

Effects of microbial inoculants on agronomic characters, physicochemical properties and nutritional qualities of lettuce and celery in hydroponic cultivation

Qiu-Ying Wang^{a,b}, Ming-Rui Zhao^a, Jin-Qi Wang^a, Bo-Yang Hu^a, Qing-Jun Chen^a, Yong Qin^{b,*}, Guo-Qing Zhang^{a,*}

^a Beijing Key Laboratory for Agricultural Application and New Technique, College of Plant Science and Technology, Beijing University of Agriculture, Beijing 102206, China

^b College of Horticulture, Xinjiang Agricultural University, Urumqi 830052, China

ARTICLE INFO

Keywords:

Lactuca sativa L.
Apium graveolens L.
Arthrobacter pascens
Bacillus subtilis
Vitamin C

ABSTRACT

Leafy vegetables are rich in nutrients such as vitamins and dietary fiber, which are essential to people's daily diet. Microbial inoculants play an important role in promoting plant growth and nutritional qualities. In this study, two combined microbial inoculants of *Arthrobacter pascens* BUAYN-122 and *Bacillus subtilis* BUABN-01 were applied in the hydroponic system for lettuce (*Lactuca sativa* L.) and celery (*Apium graveolens* L.) cultivation. After harvesting, the agronomic characters, physicochemical properties and nutritional qualities of lettuce and celery were determined. The paper aimed to evaluate the application of the combined microbial inoculants on hydroponic cultivation of lettuce and celery. The results showed that the microbial inoculants significantly improved the aboveground fresh weight, underground fresh weight, root length, leaf length and leaf number of both lettuce and celery. The root dehydrogenase activity, net photosynthetic rate, stomatal conductance and total chlorophyll content of the two vegetables were significantly improved, indicating that the microbial inoculation can promote the root nutrient uptake and leaf photosynthesis. Furthermore, the microbial inoculants could significantly increase the total protein, vitamin C and total phenol contents of lettuce and celery, anthocyanin and total flavonoid contents of lettuce, and soluble sugar and total dietary fiber contents of celery. The results of this study confirmed that the application of microbial inoculants in hydroponics systems can promote the yield and the quality of lettuce and celery.

1. Introduction

Vegetable is one of the essential foods in people's daily diet, which can provide the necessary nutrients such as vitamins and minerals for the human body (Renna et al., 2018; Zhang et al., 2020). According to the data of National Bureau of Statistics, the planting area of vegetables in China in 2021 was about 2.19×10^7 hm² with the output of about 767.11 million tons. With the continuous improvement of people's living standards, vegetable consumption is also quietly changing. More and more consumers are aware of the functional qualities and biological activities of vegetables. The demand for vegetable products with high safety, nutrients and bioactivities and is continuously increasing (Bian et al., 2020; El-Nakhel et al., 2020; Kelly et al., 2020). However, a

variety of environmental challenges including climate change, soil compaction, drought and flood disasters have caused serious negative impacts on the yield and quality of vegetable crops (Zareei et al., 2021). Nowadays, the soilless culture system (SCS) for vegetable production has rapidly expanded worldwide, since it can provide high-quality and safe products, and demonstrates higher water and nutrient use efficiencies (Barrett et al., 2016; Gruda, 2022; Koukounaras, 2021).

Hydroponics, which is one way of soilless culture under controlled environmental conditions, can utilize soilless growing media or nutrient solutions to promote faster growth, higher production, and better nutrient utilization efficiency (Lee et al., 2021; Majid et al., 2021). Compared with traditional soil-based cultivation, hydroponics saves soil resources, improves water use efficiency, reduces the amount of

* Corresponding author.

** Corresponding author.

E-mail addresses: 352167610@qq.com (Y. Qin), zhangqbua@163.com (G.-Q. Zhang).

<https://doi.org/10.1016/j.scienta.2023.112202>

Received 7 January 2023; Received in revised form 23 May 2023; Accepted 30 May 2023

Available online 7 June 2023

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chemical fertilizers and pesticides, and reduces greenhouse gas emissions (Muller et al., 2017; Specht et al., 2014). At the same time, the establishment of hydroponic systems in artificially controlled greenhouses can also avoid the effects of extreme weather and soil pollution on vegetable yield and quality (Lee and Lee, 2015). At present, a variety of horticultural plants represented by lettuce, celery and tomato can be produced by hydroponics. Lei and Engeseth (2021) compared the growth characteristics and functional quality of hydroponic and native lettuce, and found that the contents of ascorbic acid, chlorophyll, β -carotene and total phenol in fresh hydroponic lettuce were significantly higher than those in native lettuce. Verdoliva et al. (2021) found that compared with traditional soil-cultured tomatoes, hydroponic tomatoes had higher water use efficiency and higher lycopene and β -carotene contents. However, compared with commercial fertilizers available for traditional soil cultivation, commercial nutritional supplements for hydroponic cultivation are relatively limited. The nutrient solution management was an effective cultivation method to improve the biological activity and functional quality of hydroponic lettuce (El-Nakheel et al., 2020). A certain concentration of proline can improve the yield and quality of lettuce by regulating the biochemical process of plants (Zhang et al., 2020). Therefore, further development of hydroponic nutrients is of great significance to improve the yield and quality of vegetables worldwide.

