soils, increased soil mechanical impedance and decreased soil O_2 content together create unfavorable conditions for root growth rate and root system development and thus limiting water and nutrient availability (Cook et al., 1996). Root growth experiences limitations when the soil penetration resistance reaches 2 MPa (defined as a threshold, Bengough et al., 2011), and a decrease in root length is typically observed with the increase in soil bulk density (Lipiec et al., 1991). Moreover, microorganisms with aerobic lifestyles can become severely restricted in a compacted soil, which can alter nutrient cycling and reduce crop yields (Tracy et al., 2011; Pupin et al., 2009). Soil compaction has been reported to result in significant reductions in nutrient uptake, by 12–35 %, for nitrogen (N), and by 17–27 % for phosphorus (P), in wheat (Ishaq et al., 2001). This reduction can be attributable to lowered nutrient availability due to physical compaction, but also to the establishment of hypoxic conditions for soil microorganisms involved in nutrient cycling (Kirk and Kronzucker, 2005). For plant roots, whose nutrient acquisition apparatus is very sensitive to reductions in soil O_2 supply as the respiratory O_2 demand of nutrient uptake can account for the majority of root respiratory activity (Kronzucker et al., 2001, 1998). Soil compaction has been identified as a special problem for soils involved in vegetable cultivation (Wolfe et al., 1995), owing to higher frequencies of machine-assisted fertilizer application, diverse crop rotations, and intensive cropping schedules. Vegetable growth are highly sensitive to soil compaction (Shubha et al., 2020), low soil O_2 also reduced root growth rate and increased the metabolic, i.e., carbon or energy demand of root growth due to the shift from aerobic respiration to anaerobic fermentation, especially given that vegetable root distribution tends to be shallow and sparse. Therefore, in the interest of the sustainable development of vegetable production systems, a focus on soil compaction in such systems is of particular urgency.

No-tillage, reduced tillage, and biochar application have all been proposed to alleviate soil compaction problems (Blanco-Canqui et al., 2022, 2009; Alkharabsheh et al., 2021; Liu et al., 2017). However, there have as well been circumstances under which no-tillage increased soil penetration resistance and biochar applications exacerbated soil structure by clogging soil micropores, leading to yield reduction (López-Garrido et al., 2014; Mukherjee and Lal, 2014; Herath et al., 2013). One of the significant features of compacted soil lie in restricted gas diffusion through soil and, thus, reduced O_2 content of soil (Topp et al., 2000). It has been shown, in a loam soil, that the O_2 diffusion rate (ODR) decreased from 98.1 mg m^{-2} s^{-1} at 1.54 g cm^{-3} soil bulk density to 57.9 mg m^{-2} s^{-1} at 1.64 g cm^{-3} density (Czy, 2004). Rhizosphere hypoxia reduces plant growth through its effects on root physiological function (Kronzucker et al., 2001, 1998; Shi et al., 2007). Microbial activity and available carbon concentrations are higher in the rhizosphere and hence O_2 consumption in the rhizosphere is higher. The decrease in soil O_2 levels also affects aerobic soil microorganisms and their enzyme activities (Li et al., 2016), and hypoxia/anoxia can furthermore aggravate problems related to soil-borne diseases (Bhattarai et al., 2005). Several techniques, including physical and chemical oxygenation measures have been developed for improving soil aeration, mostly in aerobic soil, a few for dryland soils (Bhattarai et al., 2006, 2004; Kirk and Kronzucker, 2005). Physical oxygenation usually includes pumping pressurized air or sucking air/bubbles into the irrigation water, and the larger-scale use of physical oxygenation has been limited by oxygenation equipment and nonuniform aeration in the field (Lei et al., 2016). Chemical oxygenation is achieved by adding O_2 fertilizer, like H_2O_2, urea hydrogen peroxide (UHP), and potassium peroxide, into the soil or irrigation water, which is convenient and targeted, providing O_2 in the root zone by direct application to the rhizosphere soil (Wang et al., 2022). UHP is an environmentally friendly hydrogen peroxide that provides higher O_2 concentrations than physical oxygenation by irrigation water venting (Frankenberger, 1997). Aeration of soil through UHP treatment can contribute to improved absorption of nutrients and the formation or maintenance of sound root-morphological structures, protecting yield (Wang et al., 2022). High aeration frequencies can furthermore effectively promote aerobic soil microbial proliferation, in turn assisting with improved plant-available nutrient supply (Li et al., 2016). We here wished to explore by what principal mechanism(s) oxygenation alleviates inhibition of vegetable crop growth in compacted soil.

Although we have previously identified positive effects of oxygenation on root growth (Wang et al., 2022), the specific mechanisms underlying the influence of oxygenation on root growth and physiological root characteristics in compacted soil have remained largely unresolved. We here evaluate changes in the soil microbial community in response to oxygenation for a popular vegetable in China, amaranth (*A. mangostanus*), and whether such changes contribute significantly to soil nutrient cycling. We focus in particular on soil P, which tends to be highly immobilized, and whose uptake in compacted soil is mainly influenced by the root structure (Shaheb et al., 2021). Thus, the objectives of this study are to (1) quantify the contribution of oxygenation to the content and temporal dynamic of the soil O_2 in compacted soil, (2) clarify the effect of oxygenation on the vegetable root system in compacted soil, and (3) understand the oxygenation mechanism on vegetable yield improvement from the perspective of nutrients, in particular P, and microorganisms in compacted soil.

2. Materials and methods

2.1. Soil collection

Soil samples were collected from open vegetable fields that had been utilized for 7 years for Chinese cabbage growth in Wuxi, Jiangsu Province, China (31°23′ N, 119°58′ E). Soil in the study was developed from a lacustrine deposit and has been classified as a Gleyed-Stagnant Anthrosol, according to the FAO soil taxonomy system. The soil properties were as follows: 15.6 g kg^{-1} soil organic matter (SOM), 0.89 g kg^{-1} total nitrogen (TN), 0.82 g kg^{-1} total phosphorus (TP), 119.2 mg kg^{-1} Olsen-P, pH 6.35, 55.4 % soil porosity and 1.2 g cm^{-3} soil bulk density Soil texture was powdery loam. Soil samples were air-dried, ground, sieved through a 0.85-mm mesh, and stored for further pot experiments. Plant residues were carefully removed by hand.

