Article

Study on Screening and Degradation Effect of Autotoxin-Degrading Bacteria in Muskmelon

Shuangshuang Tang , Zhaoran Zhang , Xiaodi Liu and Zenggui Gao *

College of Plant Protection, Shenyang Agricultural University, Shenyang 110866, China
* Correspondence: gaozenggui@syau.edu.cn

Abstract: The autotoxins of muskmelon are one of the most important reasons for the continuous cropping obstacle of muskmelon, of which the main components are phenolic acids. Phenolic acids can inhibit the growth and development of muskmelon plants. The purpose of this study was to screen the strains that can degrade phenolic acids in soil. Using phenolic acids as the sole carbon source, the strains were isolated and screened by the dilution plate method, which could efficiently degrade various phenolic acids. The abilities of the strains to degrade phenolic acids were measured by HPLC, and the effects of degrading phenolic acids in soil were verified by a pot experiment. After identification, strain T58 was identified as *Burkholderia* sp., strain T79 was identified as *Burkholderia* sp., strain H16 was identified as *Pseudomonas* sp., and strain T15 was identified as *Burkholderia* sp. The results showed that, after 21 days of culture, the degradation rates of ferulic acid, p-coumaric acid, vanillin and sinapic acid by strain H16, strain T79, strain T15 and strain T58 were 100%, respectively. Additionally, the degradation rates of gallic acid by the four strains were also 100%. In this study, it was found that the four strains of autotoxin-degrading bacteria had good degradation effects on various phenolic acids, which could not only alleviate the toxic effects of phenolic acids on muskmelon, but also promote the growth of muskmelon seedlings.

Keywords: muskmelon; autotoxins; phenolic acids; autotoxin-degrading bacteria; HPLC

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1. Introduction

Muskmelon (*Cucumis melon* L.), as an economically important vegetable crop, is widely cultivated worldwide [1]. As the demand for muskmelon continues to grow, its planting area in China is also increasing. The continuous cropping obstacle in the process of intensive muskmelon planting is becoming increasingly serious [2]. Continuous cropping obstacles can lead to weakened growth, reduced yields, lower quality and increased soil-borne pests and diseases in successive crops of the same or closely related crops, even if they are under normal cultivation management [3,4]. The main reasons for continuous cropping obstacles include the deterioration of the soil's physical and chemical properties, the changes in the soil microbial community, and the autotoxicity of autotoxins [5,6]. Autotoxicity is when crops release substances to inhibit the growth of the same plant or family plants through root exudates, aboveground leaching and plant stubble decomposition [7,8]. Phenolic acids are the main components of autotoxins [9–13]. Phenolic acids can inhibit plant growth by affecting the plant membrane system, photosynthesis, enzyme activity, soil microbial activity and the soil's physical and chemical properties [14–17]. The accumulation of phenolic acids can change the structure of the soil microbial community, transform soil microorganisms from bacterial to fungal, and increase pathogenic microorganisms [18,19]. It is difficult to eliminate phenolic acids through physical or chemical methods. Reducing the accumulation of phenolic acids has become an urgent problem to be solved [20].

Studies have shown that the autotoxins of phenolic acids secreted by muskmelon accumulate with the increase in planting years, and the accumulation of these phenolic acids is an important reason for the continuous cropping obstacles of muskmelon [21–24].

The phenolic acids in muskmelon autotoxins mainly include gallic acid, salicylic acid, ferulic acid, vanillic acid, syringic acid, vanillin, coumaric acid, ferulic acid, phthalic acid, p-hydroxybenzoic acid, benzoic acid, cinnamic acid and so on [25–28]. Previous studies have reported that the total content of phenolic acids in muskmelon continuous cropping soil for three years is significantly higher than that in non-continuous cropping soil [29]. At present, there are few reports on the muskmelon autotoxin-degrading strains. For example, *Trichoderma harzianum* and *Trichoderma viride* could degrade three autotoxins of muskmelon [30].

Compared with organic fertilizer or grafting, the use of strains that can efficiently degrade phenolic acids is more conducive to the sustainable development of agriculture [31,32], and is expected to become an economical and effective measure [33,34].

In this study, four strains of autotoxin-degrading bacteria were isolated from the continuous cropping soil of muskmelon and muskmelon plants and were screened in the laboratory. The degradation effects of ten phenolic acids were determined by HPLC. This study found that four strains of autotoxin-degrading bacteria had significant degradation effects on various phenolic acids, such as gallic acid, ferulic acid, p-coumaric acid, vanillin and sinapic acid.

2. Materials and Methods

2.1. Test Materials

The tested muskmelon variety was a thin-skinned muskmelon named "Super Sweet" (produced by Xin Shuo Seed Industry Co., Ltd., Changchun, China). The tested soil samples were collected from the muskmelon experimental protected area of Shenyang Agricultural University, and the rhizosphere soil of muskmelon was taken for 1 year, 2 years and 3 years of continuous cropping. Tested phenolic acids were ferulic acid, caffeic acid, cinnamic acid, salicylic acid, vanillin, gallic acid, protocatechuic acid, vanillic acid, p-coumaric acid and sinapic acid.

Nutritional broth medium (NB): peptone 10 g; beef powder 3 g; sodium chloride 5 g; distilled water 1000 mL.

Basic salt medium: KH_2PO_4 1.3 g; Na_2HPO_4 0.12 g; $CaCl_2$ 0.5 g; $MgSO_4 \cdot 7H_2O$ 0.5 g; K_2HPO_4 1 g; NaCl 0.5 g; distilled water 1000 mL.

Screening medium: ferulic acid, caffeic acid, cinnamic acid, salicylic acid, vanillin, gallic acid, protocatechuic acid, vanillic acid, p-coumaric acid and sinapic acid were added to the basic salt medium. The final concentration of each component was 25 mg/L, and 20 g of agar powder were added to the solid medium.