Moreover, some beneficial microbial inoculants for plants have been also explored. They can produce a large number of active substances, promote the absorption of mineral elements, improve the metabolism of plants, promote plant growth, and enhance plant resistance to pathogens and pests (Jack et al., 2021; Qiu et al., 2019). Plant growth-promoting rhizobacteria (PGPR) are a group of bacteria that can be colonized in plant roots, improve the nutritional status of host plants and form a reciprocal relationship with them. PGPRs can promote plant growth by producing phytohormone (cytokinin, gibberellin, indole-3-acetic acid, etc.), antibiotics, antifungal metabolites, and solubilizing phosphorus and nitrogen fixation (Elnahal et al., 2022; Pathania et al., 2020). Moreover, PGPRs are also considered as 'natural fertilizers' that can replace conventional industrial fertilizers and pesticides, and maintain sustainable agricultural development (Harris et al., 2021; Thilagar et al., 2016). Microbial inoculation of *Bacillus subtilis* and *Rhodotorula glutinis* can not only promote the lettuce growth, but also stimulate beneficial microbes and inhibit potentially pathogenic microbes of plants (Xu et al., 2022). Moreover, the application of microbial inoculants during the romaine lettuce cultivation can help to maintain the nutritional, functional and perceived quality attributes of lettuce during the shelf life (Cocetta et al., 2021). Furthermore, the current research on microbial inoculants mainly focuses on soil or substrate cultivation, and there are relatively few studies on microbial inoculants in hydroponic system.

Lettuce (*Lactuca sativa* L.) and celery (*Apium graveolens* L.) are widely consumed green vegetables worldwide. They are not only rich in various nutrients and phytochemicals, including dietary fiber, Vitamin C (V_C), phenols and flavonoids, but also have the characteristics of short growth cycle, high economic value, good ecological benefits and suitable for various cultivation environments (Aksakal et al., 2017; Li et al., 2013; Zhang et al., 2020). In this study, two combined microbial inoculants *Arthrobacter pascens* BUAYN-122 and *Bacillus subtilis* BUABN-01 were applied in the hydroponic system of lettuce and celery. After the cultivation tests, the agronomic characters, physicochemical properties and nutritional qualities of lettuce and celery were monitored. The aim of this study was undertaken to evaluate the application of microbial inoculants in hydroponic system during lettuce and celery cultivation.

2. Materials and methods

2.1. Plant materials, microbial inoculants and growth-promoting experiment on plates

Lettuce "BeiZi NO.4" seeds were generously donated by the Lettuce

Research Group of Beijing University of Agriculture (BUA), Beijing, China. Celery "CuiQin NO.1" seeds were purchased from Beijing Academy of Agriculture and Forestry Sciences, Beijing, China. *A. pascens* BUAYN-122 (T1) and *B. subtilis* BUABN-01 (T2) were isolated and preserved by our laboratory, BUA. The lettuce and celery seeds were sterilized by 1–25% sodium hypochlorite, followed by cultured on 1/2 MS medium plate (MS powder 2.37 g/L, sucrose 20.00 g/L, agar 8.00 g/L) in a light incubator (16 h light, 8 h dark, 21 °C). BUAYN-122 and BUABN-01 strains were inoculated in liquid LB medium (tryptone 10.00 g/L, yeast extract 5.00 g/L, sodium chloride 10.00 g/L), incubated in a constant temperature shaker at 28 °C and 180 r/min for 24 h, centrifuged at 5000 rpm for 10 min. The supernatant was discarded, and the bacteria were resuspended with appropriate sterile water and diluted to 5×10^6 CFU/mL (Xu et al., 2022). After 3–10 days' seed germination, the seedlings with similar growth and root length (about 1 cm) were selected and moved to the new 1/2 MS plate. The microbial inoculants were respectively inoculated at the root tip with 2.5 μ L per seedling, and the control group was inoculated with equal volume of sterile water. The plates were subsequently cultured in a light incubator (16 h light, 8 h dark, 21 °C) for 2–3 weeks. The plant growth-promoting activity of the two microbial inoculants determined by measuring the main root length, lateral root number and fresh weight (FW) of seedlings (Li et al., 2022a).

2.2. Hydroponic experiment design

The experiments were conducted in an intelligent greenhouse in BUA from January to March 2022. Seedlings of lettuce and celery were sown in 50-cell plug-trays filled with peat, vermiculite and perlite (peat: vermiculite: perlite = 2: 1: 1; 240 cm³ each individual plug). When the seedlings grew to three leaves and one center, the seedlings with consistent growth were selected and established in a vertical hydroponic system. The hydroponic system consisted of an upper layer of a 36-well cylindrical hydroponic column, a bottom trapezoid water tank (80 L) and an automatic circulation device (Fig. 1). A standard hydroponic nutrient solution for leafy vegetables (LEAFY-500 two part hydroponic nutrient for leafy greens and herbs, Radongrow-Leafy) was used in the hydroponic system (Majid et al., 2021). The above microbial inoculants (5×10^6 CFU/mL) were mixed with equal volume (combined microbial inoculants) for further inoculation with the final concentration of 5×10^5 CFU/mL in the nutrient solution. The experiment involved four treatments: (1) CKL: the nutrient solution without the combined microbial inoculants for lettuce cultivation as the blank control; (2) TL: the nutrient solution with the combined microbial inoculants for lettuce cultivation; (3) CKC: the nutrient solution without the combined microbial inoculants for celery cultivation as the blank control; (4) TC: the nutrient solution with the combined microbial inoculants for celery cultivation. Each treatment was performed in triplicates (108 seedlings). When lettuce and celery reached commodity maturity, the plants with uniform growth in each treatment were harvested, and their related agronomic, physicochemical and nutritional characters were further evaluated.