2.2. Pot experimental design and sample collection

Urea hydrogen peroxide (UHP) was chosen as the oxygen-release compound and was applied to non-compacted and compacted soil. The fertilization protocol in the pot experiments was based on the conventional fertilization rate with 160 mg N (urea and UHP), 80 mg P_2O_5 ($CaP_2H_4O_8$), and 120 mg K_2O (K_2SO_4) for 1 kg of vegetable soil (air-dried and sieved) for all treatments. Based on our previous study, UHP need to be applied in combination with urea in the rhizosphere as a topdressing due to the strong oxidizing properties, optimum proportions of 30 % N was derived from UHP (Wang et al., 2022) were applied at the seedling (S, 13 d after transplanting), or mid-growth stage (G, 23 d after transplanting), and a non-oxygenation treatment (zero-UHP) was used as the control treatment (detailed fertilization strategy see Table 1). UHP was applied in aqueous solution injected by syringe near into the soil, 1 cm away around the root base. Soil bulk density is an important indicator of soil compaction, and soil bulk density above 1.7 g cm^{-3} is considered to be the threshold beyond which soil microorganisms are affected (Beylich et al., 2010). Therefore, soils with bulk densities of 1.2 (conventional soil bulk density), 1.5 (moderate soil compaction), and 1.7 (severe soil compaction) g cm^{-3} were chosen to represent different soil compaction treatments in this study. Sieved soils (1 kg) were uniformly mixed with 80 mg N (urea), 80 mg P_2O_5 (calcium superphosphate), and 100 mg K_2O (potassium sulfate), and then packed into pot (polyvinyl chloride cylinders, 16 cm height, 10 cm internal diameter and 1257 cm^3 volume). Each treatment with 1 kg soil and the filling heights

Table 1
O_2 fertilizer application amounts and times.

Treatments	Base fertilizer (mg kg^{-1})			Aeration at seedling stage (mg kg^{-1})		Aeration at mid-growth stage (mg kg^{-1})	
	N (Urea)	P_2O_5 ($CaP_2H_4O_8$)	K_2O (K_2SO_4)	N (Urea)	N (UHP)	N (Urea)	N (UHP)
1.2Control	80	80	120	80	-	-	-
1.2S	80	80	120	56	24	-	-
1.2G	80	80	120	-	-	56	24
1.5Control	80	80	120	80	-	-	-
1.5S	80	80	120	56	24	-	-
1.5G	80	80	120	-	-	56	24
1.7Control	80	80	120	80	-	-	
1.7S	80	80	120	56	24	-	-
1.7G	80	80	120	-	-	56	24

Note: Number (1.2, 1.5, 1.7) represents different soil bulk density. "Control" represents none oxygenation. "S" represents oxygenation at the seedling stage. "G" represents oxygenation at the mid-growth stage.

of 10.6 cm (833 cm^3 volume), 8.5 cm (668 cm^3 volume), and 7.5 cm (589 cm^3 volume) were calculated based on the soil densities of 1.2, 1.5, and 1.7 g cm^{-3}, respectively, using stainless steel compactor to obtain different volume of soil in the pot with the same size. The soil volumes used in each treatment had no effect on the plant growth based on our pre-treatment (only used the same soil volumes, and without compaction treatment) according to Poorter et al. (2012). The background dissolved O_2 concentration and soil porosity were 217 μmol L^{-1} at 1.2 g cm^{-3} and 55.4 %, 192 μmol L^{-1} at 1.5 g cm^{-3} and 44.2 %, 180 μmol L^{-1} and 36.8 % at 1.7 g cm^{-3} soil bulk density. There were nine treatments with three replicates in this study, including two-factor test with two oxygenation periods and three soil bulk density treatments.

Amaranth seeds were immersed in NaClO (1 %) for 20 min and then washed thoroughly with tap water. The seeds were then immersed in water for 3 h before being placed on moist filter paper to germinate at 25 ℃ overnight in darkness. Five seeds were sown in each pot, and 2-week-old seedlings were thinned to two with similar growth. The moisture content in the soil was maintained at 60 % of the field water-holding capacity using distilled water replenishment at a fixed time of 5:00 pm daily to avoid the effect of soil O_2 concentration caused by watering with irregular intervals. The rhizosphere soil o was gathered at the harvest stage (45 d) by removing the loose soil and collecting the remaining soil that was tightly adhered to the roots, which was divided into two parts, one part was frozen at − 20 ℃ for soil DNA extraction, then the other was air-dried for soil property analysis.

2.3. Growth parameters

Amaranth sampling was destructive, with three repetitions taken from each treatment. The amaranth samples of each treatment were divided into shoot and root, roots were rinsed with water and then thoroughly drained with absorbent paper, then weighed separately for their fresh weights. Yield was assessed by monitoring shoot fresh weight. Root morphological parameters, including total root length, root surface area, root volume, and average diameter were analyzed using the root analysis instrument WinRhizo-LA1600 (Regent Instruments Inc., Quebec, QC, Canada). Then shoot and root materials were dried at 105 ℃ for 30 min and then to constant weight at 75 ℃ for 48 h to determine the dry weight. The dried plant material was ground and digested for total P determination. The P concentration in shoots was determined after digestion with a mixture of 5 ml of concentrated sulfuric acid and 8 ml of 30 % v/v H_2O_2, followed by spectrophotometric analysis using the molybdovanado phosphate method (UVmini-1240; Shimadzu, Kyoto, Japan). Shoot P accumulation (mg pot^{-1}) calculated by shoot dry weight multiplied shoot by P concentration, as well as shoot P use efficiency (PUE, g DW g^{-1}) were expressed as the shoot dry weight relative to shoot P accumulation (Wang et al., 2022).

Determination of root physiological indicators included catalase (CAT) and malondialdehyde (MDA). CAT is the predominant H_2O_2 scavenging enzyme in plants·H_2O_2 has a characteristic absorption peak at 240 nm, and it is decomposed by CAT. The absorbance of the reaction solution at 240 nm decreased with reaction time, and the CAT activity was assayed by monitoring the decrease in the absorbance at 240 nm as a consequence of H_2O_2 disappearance (Havir and Mchale, 1987). One enzyme activity unit (U) was defined as 1 nmol H_2O_2 degradation per minute per gram of tissue catalyzed. MDA is associated with the destruction of cell membranes by oxidative stress, the MDA content of plant will increase in soil stress (Díaz et al., 2021). The content of MDA was determined by thiobarbituric acid method (Buege and Aust, 1978).

2.4. Soil property analysis

The conventional Olsen method (Olsen et al., 1954) for the plant-available P determination refers to the amount of available P per unit of soil. The diffusive gradients in thin films (DGT) technique was used to measure soil-solution P and as well as absorbed P by soil that could be easily replenished to the soil solution, which is a good measure for the soil P fraction available for plant uptake (Kruse et al., 2015). The DGT-P technique involved the following steps: 10–30 g of rhizosphere soil was placed in a container and water was added to about 60 % of the maximum field water holding capacity for 48 h. Water was then added to the above soil to 80–100 % of the maximum field water holding capacity, and the soil was mixed thoroughly until a smooth water film was detectable at the surface, and then put into the DGT device. After 24 h at constant temperature, the fixed film was removed and put it into a centrifuge tube with 1.8 ml of 1 M NaOH. The soil P concentration was determined by the molybdenum-antimony anti-spectrophotometric method (Xu et al., 2012; Ding et al., 2010). Soil phosphatase activity was measured using phenyl phosphate disodium salt (Lin, 2010), using acetate buffer at pH = 5.0 for acid phosphatase and borate buffer at pH= 10 for alkaline phosphatase, and the enzyme activity was expressed as the amount of phenol produced in the soil after 24 h (mg phenol g^{-1} d^{-1}).