2.2. Isolation, Screening and Identification of Strains

2.2.1. Isolation and Preliminary Screening of Strains

Muskmelon rhizosphere soil bacteria: The muskmelon rhizosphere soil (10 g) was added to a triangular flask containing 90 mL of sterile water, and a soil solution with a concentration of 10^{-1} was prepared after fully shaking and mixing. After the soil solution had stood and precipitated, 1 mL of the supernatant was taken, and soil solutions with concentrations of 10^{-2}, 10^{-3}, 10^{-4}, 10^{-5}, and 10^{-6} were prepared by the gradient dilution method. A total of 100 µL of soil solution at each concentration were added to the solid screening medium plate containing ten phenolic acids, which were evenly coated. Each concentration was replicated three times, and sterile water was used as the control group. The culture dishes were placed in a 37 °C incubator, and the results were observed after 48 h.

Muskmelon endophytic bacteria: The stems and leaf parts of muskmelon plants at four true leaf stages were selected and then rinsed with sterile water and dried. The plants were cut to about 1 cm, disinfected with 75% alcohol and 0.5% sodium hypochlorite for 1 min and 5 min, respectively, and rinsed with sterile water 3 times. The plant fragments were placed in a mortar, ground into a slurry, and diluted with sterile water into a solution. A total of 100 µL of the solution were added to the solid screening medium plate containing ten phenolic acids, and evenly coated. The sterile water was used as the control group. All

treatments were replicated three times. The culture dishes were placed in a 37 °C incubator, and the results were observed after 48 h.

2.2.2. Rescreening of Strains

After the colonies grew on the primary screening plate, single colonies were picked and streaked on a solid screening medium plate containing ten phenolic acids. The single colonies were streaked and separated 3–4 times, then purified and cultured.

After the purified strains were activated by NB medium, the bacteria fermentation broth was placed in a centrifuge tube, centrifuged at 5000 r/min for 10 min, and the supernatant was discarded. The bacteria were washed and diluted with the basic salt medium solution, and the NB medium was removed to prepare a bacteria solution with a concentration of 10^8 cfu/mL. The bacteria solution was inoculated into the screening medium solution containing ten phenolic acids at 5% inoculation amount and was cultured in a constant-temperature oscillation incubator at 37 °C in the dark. The control group was inoculated with the same amount of sterile water. After 7 days of culture, 1 mL of the degradation solution was taken and filtered with a 0.22 μm microporous membrane. The degradation rates of phenolic acids were determined by HPLC. The strains were screened for use, which could degrade phenolic acids.

2.2.3. Identification of Strains

After the screened strains were activated, the DNA of the strains was extracted by the Shanghai Sangon Ezup column bacterial genomic DNA extraction kit. After the DNA sample extraction was complete, DNA concentration was detected by an ultra-micro spectrophotometer. PCR amplification was performed using bacterial universal primers, and the amplified products were detected by gel electrophoresis. The primers were 27F: 5′-AGAGTTTGATCCTGGCTCAG-3′; 1492R: 5′-GGTTACCTTGTTACGACTT-3′. The PCR reaction conditions were as follows: pre-denaturation at 94 °C for 4 min; 30 cycles (94 °C denaturation 45 s, 55 °C annealing 45 s, 72 °C extension 1 min); an extended culture at 72 °C for 10 min; 4 °C heat preservation [35,36]. A total of 10 μL of PCR amplification products were detected by 1% agarose gel electrophoresis and viewed in the gel imaging system.

The PCR products were sent to Shanghai Sangon Bioengineering Co., Ltd. (Shanghai, China) for sequencing. The 16S rDNA sequences of the determined strains were submitted to GenBank for Blast homology comparison, and the 16S rDNA sequences of the model strains with higher homology were found for comparison. The sequences of the model strains that had high similarity with the measured strains were downloaded and imported into Mega11 software (version 11.0.13). The phylogenetic tree was constructed by the neighbor-joining method. The number of self-expansions was set to 1000, and the genetic relationship with the model strains was analyzed. The 16S rDNA sequences of the strains were submitted to GenBank to obtain the sequence accession numbers.

2.3. Determination of the Degradation Effect of Autotoxin-Degrading Bacteria on Phenolic Acids

2.3.1. Preparation of Phenolic Acid Solution

Each standard of phenolic acid in Section 2.1 was dissolved in methanol to prepare standard solutions with mass concentrations of 1000 mg/L. The standard solutions of 1000 mg/L were diluted with methanol to 10 mg/L, 20 mg/L, 40 mg/L, 80 mg/L and 160 mg/L, respectively, filtered with a 0.22 μm microporous membrane, and stored at 4 °C in the dark.

2.3.2. HPLC Conditions

The Agilent 1260 high-performance liquid chromatograph was used for sample detection. Chromatographic column: Agilent Zorbax SB-C18 (250 mm × 4.6 mm × 5 μm); column temperature: 30 °C; flow rate: 1 mL/min; injection volume: 10 μL; mobile phase A: methanol (chromatographic grade); mobile phase B: 0.5% aqueous acetic acid solution (chromatographic

grade); the detection wavelength was determined according to the maximum absorption wavelength of each phenolic acid, ranging from 225 nm to 329 nm. The linear gradient elution conditions were 0.0–15.0 min, 30% mobile phase A + 70% mobile phase B; 15–16.0 min, 50% mobile phase A + 50% mobile phase B; 16.0–30.0 min, 70% mobile phase A + 30% mobile phase B; and 30.0–40.0 min, 100% mobile phase A + 0% mobile phase B.

2.3.3. Standard Curve Drawing of Phenolic Acids

Using the Agilent off-line working platform (C.01.07SR2), according to the data of the standard solution detection in Section 2.3.1, the standard curves of phenolic acids were drawn. The concentration of the standard solution was taken as the abscissa, and the signal area detected by the standard solution was taken as the ordinate. The standard curves were drawn by the five-point drawing method, and the standard curves and regression equations of each standard solution were obtained.