2.3. Assay for agronomic and physicochemical characters

The agronomic characters of lettuce and celery included above-ground fresh weight (AGFW), underground fresh weight (UGFW), plant height, root length, leaf length, leaf width and leaf number. Eighteen plants selected randomly from each treatment were performed for the agronomic assays (Xu et al., 2022). Plant dehydrogenase (PDHA) activity was measured in quadruplicate with fresh root tissue by the plant dehydrogenase assay kit (BC3125, Solarbio, China) (Hou et al., 2020). The photosynthetic parameters, including net photosynthetic rate (P_n), intercellular CO₂ concentration (G_i), stomatal conductance (G_s), and transpiration rate (T_r), were evaluated on a sunny morning between 9:00 am and 11:00 am, and as described by Xu et al. (2022). The parameters

were determined using a portable non-destructive photosynthesis system CIRS-3 (Hansatech, UK) and eighteen repetitions in each treatment (Teng et al., 2022; Xia et al., 2021). The content of chlorophyll a (Chl a), chlorophyll b (Chl b), and carotenoid of fully expanded leaves was determined by using a spectrophotometer (Shanghai Aoyi Instrument Co., LTD). Fresh leaf samples (0.2 g) were put into a clean test tube, and 8.0 mL acetone alcohol mixture (acetone: alcohol = 1:1, V/V) was added. The leaves were incubated at 25 °C for 24 h in the dark until they completely faded. The absorbance of the supernatant at 645, 663 and 440 nm was measured. Chlorophyll and carotenoid contents were calculated as described by He et al. (2021).

2.4. Assay for nutritional and bioactive composition

The nutritional and bioactive composition of lettuce and celery were evaluated by measuring the contents of total protein, soluble sugar, total dietary fiber (TDF), ascorbic acid (Vc), anthocyanins, total phenols and flavonoids. The total protein content of fresh leaf samples was determined at 595 nm according to the Coomassie brilliant blue G-250 dye method (Bradford, 1976). Fresh plant samples (1.0 g) were homogenized in the phosphate buffer saline (10 mL, pH 7.0) and a small amount of quartz sand, followed by the centrifugation at 12,000 rpm for 5 min. Subsequently, the supernatant (0.1 mL) was mixed with the Coomassie brilliant blue G-250 solution (10 mg/L). The UV absorbance at 595 nm was determined after 2 min. The protein content was calculated based on the standard curve of the absorbance vs the content of standard protein (He et al., 2021).

The soluble sugar content of fresh leaf samples was determined at 630 nm by the anthrone colorimetric method (Mei et al., 2023). In brief, Fresh plant samples (1.0 g) were fully homogenized with 15 mL distilled water and set volume to 100 mL, followed by the extraction in boiling water for 30 min. The extract was cooled to room temperature and filtered using qualitative filter paper. The filtrate was set to 100 mL with distilled water. Subsequently, the filtrate (1.0 mL) was mixed with anthrone reagent (4.0 mL) in the ice bath for 5 min, followed by boiling water bath for 10 min. The UV absorbance at 630 nm was measured after cooling. According to the standard curve equation, the sugar concentration of the corresponding samples can be found. The calculation formula of total sugar content of plant materials is as follows:

$$\text{Sample sugar content} = (\text{sample sugar concentration} \times \text{total extract volume}) / \text{sample fresh weight}.$$

The anthocyanin content of fresh leaf samples was determined by spectrophotometry as described by Nakata et al. (2013). Fresh plant samples (1.0 g) were fully homogenized with liquid nitrogen, followed by the addition of hydrochloric acid-methanol (10 mL, 1%, v/v). The mixture was centrifuged at 4500 rpm for 10 min. The supernatant was collected and filtered by 0.22 µm nylon filter. The absorbance of the supernatant at 530 nm was measured. The anthocyanin concentration was one unit (U) when the light density was 0.1. The relative concentration unit of anthocyanin per gram material: $U = OD_{530} \times 10 / \text{g FW}$.

The V_C content of fresh leaf samples was determined at 243 nm (Yuan et al., 2012). In brief, fresh leaf samples (5.0 g) were grinded with liquid nitrogen and further homogenized with 2.5 mL HCl (10%, V/V). The homogenate was set volume to 5.0 mL with distilled water, followed by a centrifugation at 3000 rpm for 10 min. The supernatant (0.1 mL) was added with 0.2 mL HCl (10%, V/V) and 4.7 mL distilled water. The UV absorbance at 243 nm (A_{243nm}) was measured with distilled water as the control. A standard curve of A_{243nm} vs standard L-ascorbic acid was determined. The calculation formula of V_C content of plant materials is



Fig. 1. The hydroponic cultivation system (A) and its schematic diagram (B).

as follows:

$$V_{C\text{content}} = (C \times V_t \times V_s \times 100) / (V_1 \times W_t \times 1000)$$

C : Concentration of V_C obtained from standard curve

V_t : Total volume after constant volume

V_s : Total volume of sample to be tested

V_1 : Volume of sample solution absorbed in determination of absorbance

W_t : Sample mass

Fresh leaf samples were dried at 75 °C in a drying box (DHG-9070, Shanghai Yiheng, China) until constant weight, then pulverized, and sifted through a 30-mesh sieve. The powder was used for the determination of TDF, total phenols and flavonoids contents. The TDF was calculated based on insoluble dietary fiber (IDF) and soluble dietary fiber (SDF) as described by Rebeira et al. (2022).