2.5. In situ measurements of soil O_2 concentration

The O_2 microelectrode, a miniaturized Clark-type O_2 electrode with a guard cathode (OX 50, ø = 40–60 μm, Unisense, Aarhus, Denmark), was used to measure soil O_2 concentration in situ at 20 d (7 days after aeration at seedling stage), 30 d (7 days after aeration at mid-growth stage), and 45 d (harvest) of amaranth growth. The soil O_2 profile measurements were performed in the center of the range at a distance of 1 cm from the stem base and a depth of 4 cm for all treatments. All measurements were performed with a 1-mm depth interval, and the periods for "wait before measure" and "measure" were both set to 5 s. The picture of measurement was shown in the Supporting information (Fig. S1).

2.6. Soil DNA extraction and high-throughput sequencing

Microbial DNA was extracted using the E.Z.N.A.® soil DNA Kit (Omega Bio-tek, Norcross, GA, U.S.) according to the manufacturer's protocol. The bacterial 16S rRNA gene was amplified with primers 515 F/907 R. The resultant PCR products were extracted from a 2 % agarose gel and further purified using the AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, CA, USA) and quantified using QuantiFluor™-ST (Promega, USA), and paired-end-sequenced on an Illumina MiSeq platform (Illumina, San Diego, USA).

2.7. Molecular ecological network analysis

The network analysis was performed using the Molecular Ecological Network Analysis Pipeline based on random matrix theory-based methods (http://ieg4.rccc.ou.edu/mena/) (Deng et al., 2012), with a cutoff of 0.96 to construct the network. Network properties, including total nodes, total links, modularity, R square of the power-law, average degree (avgK), and average path distance (GD) were used to evaluate the topological structure of the co-occurrence networks.

2.8. Data analysis

Data were analyzed statistically using the statistical software program SPSS version 20 (SPSS Inc., Chicago, IL, USA). Means were compared using one-way analysis of variance (ANOVA) with Duncan's multiple-range test. Significant differences ($P < 0.05$) between treatments are indicated by different letters in the figure and table legends. Graphs were produced using Origin Pro 2021. The constructed networks for bacterial species' connection were visualized using Gephi software.

3. Results

3.1. Dissolved O_2 concentration affected by oxygenation in compacted soil

Soil dissolved O_2 concentration decreased with increasing soil density (Fig. 1). Soil dissolved O_2 concentration without oxygenation at harvest was significantly lower than the background soil dissolved O_2 concentration (0 d, no planting and without oxygenation), which were 217, 192 and 180 μmol L^{-1} corresponding to 1.2, 1.5, and 1.7 g cm^{-3} soil bulk density, respectively (Fig. 1). Oxygenation could significantly increase soil dissolved O_2 concentration compared with control, especially oxygenation at mid-growth period, where soil O_2 concentration of 1.2 G treatment increased by 17.9 % compared with 1.2Control, 1.5 G treatment increased by 20.1% compared with 1.5Control, and 1.7 G treatment increased by 20.4 % compared with 1.7Control (Fig. 1). Thus, although soil dissolved O_2 concentration decreased significantly than before transplanting, the soil dissolved O_2 concentration could be significantly increased with O_2 fertilizer applied, and the oxygenation effect could be maintained even until the harvest period.

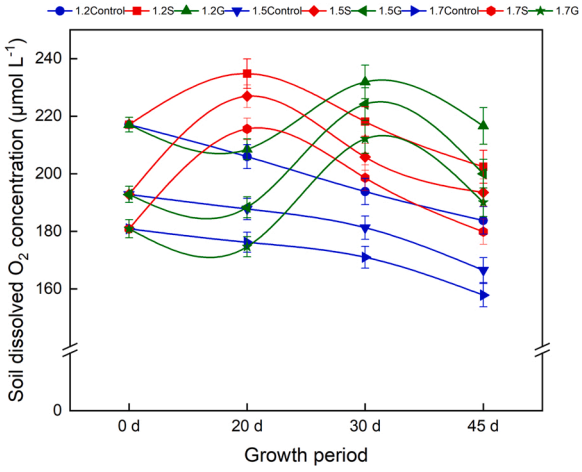

Fig. 1. Temporal variation of mean dissolved O_2 concentration in soil profiles on different soil compaction treatments. The measurement of soil O_2 concentration in situ at 20 d (7 days after aeration at seedling stage), 30 d (7 days after aeration at mid-growth stage), and 45 d (harvest) of amaranth growth. The bule line represents control, the red line represents oxygenation at seedling stage, the green line represents oxygenation at mid-growth stage. The background oxygen dissolved concentration was 217 μmol L^{-1} at 1.2 g cm^{-3}, 192 at 1.5 g cm^{-3}, 180 at 1.7 g cm^{-3} soil bulk density. Mean values were shown for a sample size of three replicates. Bars indicate the mean ± SD. The same as below. Mean values were shown for a sample size of three replicates. Bars indicate the mean ± SD. The same as below.

3.2. Vegetable growth, P absorption and P utilization affected by oxygenation in compacted soil

Soil compaction significantly affected the development of amaranth. With the increase of soil bulk density, the yield of amaranth decreased significantly ($P < 0.05$) (Fig. 2a). The yield in the 1.2Control treatment was 1.09 and 1.27 times that in the 1.5Control and 1.7Control treatments, respectively. The increase in the degree of soil compaction progressively inhibited the growth of amaranth, especially when the soil bulk density reached 1.7 g cm^{-3}. At the same soil bulk density, vegetable yields with oxygenation increased by 5.50 %, 6.88 %, and 16.1 % at 1.2, 1.5, and 1.7 g cm^{-3} soil bulk density compared with control, respectively (Fig. 2a). The yield-enhancing effect with oxygenation at the mid-growth stage was significantly superior to that at the seedling stage ($P < 0.05$) (Fig. 2a). The trends in P accumulation and shoot PUE were consistent with the trends in yield (Fig. 2b; Fig. 2c). Oxygenation significantly promoted amaranth P accumulation by 8.56 %– 28.1 % and PUE by 9.13 %– 20.4 % ($P < 0.05$) in the same soil bulk density treatment compared to control (Fig. 2b; Fig. 2c). There was no significant difference in P uptake at different oxygenation period ($P < 0.05$). Shoot PUE with oxygenation at mid-growth was significantly higher than that of seedling oxygenation in the soil bulk density of 1.5 g cm^{-3} and 1.7 g cm^{-3} treatments (Fig. 2b; Fig. 2c).

3.3. Root morphology and root protective system affected by oxygenation in compacted soil

The root growth of amaranth was inhibited with increasing of soil bulk density, and this manifested in the development of shorter and thicker roots (Table 2). Root length was shortened by 53.2 % and the average diameter increased by 55.6 % in the high soil bulk density treatment without oxygenation compared with the low soil bulk density treatment (Table 2). Oxygenation significantly promoted root development, mainly in the form of longer root length and increased root surface area. Compared with control, root length and root tip number with oxygenation increased by 28.5 % and 53.1 %, 76.3 % and 53.5 %, and 74.7 % and 68.1 % at 1.2, 1.5, and 1.7 g cm^{-3} soil bulk density, respectively (Table 2). The growth-promoting effect with oxygenation on vegetable root morphology at a density of 1.5 g cm^{-3} was particularly obvious. Moreover, total root length with mid-growth oxygenation increased by 72.3 % in the seedling oxygenation treatment, while it increased by 80.3 % compared with control at a soil bulk density of 1.5 g cm^{-3} (Table 2). Interestingly, we observed a significant increase in root tip number with oxygenation compared to the control (Table 2), in other words, oxygenation could promote root number. We provided the scanning picture of the root system for the different treatments in Supporting information (Fig. S2).