2.3.4. Determination of the Degradation Effect of Phenolic Acids by Autotoxin-Degrading Bacteria

After the strain was activated by the NB medium, the bacteria fermentation broth was placed in a centrifuge tube, centrifuged at 5000 r/min for 10 min, and the supernatant was discarded. The bacteria were washed and diluted with the basic salt medium solution, and the NB medium was removed to prepare a bacteria solution with a concentration of 10^8 cfu/mL.

Phenolic acid was added to the basic salt medium to a concentration of 25 mg/L, and then 50 mL of solution were placed in the 150 mL triangular flask. Each triangular flask was inoculated with 10^8 cfu/mL bacteria solution at a 5% inoculation amount and cultured in a constant-temperature oscillation incubator at 37 °C in the dark. The control group was inoculated with the same amount of sterile water. After 0 day, 7 days, 14 days and 21 days, the degradation solution was taken and filtered with a 0.22 μm microporous membrane. The content of phenolic acid in the degradation solution was detected by HPLC, and the degradation rate of each phenolic acid was calculated, as shown below:

Degradation rate (%) $= \frac{C_{ck} - C_t}{C_{ck}} \times 100$, where C_{ck} is the phenolic acid concentration of the control group, and C_t is the phenolic acid concentration of the treatment group.

2.4. Pot Experiments

2.4.1. Autotoxin-Degrading Bacteria Alleviate the Toxic Effects of Phenolic Acids on Muskmelon

The soil of the unplanted cucurbitaceae plants was air-dried and fully mixed. Each pot was placed in 5 kg of soil, and ten phenolic acids were added to the soil at concentrations of 25 mg/kg. The treatment of adding the same amount of sterile water without phenolic acids was used as the control group CK. Each pot except the CK group was inoculated with 10^8 cfu/mL bacteria solution at a 5% inoculation amount. The treatment of adding the same amount of sterile water without inoculating the bacteria solution was used as the control group CKP. There were 6 treatments in this experiment, with 10 pots in each treatment. The seedlings were raised in nutrient pots. When the muskmelon seedlings grew to two true leaves, they were selected for transplanting with basically the same growth and plant height. Three seedlings were transplanted into each pot. After 21 days of transplanting, the plant height, root length, fresh weight, dry weight and phenolic acid content in the soil were measured.

2.4.2. Determination of Degradation Effect of Phenolic Acids by Autotoxin-Degrading Bacteria in the Soil

The soil samples were naturally dried in the shade after removing impurities, and then ground and sieved. The phenolic acids in the soil were extracted according to the method of Dalton [37]. A total of 25 g of each soil sample were placed in a 50 mL centrifuge tube, and 25 mL of 1 mol/L sodium hydroxide solution were added. The samples were shaken for 1 h, ultrasonically oscillated for 30 min, and fully mixed. After standing for 24 h, the samples were shaken at 200 r/min for 30 min and centrifuged at 8000 r/min for

10 min. The supernatant was separated, and the pH value of the samples was adjusted to 2.5 with 12 mol/L hydrochloric acid to precipitate humic acid. After standing for 2 h, the supernatant was centrifuged at 8000 r/min for 10 min to remove the precipitate. The supernatant was stored at 4 °C for analysis. The chromatographic conditions and methods for the determination of phenolic acids by HPLC were the same as in Section 2.3.4.

2.5. Stability Detection of Degradation Ability of Autotoxin-Degrading Bacteria

The strains were subcultured once every 3 days for 20 generations in the laboratory. In order to detect the stability of the degradation ability of the strains, the degradation rates of phenolic acids by the strains that were subcultured for 0–20 generations were determined.

3. Results

3.1. Isolation and Screening of Autotoxin-Degrading Bacteria

According to the growth status of the initial screening, 234 strains of bacteria were obtained. Among them, 75 strains were isolated from the 1-year continuous cropping soil of muskmelon, 80 strains were isolated from the 2-year continuous cropping soil, 62 strains were isolated from the 3-year continuous cropping soil, and 17 strains of endophytic bacteria were isolated from muskmelon plants. A total of nine strains of bacteria were obtained by re-screening, all of which had obvious degradation effects on phenolic acids.

3.2. Identification of Autotoxin-Degrading Bacteria

The PCR amplification product was detected by gel electrophoresis, and a product with the length of about 1500 bp was obtained. Under the gel imaging system, the electrophoresis bands were clear, and there was no degradation trace (Figure 1).

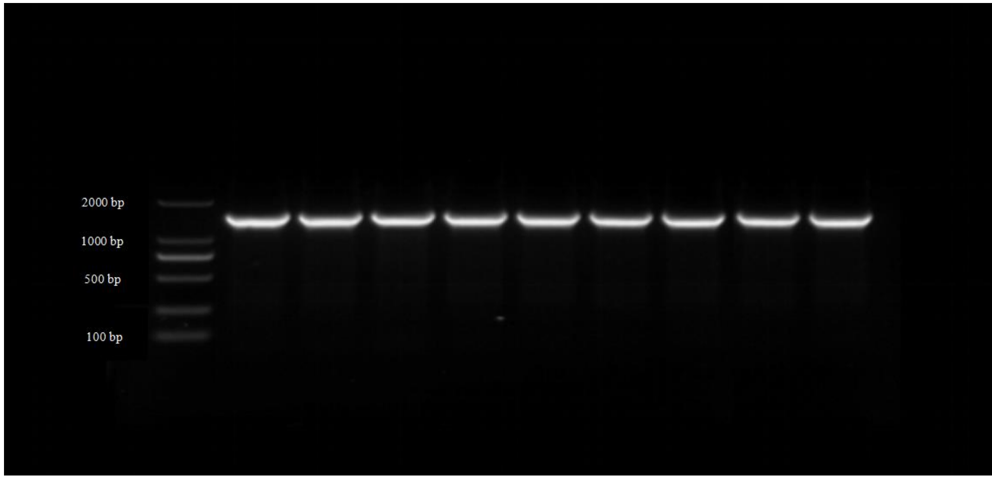

Figure 1. 16S rDNA-PCR electrophoresis maps of autotoxin-degrading bacteria T15, T31, T58, T79, T113, T147, T182, T194 and H16.