Total phenol and flavonoid contents were determined by the plant total phenol (BC1340, Solarbio, China) and flavonoid (BC1330, Solarbio, China) kits, respectively (Li et al., 2022b; Wang et al., 2020). The total phenol and flavonoid contents were calculated as gallic acid and rutin equivalents, respectively.

2.7. Statistical analysis

All data were presented as mean \pm standard deviation (mean \pm SD). The significance of the different treatments was tested by one-way ANOVA using SPSS (v.25.0). For each species, the significance of the applied treatment was analyzed using Student's *t*-test. When analyzing the effects of the two treatments on growth-promoting activities, one-way ANOVA was carried out and the means were compared using Tukey's test. Statistically significant differences were accepted at the minimum probability level of $P < 0.05$.

3. Results

3.1. Growth promoting activities of microbial inoculants

The growth promoting activities of microbial inoculants towards lettuce and celery on the plates were shown in Fig. 2. The morphological characteristics of the assayed seedlings revealed that both *A. pascens* BUAYN-122 and *B. subtilis* BUABN-01 can promote the growth of the aboveground part of lettuce and celery (Fig. 2A). *A. pascens* BUAYN-122 significantly promoted the main root length, lateral root number and fresh weight of lettuce and celery seedlings (Fig. 2B–2D). Compared with the control group, the fresh weight of lettuce and celery inoculated with *A. pascens* BUAYN-122 increased by 144.4% and 300.9%, respectively. Moreover, *B. subtilis* BUABN-01 demonstrated significant growth promoting activities towards the lateral root number and fresh weight of lettuce and celery seedlings, but significant inhibitory activity towards the main root length of lettuce seedlings.

3.2. Agronomic and physicochemical characters

The agronomic and physicochemical characters of mature lettuce and celery were evaluated after a 30-day and 45-day hydroponic cultivation, respectively. The microbial inoculation significantly improved the morphological characters of both lettuce and celery (Fig. 3). The agronomic characters and plant dehydrogenase (PDHA) activity of lettuce and celery were listed in Table 1. The AGFW of TL and TC was 50.60 ± 4.16 g and 58.87 ± 3.16 g, which was 1.98 and 1.30 times as high as that of the control group (CKL and CKC), respectively. The UGFW of TL and TC was 10.00 ± 2.64 and 24.80 ± 3.53 g respectively, which was 1.88 and 1.21 times as high as that of the control group, respectively. The TL manifested a plant height of 15.71 ± 1.11 cm, which was significantly higher than that of the CKL. Moreover, there was no significant difference in the plant height of celery between CKC and TC. The root length of TL and TC was 24.29 ± 2.16 and 31.53 ± 5.46 cm, which was significantly higher than CKL and CKC, respectively. Meanwhile, the microbial inoculants did not significantly improve the leaf length and leaf width of lettuce and leaf width of celery. Moreover, TL and TC demonstrated significantly higher leaf number and PDHA activity.

The photosynthetic parameters were visualized in Table 2. The P_n of TL and TC was 6.09 ± 0.67 and 13.11 ± 0.99 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ respectively, which was significantly higher than that of CKL and CKC. Moreover, the G_i of CKL and CKC was significantly higher than that of TL and TC, respectively. Furthermore, the microbial inoculants significantly improved the G_s of TL and TC and T_r of TL and TC. Subsequently, the photosynthetic pigment contents of lettuce and celery in each treatment were further determined and shown in Table 3. The microbial inoculants significantly improved the content of Chl a, total Chl and