As soil bulk density increased, root MDA content increased by 79.2 % and 116 % in the 1.5Control and 1.7Control treatments, respectively, compared with the 1.2Control treatment (Fig. 3a). Root CAT enzyme activity was significantly reduced when the soil bulk density increased,

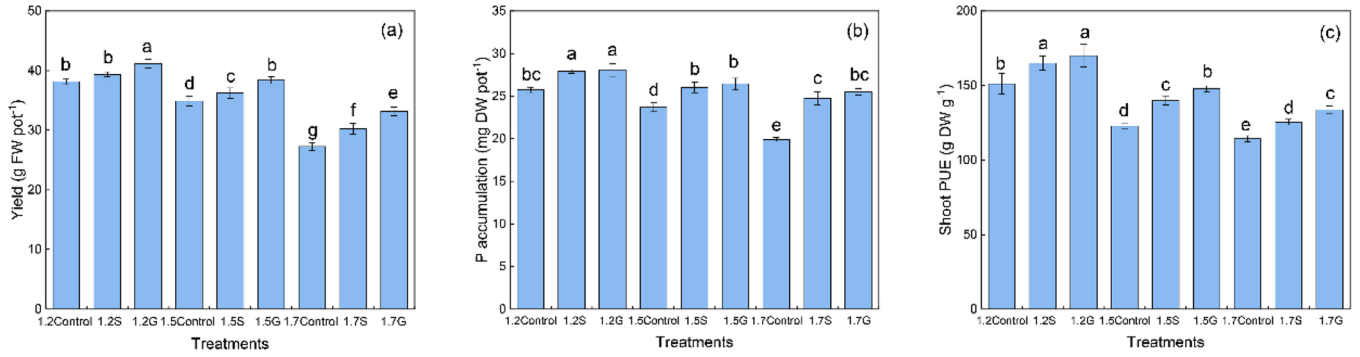

Fig. 2. Effect of oxygenation on (a) vegetable yield, (b) absorption, and (c) utilization of P under different soil compaction treatments. FW means fresh weight, DW means dry weight. The same as below.

Table 2
Effect of oxygenation on root development characteristics of amaranth at harvest under different soil compaction treatments.

Treatments	Total root length (cm)	Total root surface area (cm^2)	Root average diameter (mm)	Total root volume (cm^3)	Root tips
1.2Control	5339 ± 174c	432 ± 26.0c	0.27 ± 0.01d	2.72 ± 0.15c	13,208 ± 871cd
1.2S	6817 ± 287a	527 ± 18.6a	0.29 ± 0.01cd	2.98 ± 0.09b	19,525 ± 3003a
1.2G	6900 ± 130a	540 ± 10.3a	0.30 ± 0.02c	3.43 ± 0.14a	20,917 ± 1587a
1.5Control	3361 ± 112e	324 ± 5.40e	0.35 ± 0.01b	2.22 ± 0.04d	10,332 ± 908d
1.5S	5792 ± 491b	460 ± 41.1bc	0.30 ± 0.01c	3.04 ± 0.15b	15,757 ± 1226b
1.5G	6060 ± 156b	471 ± 13.1b	0.32 ± 0.01c	2.94 ± 0.11b	15,968 ± 769b
1.7Control	2500 ± 255f	247 ± 10.9f	0.42 ± 0.02a	2.02 ± 0.06e	6481 ± 789e
1.7S	3817 ± 144c	351 ± 7.40e	0.34 ± 0.01b	2.59 ± 0.02c	9779 ± 815d
1.7G	4919 ± 146d	393 ± 10.3d	0.36 ± 0.02b	2.63 ± 0.10c	12,016 ± 242cd

Note: Values represent means ± SDs with three replicates. Different letters in the same column indicate a significant difference ($P < 0.05$).

by 37.9 % and 49.7 % in the 1.5Control and 1.7Control treatments, respectively, compared with the 1.2Control treatment ($P < 0.05$) (Fig. 3b). At the same soil bulk density, root MDA content was significantly reduced by 35.8–52.6 %, while CAT enzyme activity was significantly increased by 13.4–110 % with oxygenation compared with control ($P < 0.05$) (Fig. 3).

3.4. Soil P turnover affected by oxygenation in a compacted soil

Available-P content decreased significantly with increasing soil density, and Olsen-P content in the 1.2Control treatment was 10.2 % and 14.5 % higher than that in the 1.5Control and 1.7Control treatments, respectively (Fig. 4a), while DGT-P concentration in the 1.2 Control treatment was 1.2 and 1.31 times higher than that in the 1.5Control and 1.7Control treatments, respectively (Fig. 4b). Oxygenation significantly increased available-P content, with Olsen-P content increased by 7.17–12.1 % and DGT-P concentration by 10.5–23.6 % compared with control at the same soil bulk density (Fig. 4a; Fig. 4b). There was no significant difference in Olsen-P content at different oxygenation periods at the same soil bulk densities, but the DGT-P content was significantly higher with mid-growth rather than seedling oxygenation (Fig. 4a; Fig. 4b).

ACP activity was 0.35–0.47 mg phenol g^{-1} d^{-1}, which was significantly higher than ALP activity (0.24–0.33 mg phenol g^{-1} d^{-1}) ($P < 0.05$) (Fig. 4c; Fig. 4d), showing that ACP was the more important phosphatase in this system. Both phosphatase activities decreased significantly with increasing soil density, and oxygenation increased phosphatase activity. ACP with oxygenation increased by 9.52–22.9 % and ALP increased by 6.9–14.8 % compared with no oxygenation, especially in compacted soil (Fig. 4c; Fig. 4d). Under identical capacitance conditions, ALP was significantly higher with mid-growth rather than seedling oxygenation, and there was no significant difference seen

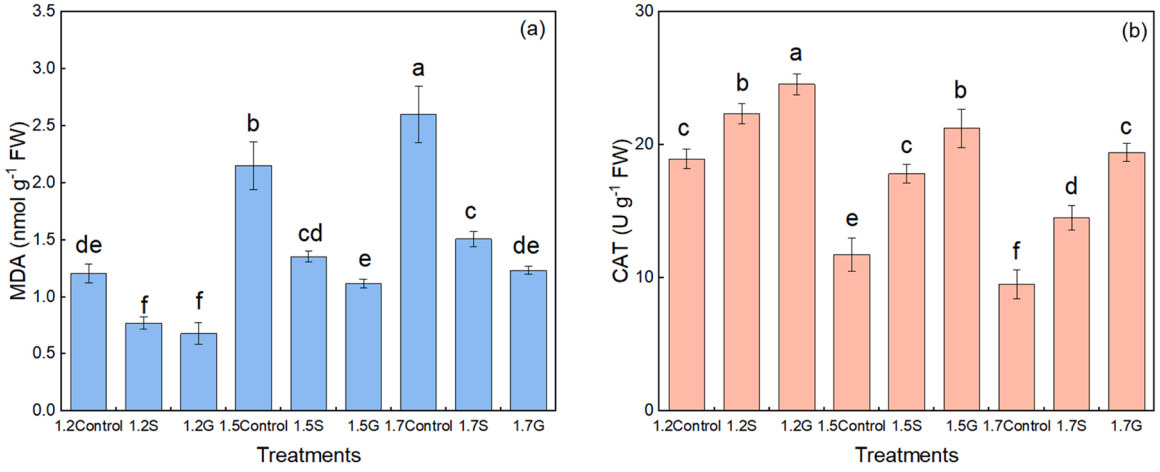

Fig. 3. Effect of oxygenation on root CAT enzyme activity and MDA content. (a) MDA and (b) CAT of amaranth roots at harvest under different soil compaction treatments.