According to the results of the 16S rDNA sequence homology and phylogenetic tree, all strains except for H16 belonged to *Burkholderia* sp. and had a high similarity with strain H16. Strain H16 belonged to *Pseudomonas* sp.; T58(OQ733247) and T194(OQ733254) were preliminarily identified as *Burkholderia* sp.; T79(OQ733251) and T147(OQ733253) were *Burkholderia* sp.; T15(OQ733249), T31(OQ733248), T113(OQ733252) and T182(OQ733255) were *Burkholderia* sp.; H16(OQ733257) was *Pseudomonas* sp. (Figure 2).

Burkholderia sp. strain T58, *Burkholderia* sp. strain T79, *Burkholderia* sp. strain T15 and *Pseudomonas* sp. strain H16 were selected in the following experiment.

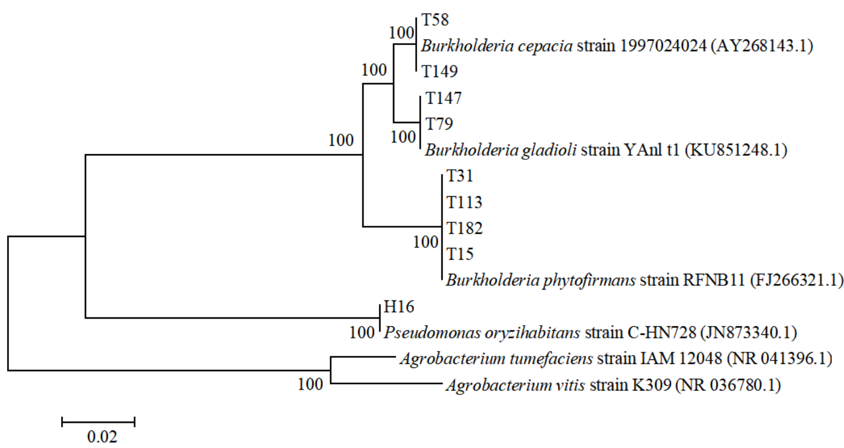

Figure 2. Phylogenetic tree of autotoxin-degrading bacteria.

3.3. Standard Curve of Phenolic Acid Solution

According to the results of the HPLC, the regression equation of each phenolic acid (Table 1) could be obtained. The results showed that when the concentration of each phenolic acid ranged from 10 mg/L to 160 mg/L, the peak area had a good linear relationship with its concentration. This regression equation can be used in future detection work.

Table 1. Regression equations of phenolic acids and related parameters.

Number	Phenolic Acid	Regression Equation	Correlation	Detection Wavelength	Retention Time (min)
1	Ferulic acid	y = 121.34 − 85.90	0.99990	310	12.007
2	Caffeic acid	y = 104.42x − 105.53	0.99919	323	7.773
3	Cinnamic acid	y = 173.84x + 73.20	0.99975	270	19.772
4	Salicylic acid	y = 36.60x − 2.39	0.99990	300	16.267
5	Vanillin	y = 89.79x − 0.75	0.99999	275	9.633
6	Gallic acid	y = 67.86x + 2.14	1.00000	273	3.139
7	Protocatechuic acid	y = 74.96x + 11.96	0.99999	260	4.658
8	Vanillic acid	y = 76.64x + 3.53	0.99997	260	7.759
9	p-Coumaric acid	y = 247.96x + 37.29	0.99999	310	11.432
10	Sinapic acid	y = 79.41x − 5.13	0.99998	320	12.863

Note: x represents the concentration of phenolic acids (mg/L), y represents the peak area.

3.4. Degradation of Phenolic Acids by Autotoxin-Degrading Bacteria

With the extension of culture time, the degradation rates gradually increased. The four strains had significant degradation effects on the ten phenolic acids. After 21 days of culture, the degradation rates of gallic acid by the four strains were 100%. The degradation rates of ferulic acid and p-coumaric acid by strain H16 and strain T79 were 100%. The degradation rate of vanillin by strain T15 was 100%. The degradation rate of sinapic acid by strain T58 and strain T79 was 100%.

Table 2 shows that strain T58 had different degradation effects on the ten phenolic acids after seven days of culture, but the degradation effects were not obvious. After 14 days of culture, the concentration of phenolic acids changed significantly, and the degradation rate of sinapic acid was the highest, reaching 63.77%. After 21 days of culture, the degradation rates of the different phenolic acids were significantly different. The degradation rates of sinapic acid and gallic acid were the highest (100%), and there were significant differences between the degradation rates of other phenolic acids. The degradation rate of salicylic acid was 98.09%. The degradation rates of cinnamic acid and p-coumaric acid were 89.04% and 75.35%, respectively. The degradation rates of ferulic acid, caffeic acid, vanillin, protocatechuic acid and vanillic acid were between 30.44% and 41.77%, and all were lower than 50%. The results showed that strain T58 could not only efficiently degrade sinapic

acid, gallic acid, salicylic acid, cinnamic acid and p-coumaric acid, but also have different degrees of degradation effects on the other five phenolic acids.

Table 2. Degradation rates of 10 phenolic acids by *Burkholderia* sp. strain T58.