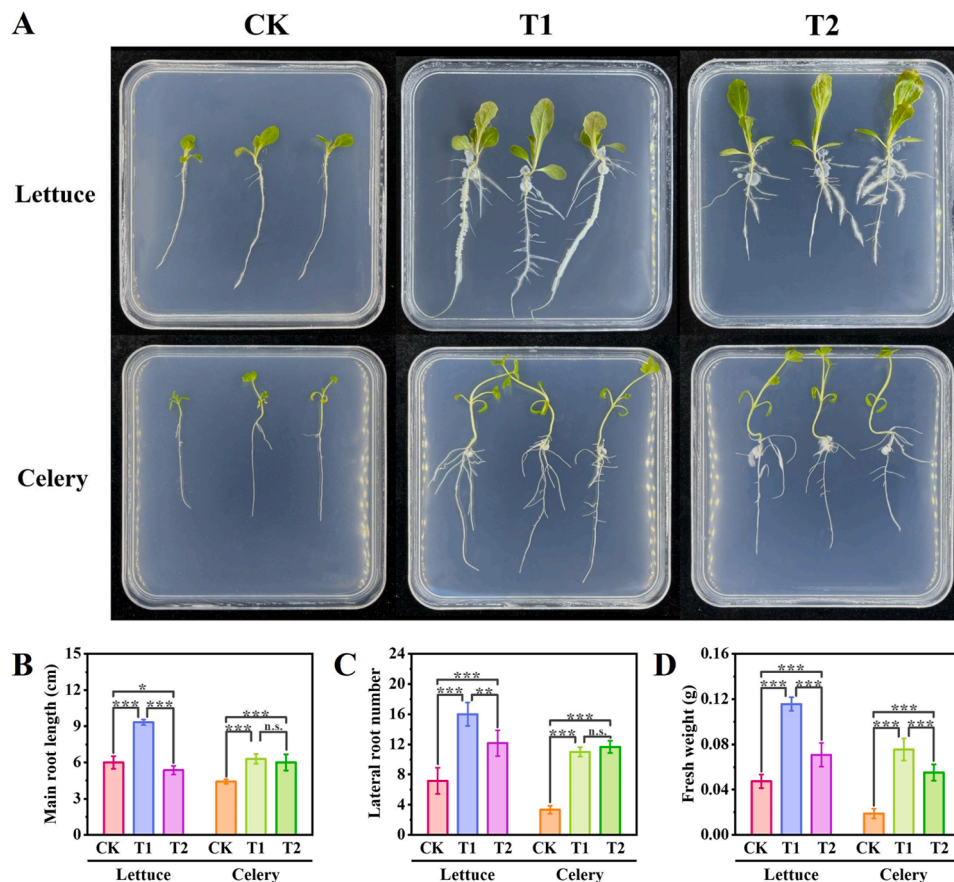


Fig. 2. Growth promoting activities of *A. pascens* BUAYN-122 (T1) and *B. subtilis* BUABN-01 (T2) on lettuce and celery seedling. All the data were expressed as mean \pm SD ($n = 6$). Data were analyzed using one-way ANOVA. Different letters indicate means significantly different according to Tukey's post-hoc test (Significance level: n.s. = not significant; *, $0.01 \leq P < 0.05$; **, $0.001 \leq P < 0.01$; ***, $P < 0.001$).

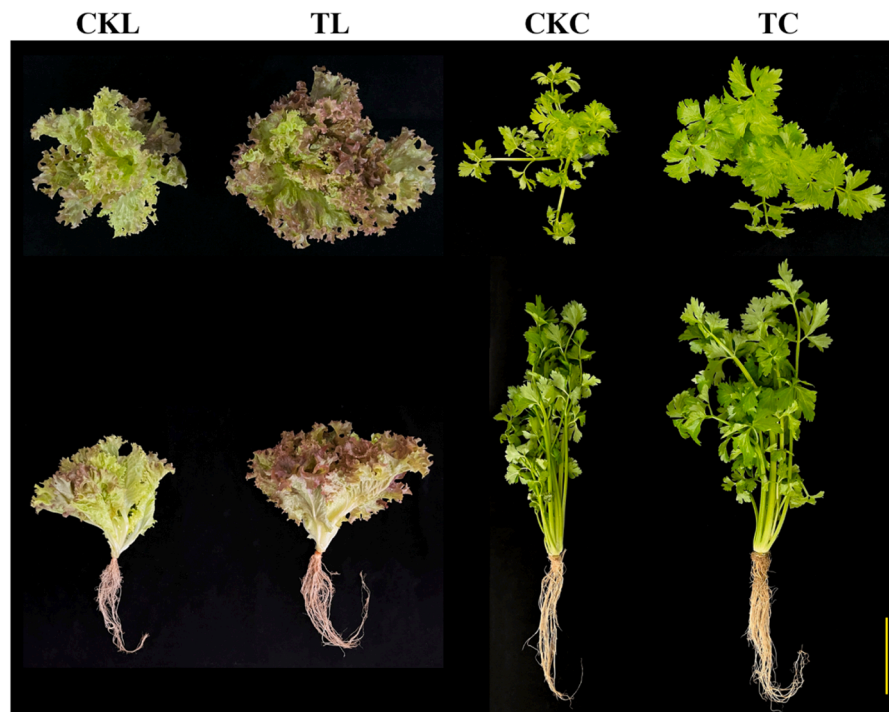


Fig. 3. Plant morphology of different treatment groups. CKL: control group of lettuce; TL: test group of lettuce; CKC: control group of celery; TC: test group of celery.

Table 1

Effects of microbial inoculants on aboveground fresh weight (AGFW), underground fresh weight (UGFW), plant height, root length, leaf length, leaf width, leaves/petiole number, plant dehydrogenase (PDHA) activity of lettuce and celery in hydroponic cultivation.

Treatment	AGFW (g)	UGFW (g)	Plant height (cm)	Root length (cm)	Leaf length (cm)	Leaf width (cm)	Leaves/petiole number (piece)	PDHA activity (U/g FW)
CKL	25.50 ± 2.70	5.33 ± 1.40	14.93 ± 1.06	21.5 ± 4.14	13.32 ± 1.00	11.59 ± 1.27	10.35 ± 1.00	21.70 ± 1.77
TL	50.60 ± 4.16	10.00 ± 2.64	15.71 ± 1.11	24.29 ± 2.16	13.72 ± 1.16	13.24 ± 1.29	13.47 ± 0.74	27.64 ± 1.36
<i>P</i>	***	***	*	*	ns	***	***	**
CKC	45.26 ± 3.21	20.55 ± 3.80	38.92 ± 2.70	27.92 ± 3.26	4.78 ± 0.51	4.21 ± 0.45	12.06 ± 1.83	23.10 ± 1.35
TC	58.87 ± 3.16	24.80 ± 3.53	39.24 ± 3.23	31.53 ± 5.46	5.14 ± 0.58	4.51 ± 0.33	14.00 ± 1.24	32.59 ± 1.58
<i>P</i>	***	**	ns	*	ns	ns	**	***

CKL: control treatment of lettuce; TL: test treatment of lettuce; CKC: control treatment of celery; TC: test treatment of celery. The values of agronomic characters and PDHA shown were the mean ± SD ($n = 18$ and 4 , respectively). For each treatment, means in the same column were compared using Student's *t*-test.