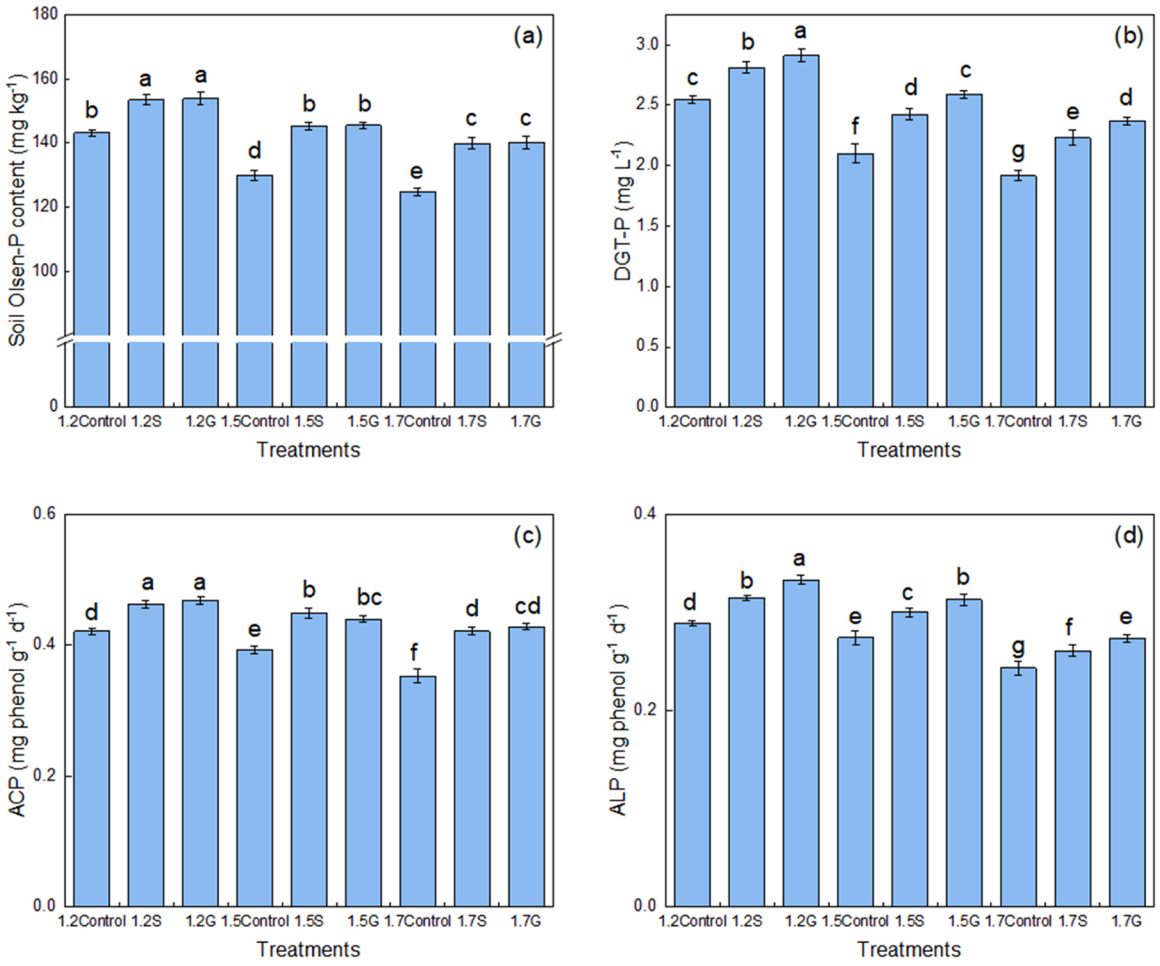

Fig. 4. Effect of oxygenation on soil physical properties. (a) Olsen-P, (b) DGT-P, (c) ACP, and (d) ALP under different soil compaction treatments.

in ACP with different oxygenation periods (Fig. 4c; Fig. 4d).

3.5. Soil microbial community affected by oxygenation in compacted soil

The soil-microbial phyla with relative abundance above 1 % are displayed in Fig. 5a, and these were: *Firmicutes*, *Proteobacteria*, *Actinobacteriota*, *Acidobacteriota*, *Chloroflexi*, *Gemmatimonadota*, *Cyanobacteria*, *Bacteroidota*, and *Myxococcota*. The phyla *Firmicutes* and *Proteobacteria* were the most dominant group, totally accounting for 50.3 %, 52.0 %, and 52.2 % of the soil bacterial communities corresponding to the 1.2Control, 1.5Control and 1.7Control treatments, respectively (Fig. 5a). Redundancy analysis (RDA) revealed that the microbial community structure was associated with primary soil variables, including soil O_2 ($r^2 = 0.66$, $P = 0.001$), DGT-P ($r^2 = 0.61$, $P = 0.001$), ACP ($r^2 = 0.60$, $P = 0.001$), Olsen-P ($r^2 = 0.60$, $P = 0.001$), SOM ($r^2 = 0.47$, $P = 0.001$), ALP ($r^2 = 0.45$, $P = 0.001$), and pH ($r^2 = 0.45$, $P = 0.002$) (Fig. 5b). Soil microbiota richness and diversity were significantly reduced with increasing soil bulk density (Fig. 5c; Fig. 5d). Oxygenation had no significant effect on microbial richness, but significantly increased the diversity of microorganisms at a soil bulk density of 1.7 g cm^{-3} ($P < 0.05$) (Fig. 5d).

4. Discussion

4.1. Contribution of oxygenation to the O_2 content increase in compacted soil

A significant feature of soil compaction is the limitation of gas diffusion through soil (Topp et al., 2000). The decreased gas transport capacity of the soil can ultimately result in lower levels of O_2 concentration in soil air (Reiser et al., 2020). Dissolved O_2 concentrations were 183 μmol L^{-1} at 1.2 g cm^{-3}, decreased to 166 μmol L^{-1} at 1.5 g cm^{-3}, and 157 μmol L^{-1} at 1.7 g cm^{-3} soil bulk density, significantly lower than background values (Fig. 1). Oxygenation of soil resulting from UHP application contributed to dissolved O_2 concentration increases by 17.9–20.4 %, and especially oxygenation at the mid-growth stage offered an additional 32.2–33.5 μmol L^{-1} of dissolved O_2 to soils (Fig. 1). However, soil O_2 concentration decreased gradually due to consumption by amaranth during its growth and development, and the effect was maintained until harvest with oxygenation at the middle growth stage compared with background values (217 μmol L^{-1} at 1.2 g cm^{-3}, 192 at 1.5 g cm^{-3}, 180 at 1.7 g cm^{-3} soil bulk density) (Fig. 1).