Phenolic Acid	Concentration of Phenolic Acid (mg/L)				Degradation Rate (%)		
	0 day	7 days	14 days	21 days	7 days	14 days	21 days
Ferulic acid	25.06 ± 0.18 d	21.61 ± 0.33 b	16.57 ± 0.45 d	14.59 ± 0.30 d	13.75 ± 0.70 cd	33.88 ± 1.31 cd	41.77 ± 0.77 e
Caffeic acid	25.16 ± 0.33 d	23.75 ± 0.17 a	18.16 ± 0.82 c	15.62 ± 0.11 c	5.59 ± 1.88 f	27.80 ± 4.15 e	37.92 ± 0.48 f
Cinnamic acid	25.99 ± 0.54 bc	20.49 ± 1.14 c	19.58 ± 0.28 b	2.85 ± 0.11 f	21.09 ± 5.75 ab	24.67 ± 1.63 e	89.04 ± 0.39 c
Salicylic acid	26.09 ± 0.07 bc	20.33 ± 0.84 c	15.14 ± 0.13 f	0.50 ± 0.06 g	22.09 ± 3.03 ab	41.98 ± 0.34 b	98.09 ± 0.23 b
Vanillin	26.88 ± 0.04 a	21.63 ± 0.37 b	18.52 ± 0.17 c	16.91 ± 0.10 b	19.54 ± 1.44 ab	31.09 ± 0.70 d	37.08 ± 0.44 g
Gallic acid	25.80 ± 0.69 c	20.39 ± 0.57 c	16.59 ± 0.29 d	0.00 ± 0.00 h	20.87 ± 4.37 ab	35.62 ± 2.85 c	100 ± 0.00 a
Protocatechuic acid	26.48 ± 0.29 ab	23.45 ± 0.12 a	19.73 ± 0.11 ab	17.35 ± 0.05 a	11.40 ± 1.40 de	25.46 ± 0.78 e	34.45 ± 0.88 h
Vanillic acid	25.13 ± 0.13 d	23.48 ± 0.54 a	20.25 ± 0.05 a	17.48 ± 0.04 a	6.58 ± 2.62 ef	19.44 ± 0.60 f	30.44 ± 0.46 i
p-Coumaric acid	26.76 ± 0.08 a	21.97 ± 0.70 b	15.83 ± 0.20 e	6.60 ± 0.12 e	17.88 ± 2.71 bc	40.86 ± 0.84 b	75.35 ± 0.47 d
Sinapic acid	25.87 ± 0.13 c	19.46 ± 0.21 c	9.37 ± 0.07 g	0.00 ± 0.00 h	24.77 ± 0.46 a	63.77 ± 0.28 a	100 ± 0.00 a

Different lowercase letters in rows indicate significant differences at $p < 0.05$.

Table 3 shows that strain T79 had different degrees of degradation effects on the ten phenolic acids after seven days of culture, and the degradation rate of ferulic acid was significantly higher than those of the other phenolic acids. The concentration of ferulic acid in the degradation solution decreased rapidly, and the degradation rate was the highest. After 14 days of culture, the concentration of phenolic acids changed significantly, and the degradation rates of ferulic acid, sinapic acid, p-coumaric acid, cinnamic acid, gallic acid and salicylic acid were higher than those of the the other phenolic acids. After 21 days of culture, the degradation rates of ferulic acid, sinapic acid and p-coumaric acid were the highest, which were 100%, and there were significant differences between the degradation rates of other phenolic acids. The degradation rates of gallic acid, salicylic acid and cinnamic acid were 98.47%, 98.27% and 92.38%, respectively. The degradation rates of vanillin, protocatechuic acid, caffeic acid and vanillic acid were between 34.29% and 46.23%, and all were lower than 50%. The results showed that strain T79 could not only efficiently degrade ferulic acid, sinapic acid, p-coumaric acid, gallic acid, salicylic acid and cinnamic acid, but also have different degrees of degradation effects on the other four phenolic acids.

Table 3. Degradation rates of 10 phenolic acids by *Burkholderia* sp. strain T79.

Phenolic Acid	Concentration of Phenolic Acid (mg/L)				Degradation Rate (%)		
	0 day	7 days	14 days	21 days	7 days	14 days	21 days
Ferulic acid	25.10 ± 0.11 d	1.09 ± 0.09 h	0.64 ± 0.04 i	0.00 ± 0.00 g	95.64 ± 0.32 a	97.44 ± 0.19 a	100.00 ± 0.00 a
Caffeic acid	25.12 ± 0.07 d	23.18 ± 0.10 b	18.37 ± 0.06 b	15.87 ± 0.06 b	7.75 ± 0.53 gh	26.90 ± 0.36 i	36.84 ± 0.21 f
Cinnamic acid	26.59 ± 0.18 b	19.55 ± 0.13 d	6.88 ± 0.15 f	2.03 ± 0.11 e	26.47 ± 0.03 e	74.13 ± 0.72 d	92.38 ± 0.37 c
Salicylic acid	26.10 ± 0.09 c	17.69 ± 0.28 e	8.92 ± 0.09 d	0.45 ± 0.04 f	32.24 ± 0.84 d	65.81 ± 0.46 f	98.27 ± 0.13 b
Vanillin	26.85 ± 0.11 a	22.7 ± 0.21 c	17.28 ± 0.27 c	14.44 ± 0.31 d	15.46 ± 0.43 f	35.66 ± 0.74 g	46.23 ± 0.92 d
Gallic acid	25.98 ± 0.12 cd	19.42 ± 0.10 d	7.39 ± 0.09 e	0.40 ± 0.03 f	25.23 ± 0.70 e	71.55 ± 0.46 e	98.47 ± 0.09 b
Protocatechuic acid	26.43 ± 0.11 b	24.62 ± 0.51 a	18.38 ± 0.15 b	15.04 ± 0.07 c	6.85 ± 2.28 h	30.47 ± 0.27 h	43.08 ± 0.03 e
Vanillic acid	25.04 ± 0.14 d	22.80 ± 0.05 c	20.38 ± 0.07 a	16.46 ± 0.01 a	8.95 ± 0.47 g	18.62 ± 0.60 j	34.29 ± 0.35 g
p-Coumaric acid	26.84 ± 0.03 a	13.29 ± 0.02 g	6.28 ± 0.03 g	0.00 ± 0.00 g	50.50 ± 0.05 b	76.62 ± 0.10 c	100.00 ± 0.00 a
Sinapic acid	25.87 ± 0.08 d	14.06 ± 0.06 f	3.50 ± 0.02 h	0.00 ± 0.00 g	45.63 ± 0.25 c	86.46 ± 0.05 b	100.00 ± 0.00 a

Different lowercase letters in rows indicate significant differences at $p < 0.05$.