* $0.01 \leq P < 0.05$.

** $0.001 \leq P < 0.01$.

*** $P < 0.001$.

ns $P > 0.05$.

carotenoid content of lettuce and celery.

3.3. Nutritional and bioactive composition

Furthermore, the nutritional composition of total protein, soluble sugar, TDF and Vc, and bioactive composition of anthocyanins, total phenols and flavonoids of lettuce and celery were determined. The microbial inoculants significantly increased the total protein and Vc contents of lettuce and celery, and soluble sugar and TDF contents of celery (Table 4). After the hydroponic cultivation with microbial inoculation, the total protein content of lettuce and celery reached 9.21 ± 0.66 and 9.84 ± 0.76 mg/g FW respectively, which was 25% and 18% higher than that of control treatments. The soluble sugar content of TL and TC was 1.38 ± 0.25 and 3.91 ± 0.53 mg/g FW respectively, which was 18% and 33% higher than that of control treatments. The TC demonstrated the highest TDF content of 3.08 ± 0.11 g/100 g FW, whereas TL showed no significant difference in TDF content with CKL. Moreover, the Vc content of TL and TC of lettuce and celery was 33.76 ± 1.25 and 43.45 ± 0.28 mg/100 g FW respectively, which was significantly higher than

that of control treatments CKL and CKC.

The bioactive composition of anthocyanin, total phenol and flavonoid in lettuce and celery were shown in Table 5. The anthocyanin content of TL reached to be 22.16 ± 3.32 OD_{530nm}/g FW, which was 81% higher than that of CKL. The anthocyanin content of CKC and TC was relatively low and showed no significant difference. Moreover, the total phenol content of TL and TC was 1.33 ± 0.05 and 0.66 ± 0.09 mg/g DW, which was 2.05 and 2.00 times as high as the control treatment, respectively. The total flavonoid content of TL was 6.95 ± 0.36 mg/g DW and significantly higher than that of CKL. Furthermore, the microbial inoculants did not significantly affect the total flavonoid content of celery.

4. Discussion

Nowadays, hydroponic cultivation has become more and more popular and continuously increased worldwide, since it can offer higher yield and higher quality products, improve water and nutrient use efficiency, and reduce soil-borne diseases and pests (Lee et al., 2021; Lee

Table 2

Effects of microbial inoculants on net photosynthetic rate (P_n), intercellular CO_2 concentration (C_i), stomatal conductance (G_s), transpiration rate (T_r) of lettuce and celery in hydroponic cultivation.

Treatment	P_n ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	C_i ($\mu\text{mol}\cdot\text{mol}^{-1}$)	G_s ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	T_r ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)
CKL	5.29 ± 0.56	530.56 ± 11.91	177.38 ± 19.59	6.24 ± 0.33
TL	6.09 ± 0.67	504.88 ± 21.23	191.73 ± 19.12	6.52 ± 0.18
<i>P</i>	**	***	*	*
CKC	11.31 ± 1.14	561.13 ± 14.49	437.00 ± 45.32	10.38 ± 0.73
TC	13.11 ± 0.99	549.63 ± 8.07	602.77 ± 46.58	13.18 ± 0.95
<i>P</i>	***	*	***	***

CKL: control treatment of lettuce; TL: test treatment of lettuce; CKC: control treatment of celery; TC: test treatment of celery. The values shown were the mean ± SD ($n = 18$). For each treatment, means in the same column were compared using Student's t -test.

ns: $P > 0.05$.

* $0.01 \leq P < 0.05$.

** $0.001 \leq P < 0.01$.

*** $P < 0.001$.

Table 3

Effects of microbial inoculants on chlorophyll a (Chl a), chlorophyll b (Chl b), total chlorophyll, carotenoids content of lettuce and celery in hydroponic cultivation.

Treatment	Chl a (mg/100 g)	Chl b (mg/100 g)	Total Chl (mg/100 g)	Carotenoids (mg/100 g)
CKL	21.43 ± 1.66	7.41 ± 0.85	29.17 ± 2.52	5.64 ± 0.78
TL	28.90 ± 0.99	10.66 ± 0.64	40.00 ± 1.64	8.02 ± 0.42
<i>P</i>	**	**	***	**
CKC	67.30 ± 2.69	28.05 ± 0.72	96.37 ± 3.36	11.21 ± 0.72
TC	77.73 ± 1.97	35.58 ± 7.01	114.50 ± 8.16	16.47 ± 1.48
<i>P</i>	**	ns	**	**

CKL: control treatment of lettuce; TL: test treatment of lettuce; CKC: control treatment of celery; TC: test treatment of celery. The values shown were the mean ± SD ($n = 4$). For each treatment, means in the same column were compared using Student's t -test *: $0.01 \leq P < 0.05$; ***: $P < 0.001$;

** $0.001 \leq P < 0.01$;

ns $P > 0.05$.

Table 4

Effects of microbial inoculants on soluble protein, soluble sugar, total dietary fiber (TDF), ascorbic acid (Vc) content of lettuce and celery in hydroponic cultivation.