4.2. Contribution of oxygenation to vegetable growth improvement in compacted soil

Low O_2 concentrations in the root zone associated with soil compaction have been recognized as a major bottleneck for achievement of yield potential (Bhattarai et al., 2005; Agnew and Carrow, 1985). In this study, amaranth shoot biomass decreased significantly with increasing soil compaction, with yield being reduced by 8.60 % and 28.5 % in the 1.5 and 1.7 g cm^{-3} soil bulk density treatments, respectively, compared with the 1.2 g cm^{-3} soil bulk density treatment (Fig. 2a). This phenomenon was also found in root length, root surface area, and number of root tips, all of which were reduced as soil bulk density

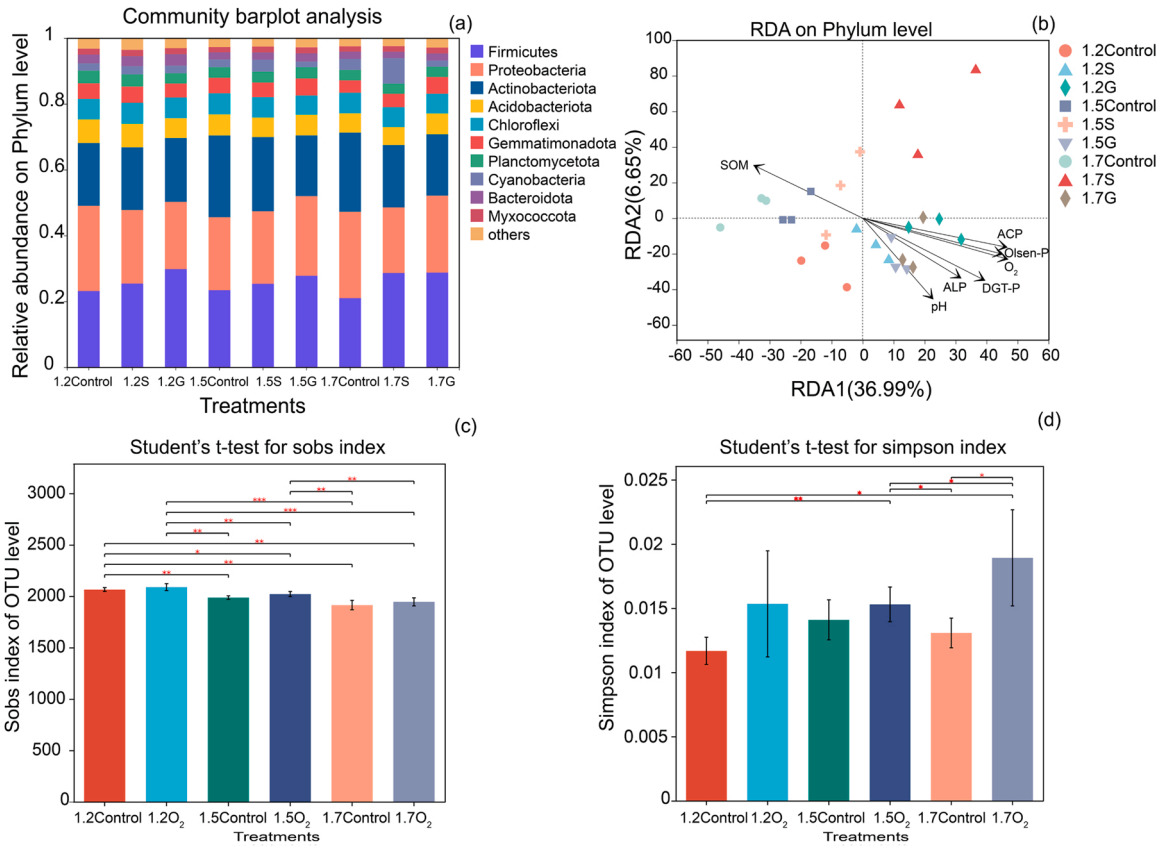

Fig. 5. Soil bacterial community response to oxygenation under different soil compaction treatments. (a) Microbiota community structure. (b) Redundancy analysis (RDA) of bacterial community structure and environmental characteristics. The correlations between the environmental factors and RDA axes are represented by the length and angle of the arrows. The longer the line is, the greater the contribution of the factor. The values of axes 1 and 2 are the percentages explained by the corresponding axis. (c) Microbiota richness. (d) Microbiota diversity. 1.2 O_2 (Oxygenation at 1.2 g cm^{-3} bulk density soil) treatment included 1.2 S and 1.2 G treatments; 1.5 O_2 (Oxygenation at 1.5 g cm^{-3} bulk density soil) treatment included 1.5 S and 1.5 G treatments; 1.7 O_2 (Oxygenation at 1.7 g cm^{-3} bulk density soil) treatment included 1.7 S and 1.7 G treatments. The same as below.

increased (Table 2). This is likely mainly attributable to impaired root respiration, which is the driving force for root metabolic activity, limited by O_2 supply in the rhizosphere (Bhattarai et al., 2005; Benjamin et al., 2003). The O_2 requirement for root growth is especially high in compacted soils, as greater amounts of energy are required for roots, i.e., energy for synthesis of anaerobic proteins and energy-dependent substrate transport, maintenance of membrane integrity and regulation of tissue pH, usually a moderate decrease in cytoplasmic pH and increase in vacuolar pH (Greenway and Gibbs, 2003), thus achieved root elongation. Furthermore, increased interception of roots with soil nutrients is expected to be critical under compacted conditions, as nutrient availability is generally reduced in compacted soils, while the acquisition of nutrients itself can carry a very high O_2 requirement (Kirk and Kronzucker, 2005; Kronzucker et al., 2001, 1998).