Table 4 shows that strain H16 had different degrees of degradation effects on the ten phenolic acids after seven days of culture, and the degradation rates were significantly different. The concentration of ferulic acid in the degradation solution decreased rapidly, and the degradation rate was the highest. After 14 days of culture, the concentration of each phenolic acid changed significantly, and the degradation rates of ferulic acid, p-coumaric acid, salicylic acid, gallic acid and sinapic acid were higher than those of the other phenolic acids. After 21 days of culture, the degradation rates of the different phenolic acids were significantly different. The degradation rates of ferulic acid and p-coumaric acid were the highest, which were 100%, and there were significant differences between the degradation rates of other phenolic acids. The degradation rates of gallic acid and salicylic acid were

99.20% and 95.94%, respectively. The degradation rates of sinapic acid, cinnamic acid, vanillin and protocatechuic acid were 69.97%, 69.63%, 52.85% and 51.61%, respectively. The degradation rates of caffeic acid and vanillic acid were 43.80% and 42.26%, which were lower than 50%. The results showed that strain H16 could not only efficiently degrade ferulic acid, p-coumaric acid, gallic acid, salicylic acid, sinapic acid and cinnamic acid, but also have different degrees of degradation effects on the other four phenolic acids.

Table 4. Degradation rates of 10 phenolic acids by *Pseudomonas* sp. strain H16.

Phenolic Acid	Concentration of Phenolic Acid (mg/L)				Degradation Rate (%)		
	0 day	7 days	14 days	21 days	7 days	14 days	21 days
Ferulic acid	25.08 ± 0.04 f	1.04 ± 0.04 h	0.63 ± 0.01 j	0.00 ± 0.00 i	95.84 ± 0.13 a	97.47 ± 0.05 a	100.00 ± 0.00 a
Caffeic acid	25.05 ± 0.06 f	23.75 ± 0.09 a	17.73 ± 0.09 b	14.08 ± 0.07 b	5.19 ± 0.17 j	29.22 ± 0.20 i	43.80 ± 0.13 h
Cinnamic acid	26.56 ± 0.07 b	19.62 ± 0.03 d	10.98 ± 0.05 e	8.06 ± 0.06 e	26.13 ± 0.28 f	58.65 ± 0.28 f	69.63 ± 0.31 e
Salicylic acid	26.08 ± 0.03 d	18.37 ± 0.02 e	8.23 ± 0.02 h	1.06 ± 0.03 g	29.57 ± 0.10 d	68.43 ± 0.09 c	95.94 ± 0.12 c
Vanillin	26.84 ± 0.05 a	22.8 ± 0.01 c	15.16 ± 0.03 d	12.65 ± 0.04 d	15.05 ± 0.17 g	43.53 ± 0.11 g	52.85 ± 0.05 f
Gallic acid	25.94 ± 0.07 e	18.35 ± 0.06 e	8.79 ± 0.03 g	0.21 ± 0.01 h	29.23 ± 0.38 e	66.11 ± 0.19 d	99.20 ± 0.02 b
Protocatechuic acid	26.47 ± 0.03 c	22.84 ± 0.02 c	15.62 ± 0.05 c	12.81 ± 0.03 c	13.69 ± 0.01 h	40.98 ± 0.15 h	51.61 ± 0.09 g
Vanillic acid	25.04 ± 0.04 f	23.64 ± 0.03 b	19.52 ± 0.05 a	14.46 ± 0.05 a	5.61 ± 0.22 i	22.08 ± 0.06 j	42.26 ± 0.29 i
p-Coumaric acid	26.83 ± 0.08 a	4.11 ± 0.01 g	1.68 ± 0.03 i	0.00 ± 0.00 i	84.69 ± 0.05 b	93.72 ± 0.11 b	100.00 ± 0.00 a
Sinapic acid	25.87 ± 0.03 e	16.23 ± 0.02 f	9.57 ± 0.04 f	7.77 ± 0.02 f	37.23 ± 0.13 c	63.01 ± 0.19 e	69.97 ± 0.02 d

Different lowercase letters in rows indicate significant differences at $p < 0.05$.

Table 5 shows that strain T15 had different degrees of degradation effects on the ten phenolic acids after seven days of culture, and the degradation rates were significantly different. The concentration of vanillin in the degradation solution decreased rapidly, and the degradation rate was the highest. After 14 days of culture, the concentration of phenolic acids changed significantly, and the degradation rates of vanillin, gallic acid, sinapic acid and salicylic acid were higher than those of the other phenolic acids. After 21 days of culture, the degradation rates of different phenolic acids were significantly different. The degradation rate of vanillin was 100%, and there were significant differences between the degradation rates of other phenolic acids. The degradation rates of gallic acid, salicylic acid and cinnamic acid were 99.00%, 96.38% and 91.55%, respectively. The degradation rates of coumaric acid, sinapic acid, ferulic acid and protocatechuic acid were 80.65%, 69.99%, 66.48% and 54.70%, respectively. The degradation rates of vanillic acid and caffeic acid were 48.37% and 38.90%, which were all lower than 50%. The results showed that strain T15 could not only efficiently degrade vanillin, gallic acid, salicylic acid, cinnamic acid, p-coumaric acid, sinapic acid and ferulic acid, but also have different degrees of degradation effects on the other three phenolic acids.

Table 5. Degradation rates of 10 phenolic acids by *Burkholderia* sp. strain T15.