Treatment	Soluble protein (mg/g, FW)	Soluble sugar (mg/g, FW)	TDF (%)	Vc (mg/100 g, FW)
CKL	7.38 ± 0.18	1.17 ± 0.11	2.32 ± 0.15	31.07 ± 0.89
TL	9.21 ± 0.66	1.38 ± 0.25	2.49 ± 0.01	33.76 ± 1.25
<i>P</i>	*	ns	ns	**
CKC	8.31 ± 1.22	2.95 ± 0.12	2.71 ± 0.07	41.22 ± 1.03
TC	9.84 ± 0.76	3.91 ± 0.53	3.08 ± 0.11	43.45 ± 0.28
<i>P</i>	*	*	**	**

CKL: control treatment of lettuce; TL: test treatment of lettuce; CKC: control treatment of celery; TC: test treatment of celery. The values shown were the mean ± SD ($n = 4$). For each treatment, means in the same column were compared using Student's t -test (***: $P < 0.001$);

* $0.01 \leq P < 0.05$;

** $0.001 \leq P < 0.01$;

ns $P > 0.05$.

and Lee, 2015; Majid et al., 2021). Moreover, optimized microbial inoculant is considered to be one of the new frontiers in agriculture productivity (Jack et al., 2021; Khan, 2022; Qiu et al., 2019). The

Table 5

Effects of microbial inoculants on anthocyanins, total phenols, flavonoids content of lettuce and celery in hydroponic cultivation.

Treatment	Anthocyanins (OD530nm/g FW)	Total phenol (mg/g, DW)	Flavonoid (mg/g, DW)
CKL	12.22 ± 1.76	0.65 ± 0.08	5.42 ± 0.42
TL	22.16 ± 3.32	1.33 ± 0.05	6.95 ± 0.36
<i>P</i>	**	***	**
CKC	5.19 ± 0.32	0.33 ± 0.05	2.60 ± 0.46
TC	5.10 ± 0.32	0.66 ± 0.09	3.25 ± 0.61
<i>P</i>	ns	**	ns

CKL: control treatment of lettuce; TL: test treatment of lettuce; CKC: control treatment of celery; TC: test treatment of celery. The values shown were the mean ± SD ($n = 4$). For each treatment, means in the same column were compared using Student's t -test (*: $0.01 \leq P < 0.05$).

** $0.001 \leq P < 0.01$;

*** $P < 0.001$;

ns $P > 0.05$.

research on hydroponics mainly focuses on the yield components, nutrient efficiency, environmental control, etc. (Fayezizadeh et al., 2021; Lee et al., 2021; Sronsri et al., 2022). However, there is little research focusing on microbial inoculants in hydroponic cultivation systems. In the present study, we aimed to evaluate the application of microbial inoculants in the hydroponic cultivation system.

Previous studies revealed that many PGPRs offer a number of benefits for host plants, including promoting plant growth, improving nutritional quality, extending shelf life and inhibiting plant pathogens (Cocetta et al., 2021; Olenska et al., 2020; Pathania et al., 2020). In this study, two microbial inoculants *A. pascens* BUAYN-122 and *B. subtilis* BUABN-01 were used. In our previous study, *B. subtilis* BUABN-01 can significantly promote lettuce growth during the seedling test using composted spent mushroom substrate (Xu et al., 2022). Moreover, *Arthrobacter* spp. are metal resistant Actinobacteria and known as bio-remediating inoculants in many polluted environments (Kong et al., 2022; Schwabe et al., 2021). Previous studies revealed that *Arthrobacter* spp. involved in the soil phosphorus metabolism and can improve the phosphate solubilizing (Olenska et al., 2020; Safdarian et al., 2019). It is reported that many PGPRs can induce lateral root formation in plants, for example *Bacillus* spp. and *Pseudomonas* spp. (Li et al., 2022a, 2021). In this study, the plate seedling test showed that both *A. pascens* BUAYN-122 and *B. subtilis* BUABN-01 can significantly promote the fresh weight and lateral root number of lettuce and celery seedlings (Fig. 2). The two microbial inoculants BUAYN-122 and BUABN-01 induced the lateral roots of both lettuce and celery, which would further improve the nutrient uptake of plant roots and plant growth. The plant growth-promoting activities can be mediated through the release of phytohormones, such as gibberellin and indole-3-acetic acid (Elnahal et al., 2022; Schwabe et al., 2021). Moreover, a previous study also revealed that the inoculation of *Pseudomonas* sp. CM11 specifically induced the genetic pathways associated with lateral root formation (Li et al., 2022a).

The application of the two microbial inoculants in the hydroponic cultivation significantly promoted the agronomic characters of mature lettuce and celery, including AGFW, UGFW, root length, and leaf number (Table 1). Previous studies showed that PGPRs applied in soilless cultivation systems could improve the efficiency of plants in using organic nutrients, thus increasing the yield, plant height and root length (Kaloterakis et al., 2021; Moncada et al., 2021). In this study, the microbial inoculation stimulated the growth of lateral roots, which further promoted the absorption and utilization of nutrients in the hydroponic environment. The AGFW of lettuce and celery with microbial inoculation was 1.98 and 1.30 higher than that of the control treatment, respectively. The root dehydrogenase (PDHA) can reflect the active state of biological cells and the ability to utilize nutrients from culture media. The two microbial inoculants can also significantly improve the PDHA

activity of both lettuce and celery. This result suggests that the microbial inoculation in the hydroponic system can promote not only the lateral root formation, but also the root activity, resulting in the increase of biomass accumulation and yield. Moreover, the application of microbial inoculants (*Bacillus amyloliquefaciens*, *Paenibacillus pasadenensis* and *Pseudomonas syringae*) during romaine lettuce cultivation can maintain the nutritional, functional and perceived quality attributes of leaves during shelf life (Cocetta et al., 2021). These findings suggest that the present microbial inoculants might further extend the produce quality during shelf life.