The root system is the first plant tissue to perceive soil stress (Zhang et al., 2018), and root cell membranes can be readily damaged in compacted soil, with the main manifestation was the increasing root thickness and decreasing root length (Bengough et al., 2006). The results were consistent with our research, root growth reduction in compacted soil (Table 2). A change in root morphological characteristics in response to oxygenation was one of the main reasons for observed differences in yield improvement in several agricultural systems, manifesting in an increased root surface area in rice (Xu et al., 2020), increased root length in cotton (Bhattarai et al., 2004), and higher root length density in soybean (Bhattarai et al., 2008). In this study, we found that the growth-protective effect of oxygenation at the level of the root system was mainly reflected in root length and in root tip number (Table 2). The trend in root growth was consistent with that in O_2 consumption (Fig. 1). Therefore, abundant O_2 is clearly an important reason for improved vegetable root growth. Generally, antioxidant capacity and oxidative metabolism in plants are maintained in a dynamic balance (Imlay, 2003). The fact that oxygenation significantly reduced root MDA content might relate to the increase in root CAT activity. Plants can protect themselves against cell damage from reactive O_2 species (ROS) by activating their antioxidant system (Pereira et al., 2010). Protective enzymes such as CAT are important for plants to scavenge ROS and reduce oxidative damage (Mølle et al., 2007). In our study, CAT activity increased significantly and MDA content decreased with oxygenation, indicating that oxygenation can increase the activity of protective enzymes and accelerate ROS scavenging, thus reducing root damage via oxidative stress in compacted soil. Furthermore, plants continuously extend roots through the action of meristems at their growing tips (Table 2). P absorption and utilization was influenced by the root morphological structure, because of P was highly immobilized in the soil. Oxygenation significantly promoted amaranth P accumulation and PUE in the same soil bulk density treatment compared to control (Fig. 2b; Fig. 2c). Interestingly, vegetable yields with oxygenation at a soil bulk density of 1.7 g cm^{-3} could be restored to 83.0 % of the 1.2Control treatment, and, both in terms of yield and root growth, the effect of mid-growth oxygenation was significantly higher than that of seedling oxygenation (Fig. 2a). It can be concluded that oxygenation is a useful means to improve vegetable growth in compacted soil, and the mid-growth stage is of particular importance in amaranth, as O_2 demand during that stage appears to be especially high.

4.3. Contribution of oxygenation to soil P turnover in compacted soil

Soil Olsen-P and DGT-P tended to decrease with increasing soil bulk density, but oxygenation significantly increased Olsen-P and DGT-P contents (Fig. 4a; Fig. 4b). There was no significant difference in the effect of oxygenation on Olsen-P content at different periods, but the DGT-P concentration was significantly higher with mid-growth oxygenation than in seedling oxygenation (Fig. 4b). DGT-P characterized soil-solution P as well as absorbed P by soil that could be easily replenished to the soil solution, therefore oxygenation might weaken soil-P adsorption and promote P desorption, thus allowing rapid replenishment of P depleted by root uptake. In our study, the increase in soil-available P might also be related to the effect of oxygenation on soil enzyme activity. Phosphatase activity is an important indicator of the mineralization potential of soil organic P, as it hydrolyzes phosphomonoesters to release orthophosphates that can be utilized by plants (Nannipieri et al., 2011; George et al., 2007). Typically, phosphatases are classified into acid phosphatase (ACP) and alkaline phosphatase (ALP) according to the enzymatic pH optima. Soil phosphatase activity decreased significantly with increasing soil compaction in our study (Fig. 4c; Fig. 4d), which is in agreement with Atwell (1990). ACP and ALP activities were significantly higher in loosened soil than in compacted soil with 1.44 soil bulk density (Atwell, 1990). Increasing soil air content can effectively increase soil phosphatase activity (Wang et al., 2013; Dodor and Tabatabai, 2003). This is consistent with the results of this study, where oxygenation increased ACP and ALP activity in the soil (Fig. 4c; Fig. 4d), thus increasing available P. Studies showed that both plant roots and microorganisms can secrete ACP, whereas ALP can be secreted by soil microorganisms (Nannipieri et al., 2011). There was no significant effect of different periods of oxygenation on ACP at the same soil bulk density, but mid-growth oxygenation significantly increased ALP (Fig. 4c; Fig. 4d), and this difference might due to changes in the soil microbial community (Fig. 5).

4.4. Contribution of oxygenation to soil microbial structure in compacted soil

The influence of soil compaction and the ensuing limited O_2 supply on microbial processes can be pronounced (De Neve and Hofman, 2000). A significant decrease in microbial diversity and richness was observed at a bulk density of 1.7 g cm^{-3}, as compared to diversity and richness at a bulk density of 1.2 g cm^{-3}, in our study (Fig. 5c; Fig. 5d). Furthermore, oxygenation significantly increased soil microbial diversity in 1.7 g cm^{-3} soil bulk density compared to 1.7Control, and there was no significant effect on soil microbial diversity in the other compaction treatments (Fig. 5c). Soil O_2 content was found to be the most important factor affecting soil community structure (Fig. 5b). Oxygenation clearly favored microbial colonization of the rhizosphere, leading to a marked microbial diversity increase in compacted soil. Soil microbial diversity is often positively correlated with ecosystem stability (Sul et al., 2013; Ptacnik et al., 2008), i.e., oxygenation can promote a more stable agroecosystem. Microbiota are important for plant growth, nutrient uptake, and disease resistance (Compant et al., 2019). We observed an increase in the relative abundance of *Firmicutes* and *Proteobacteria* phyla with oxygenation (Fig. 5a); these belong to phosphate-solubilizing microorganisms (Wei et al., 2016) and are considered the main drivers for transformation of soil-fixed P into bioavailable forms (Richardson and Simpson, 2011). This indicates that oxygenation can promote soil P transformation by regulating beneficial bacterial in the rhizosphere, which, in turn, provide additional P nutrient to vegetables and promote their growth (Fig. 2a; Fig. 4c; Fig. 4d). This finding could be of broader significance for the development of improvement strategies of vegetable production systems faced by soil compaction stress.

To understand the influence of oxygenation on microbial interactions further, we compared soil microbial molecular-ecological networks changes with different bulk density in response to oxygenation (Fig. 6a; Fig. 6b; Fig. 6c), and the topology indices are listed in Table 3. Evidence is mounting that properties of ecological networks, which reflect interactions among microorganisms, can influence the response of microbial communities to environmental change (De Vries et al., 2018). The modularity index value in each group was 0.92 (Table 3), which was greater than 0.4, indicating that they were all modularly structured co-occurrence networks (Newman, 2006). Total nodes and average path distance (GD) increased with increasing soil bulk density, but the most total links occurred in 1.5 O_2 treatment (Table 3). The small GD value indicates higher efficiency in the community in terms of material metabolism and energy transfer (Deng et al., 2012). In our study, we found that the total nodes and links of the microbial network with oxygenation in the soil bulk density of 1.2 and 1.5 g cm^{-3} was larger than that at severe soil compaction (1.7 g cm^{-3}), while the GD was lower than that at severe soil compaction (Table 3). We determined the topological role of each node according to the relative within-module degree Z and the participation coefficient P (Guimera and Amaral, 2005). According to the simplified criteria of Olesen et al. (2007), only 0.35–1.18 % of the total nodes were generalists (Fig. 6d; Fig, 6e; Fig. 6f), divided equally between module hubs and connectors, which were analogous to key microbial species for the communities as predicted from network theory (Montoya et al., 2006). It should be noted that the proportion of significant hubs in the 1.2 O_2 treatment network was higher than that in the 1.5 O_2 and 1.7 O_2 treatment networks. Overall, the interactions between the rhizosphere bacterial communities were closer at the 1.2 and 1.5 g cm^{-3} soil bulk density with oxygenation treatment (Fig. 6a; Fig. 6b). The microbial network structure was more similar in moderate compaction soil (1.5 g cm^{-3}), but more different in severe compaction soils (1.7 g cm^{-3}) compared to normal soils (1.2 g cm^{-3}) with oxygenation. This indicates that elevated soil O_2 established a more complex, balanced, and efficient microbial community, conducive to the collaborative interaction between plants and microorganisms, finally, it could establish a healthy and stable rhizosphere bacterial community. And oxygenation at moderate compaction soil led to rhizosphere bacterial structure nearly returned to that of normal soils. Although oxygenation at severe compaction soil could not restore the soil microbial community structure to normal soil levels, it could still significantly increase the soil microbial diversity of severe compaction soils, and this might be one of the reasons for elevating nutrient levels in the rhizosphere, thus promoting root growth and increasing yield.