Phenolic Acid	Concentration of Phenolic Acid (mg/L)				Degradation Rate (%)		
	0 day	7 days	14 days	21 days	7 days	14 days	21 days
Ferulic acid	25.08 ± 0.04 g	20.64 ± 0.09 c	15.85 ± 0.10 d	8.41 ± 0.02 d	17.74 ± 0.23 f	36.79 ± 0.43 h	66.48 ± 0.03 g
Caffeic acid	25.07 ± 0.02 g	22.23 ± 0.02 b	18.75 ± 0.04 a	15.32 ± 0.01 a	11.30 ± 0.02 g	25.19 ± 0.08 j	38.90 ± 0.05 j
Cinnamic acid	26.54 ± 0.04 b	18.46 ± 0.05 e	11.12 ± 0.05 e	2.24 ± 0.03 g	30.45 ± 0.10 e	58.11 ± 0.25 f	91.55 ± 0.11 d
Salicylic acid	26.12 ± 0.03 d	16.38 ± 0.05 g	9.08 ± 0.06 g	0.95 ± 0.02 h	37.30 ± 0.17 c	65.26 ± 0.19 c	96.38 ± 0.06 c
Vanillin	26.85 ± 0.07 a	13.53 ± 0.09 i	7.54 ± 0.08 i	0.00 ± 0.00 j	49.62 ± 0.32 a	71.93 ± 0.26 a	100.00 ± 0.00 a
Gallic acid	25.92 ± 0.06 e	14.11 ± 0.11 h	7.70 ± 0.03 h	0.26 ± 0.01 i	45.58 ± 0.40 b	70.29 ± 0.16 b	99.00 ± 0.05 b
Protocatechuic acid	26.44 ± 0.06 c	23.68 ± 0.04 a	16.09 ± 0.08 c	11.97 ± 0.06 c	10.41 ± 0.22 h	39.12 ± 0.41 g	54.70 ± 0.14 h
Vanillic acid	25.06 ± 0.04 g	22.26 ± 0.04 b	18.24 ± 0.04 b	12.94 ± 0.03 b	11.19 ± 0.11 g	27.21 ± 0.16 i	48.37 ± 0.11 i
p-Coumaric acid	26.81 ± 0.03 a	18.58 ± 0.03 d	10.70 ± 0.04 f	5.19 ± 0.03 f	30.69 ± 0.13 e	60.09 ± 0.16 e	80.65 ± 0.10 e
Sinapic acid	25.82 ± 0.07 f	17.38 ± 0.03 f	9.08 ± 0.03 g	7.75 ± 0.03 e	32.67 ± 0.27 d	64.81 ± 0.20 d	69.99 ± 0.06 f

Different lowercase letters in rows indicate significant differences at $p < 0.05$.

3.5. Autotoxin-Degrading Bacteria Alleviate the Toxic Effects of Phenolic Acids on Muskmelon

Figure 3 shows that the plant height, root length, fresh weight and dry weight of muskmelon seedlings in the treatment group were significantly better than those in the control group CKP and CK. The physiological indexes of CKP in the control group were the lowest, and there were significant differences between other groups. The physiological

indexes of strain T79 in the treatment group were the highest, and there were significant differences with other groups. The results showed that the four strains of autotoxin-degrading bacteria could not only alleviate the toxic effect of phenolic acids on muskmelon, but also promote the growth of muskmelon seedlings. Among the four strains of autotoxin-degrading bacteria, strain T79 had the most significant growth-promoting effects.

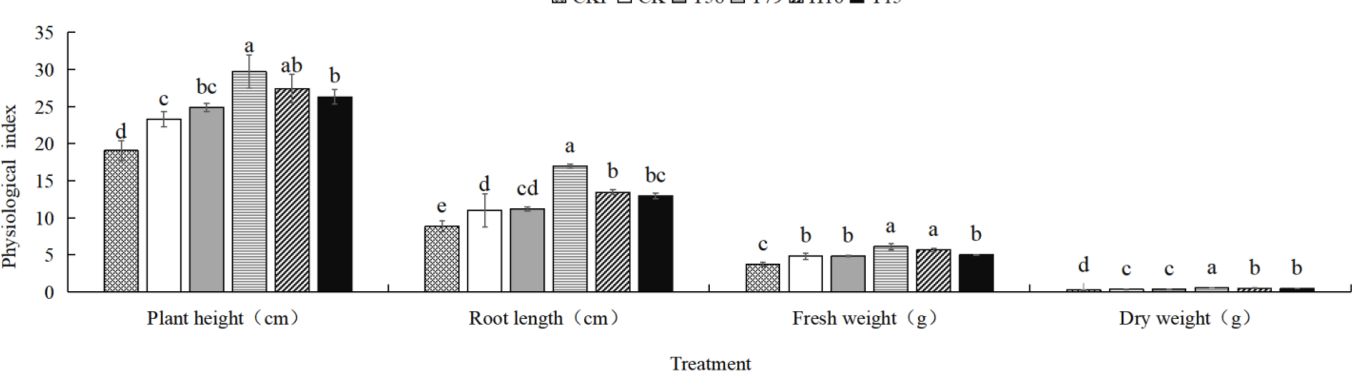

Figure 3. Autotoxin-degrading bacteria alleviate the toxic effects of phenolic acids on muskmelon. Different lowercase letters in figure indicate significant differences at $p < 0.05$.

3.6. Degradation of Phenolic Acids by Autotoxin-Degrading Bacteria in the Soil

The degradation effects of four strains of autotoxin-degrading bacteria on phenolic acids in soil were obtained by HPLC. The degradation rate of CKP in the control group was 16.29%, which was significantly lower than those in the four treatment groups. The degradation rate of strain T79 was not significantly different from that of strain T15 in the treatment group. The degradation rate of strain T79 was significantly higher than those of strain H16 and strain T58. The results showed that the content of phenolic acids in the control group decreased slowly after 21 days, while the four treatment groups had significant degradation effects on the phenolic acids, and the degradation rates were between 77.18% and 86.76%. Figure 4 shows that strain T79 was the best, which was consistent with the degradation effect under shaking flask culture in the laboratory.