Photosynthesis is a very important physiological process in plant, which contributes more than 90% of plant yield (Zhu et al., 2019). A previous study indicated that the application of *B. subtilis* BUABN-01 and *R. glutinis* RG significantly increased the P_n and G_s of lettuce in spent mushroom substrate based seedling (Xu et al., 2022). Three PGPRs, *Bacillus velezensis* SX13, *Bacillus paralicheniformis* SX21 and *Bacillus tequilensis* SX31, were found effective in improving the P_n , T_r and Chl contents (Chl a, Chl b and total Chl) of cucumber leaves (Wang et al., 2022). The combined use of *Bacillus* sp. strain and γ -aminobutyric acid significantly increased the P_n , T_r and total Chl content of rice leaves under salt stress (Wang et al., 2023). Moreover, *Pseudomonas* spp. improved the P_n , G_s , T_r and the total Chl content of tomato leaves under salt stress (Win et al., 2018). In this study, the two microbial inoculants significantly enhanced the P_n , G_s and T_r of lettuce and celery leaves, and significantly decreased the C_i (Table 2). The decrease of C_i suggested that CO_2 was more effectively absorbed and fixed. The microbial inoculants enhanced the photosynthetic efficiency of the two plants. Moreover, they also significantly improved the content of Chl a and total Chl of lettuce and celery (Table 3). These data suggest that the microbial inoculation can increase the leaf Chl contents (Chl a and total Chl), with positive effect on the P_n and G_s of lettuce and celery leaves.

In recent years, leafy vegetables are popular, since they are convenient to eat, low in calories and rich in dietary fiber, Vc and other bioactive compounds. In this study, the microbial inoculation significantly promoted the total protein content of both lettuce and celery (Table 4). Previous studies revealed that PGPRs can improve the nitrogen and phosphorus metabolism of plant, resulting in the increase of the protein content (Olenska et al., 2020; Pathania et al., 2020). Furthermore, the two microbial inoculants significantly improved the soluble sugar and TDF contents of celery, but had no significant effect on those of lettuce (Table 4). It may be due to the greatly increased yield (1.98 times as high as CKL) of lettuce by microbial inoculants, which led to the decrease of soluble sugar and TDF contents in lettuce per unit mass. Leafy vegetables are rich in Vc, anthocyanin, phenols and flavonoids, which enrich them with strong antioxidant activity and potential health-beneficial functions (Medina-Lozano et al., 2021; Schreinemachers et al., 2018). These bioactive compounds have shown anti-diabetic, anti-inflammatory and cholesterol-lowering activities in vivo and vitro (Kim et al., 2016). A recent report revealed that a higher intake of lettuce was associated with a lower risk of liver cancer and chronic liver diseases (Zhao et al., 2022). Moreover, the vegetable protein intake was negatively correlated with cardiovascular disease mortality and blood pressure, and was associated with reduced risk of breast cancer (Liu et al., 2014). In this study, the microbial inoculation significantly increased the anthocyanin, total phenol and flavonoid contents in lettuce (Table 5). The two microbial inoculants significantly promoted the growth of aboveground and underground parts of lettuce and celery (Fig. 2). The addition of microbial inoculations in the hydroponic system significantly improved the root activity (PDHA) (Table 1), which can promote plants to better absorb nutrients from the environment and produce more secondary metabolites. The application of two mycorrhizal fungi and *Trichoderma koningii* in lettuce cultivation improved the biosynthesis of secondary compounds of the plant (Saiaa et al., 2019). These results suggest that the addition of PGPRs in hydroponic systems could significantly improve the nutritional qualities and antioxidant capacity of lettuce. Moreover, the lettuce used in this

study is a purple leaf lettuce rich in anthocyanins, while the celery variety lacks anthocyanins. Therefore, it may have had less impact on celery because of the low anthocyanin content.

5. Conclusion

In conclusion, the two microbial inoculants *A. pascens* BUAYN-122 and *B. subtilis* BUABN-01 manifested significant promoting effects on the agronomic characters of hydroponic lettuce and celery, including the biomass of aboveground and underground, root length and leaf number. The microbial inoculation significantly improved the root nutrient uptake and leaf photosynthesis of the two vegetables, including the root activity (PDHA), P_n , G_s and the total Chl content. Moreover, the microbial inoculation further promoted the nutritional qualities of the two vegetables, including total protein, Vc and total phenol contents. Furthermore, the microbial inoculation highly significantly improved the anthocyanin content of the test purple leaf lettuce. These results suggest that the application of microbial inoculants in hydroponics systems is a very effective and promising cultivation method for leaf vegetables.

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.

Data availability

Data will be made available on request.

Funding

This work was financially supported by the Beijing Innovation Consortium of Agriculture Research System (BAIC03-05).

Acknowledgements

We thank Prof. Ying-Yan Han for supplying the lettuce seeds used in this study.

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