5. Conclusions

This study demonstrates that oxygenation via UHP can increase dissolved soil O_2 concentrations significantly. Oxygenation has the potential to alleviate soil compaction stress on vegetable growth by promoting root growth, increasing nutrient availability, especially P. However, the production promotion mechanism was not exactly the same at different soil bulk density. In moderate compaction soils, oxygenation led to rhizosphere bacterial structure nearly return to that of normal soils, and build of a healthy and stable bacterial community response to soil perturbation. Oxygenation at severe compaction soil increases root CAT activity and decreases root MDA content, in turn reducing soil compaction damage to roots and promoting root growth. Furthermore, we found that the mid-growth stage was the critical oxygen-sensitive period for amaranth, allowing the conclusion that oxygenation in mid-growth has a superior effect on vegetable growth than oxygenation at the seedling stage.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

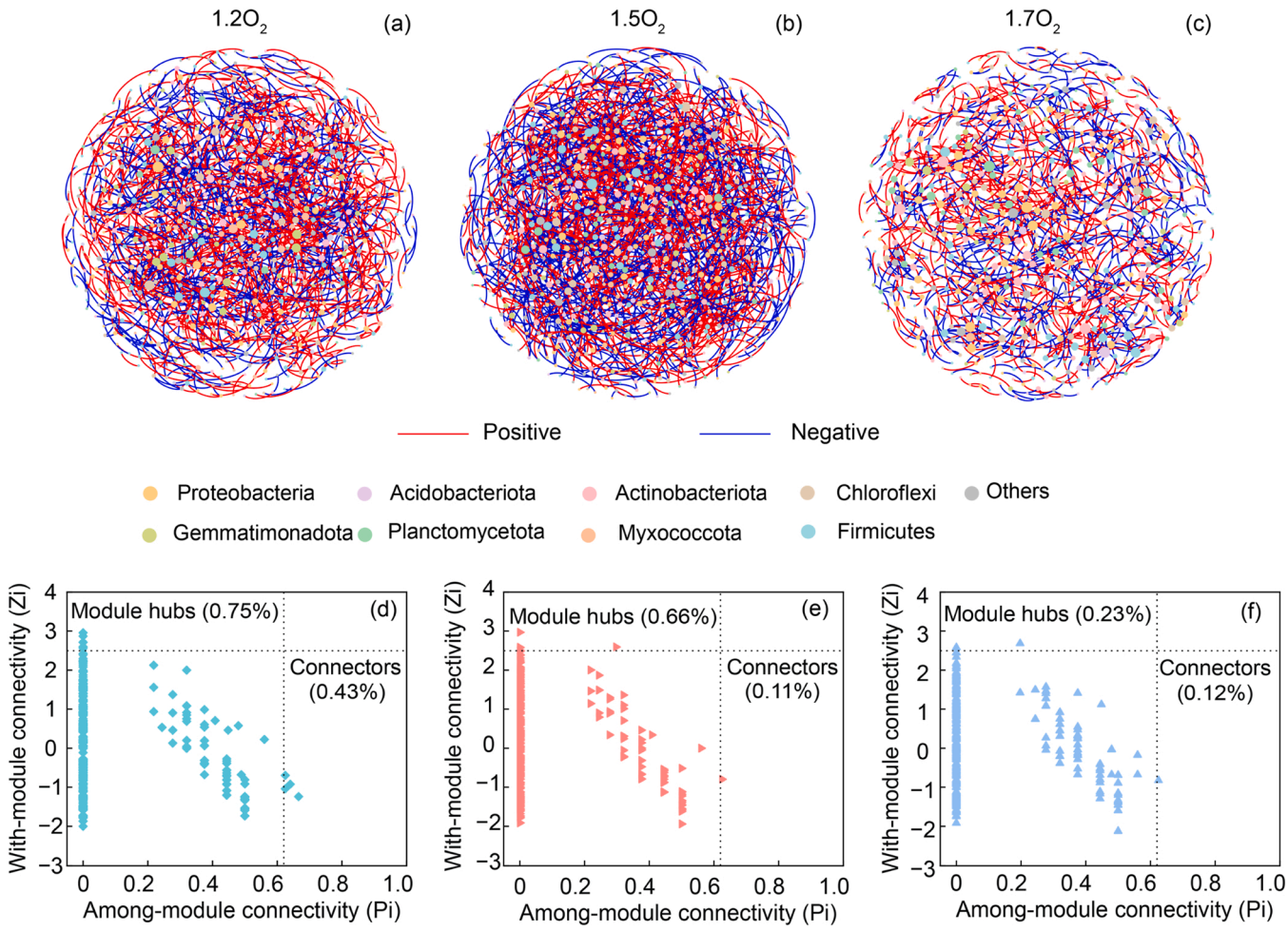

Fig. 6. Co-occurrence network interactions of bacterial community connection with oxygenation at soil bulk densities of (a) 1.2 g cm^{-3}, (b) 1.5 g cm^{-3}, and (c) 1.7 g cm^{-3}. (Each node signifies an OTU, and colors of the nodes indicate different major phyla. The size of each node is proportional to the number of connections. Red and blue lines, respectively, represent negative and positive correlations between nodes.). Zi-Pi plot showing the distribution of nodes based on their topological roles in the networks of (d) 1.2 g cm^{-3}, (e) 1.5 g cm^{-3}, and (f) 1.7 g cm^{-3} soil bulk density with oxygenation. The threshold values of Zi and Pi for categorizing OTUs were 2.50 (horizontal dashed line) and 0.62 (vertical dashed line).

Table 3
Topological properties of microbial networks with oxygenation under different soil compaction treatments.

Topological properties	1.2 O_2	1.5 O_2	1.7 O_2
Total nodes	924	909	860
Total links	1317	1372	1251
Modularity index	0.92	0.92	0.92
Average degree (avgK)	2.85	3.02	2.91
R square of power-law	0.75	0.68	0.71
Average path distance (GD)	12.3	13.7	16.6

Note: 1.2 O_2 (Oxygenation at 1.2 g cm^{-3} bulk density soil) treatment included 1.2 S and 1.2 G treatments; 1.5 O_2 (Oxygenation at 1.5 g cm^{-3} bulk density soil) treatment included 1.5S and 1.5G treatments; 1.7 O_2 (Oxygenation at 1.7 g cm^{-3} bulk density soil) treatment included 1.7S and 1.7G treatments.

Data availability

Data will be made available on request.

Acknowledgments

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.still.2023.105686.

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