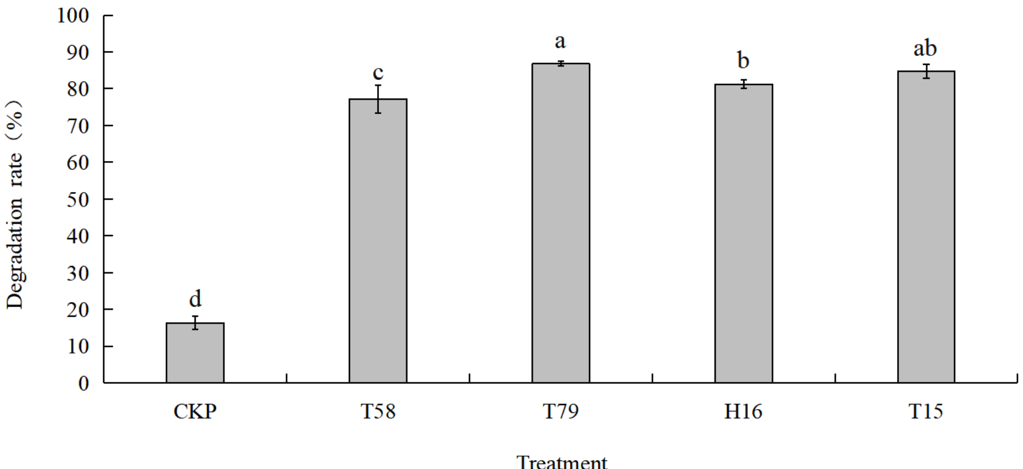

Figure 4. Degradation rates of phenolic acids by autotoxin-degrading bacteria in the soil. Different lowercase letters in figure indicate significant differences at $p < 0.05$.

3.7. Stability Detection of Degradation Ability of Autotoxin-Degrading Bacteria

The degradation rates of phenolic acids by the four strains of subculture for 0–20 generations were measured, which began to decrease slowly with the increase in subculture generations. However, the degradation rates of generation 20 were higher than

79.85% (the lowest degradation rate of generation 0 was 82.66%). For strains T58, H16 and T15, the degradation rates did not change significantly from generation 0 to generation 15 and began to change significantly from generation 20. For strain T79, the degradation rates did not change significantly from generation 0 to generation 10 but changed significantly from generation 15. However, the degradation ability of four strains after subculture was still relatively high (Figure 5), which indicates that four strains had a relatively stable ability to degrade phenolic acids.

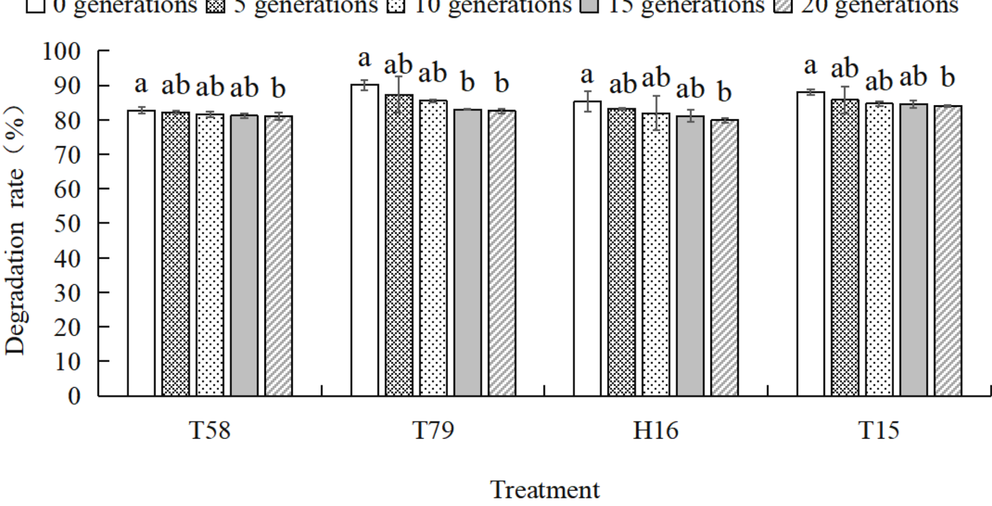

Figure 5. The stability of autotoxin-degrading bacteria on the degradation of phenolic acids. Different lowercase letters in figure indicate significant differences at $p < 0.05$.

4. Discussion

In recent years, domestic and foreign scholars have studied the biological control of continuous cropping obstacles. These studies have shown that autotoxin-degrading strains can effectively degrade phenolic acids in soil and alleviate the toxic effects of phenolic acids on plants [31]. Three strains of bacteria were screened from the continuous cropping soil of tomato, which could efficiently degrade benzoic acid, cinnamic acid and vanillic acid [38]. Cinnamic acid could be degraded up to 99% by a bacterial strain R30, which was isolated from watermelon continuous cropping soil, and was identified as *Exiguobacterium* sp. [39]. The degradation rates of phthalic acid, p-hydroxybenzoic acid and pyrogallic acid by the autotoxin-degrading bacteria, which were screened from the continuous cropping soil of apple, were higher than 50% [40]. The degradation rate of salicylic acid by the strain FD-21, which was screened from vanilla rhizosphere soil, was 93.62% [41]. Five strains of autotoxin-degrading bacteria were screened from the continuous cropping soil of ginseng, which could grow with palmitic acid as the sole carbon source, and the degradation rate of palmitic acid was close to 80% [42]. A strain of fungus was isolated from the continuous cropping soil of Chinese goldthread, which could degrade ferulic acid [43]. *Phanerochaete chrysosporium* could effectively degrade p-hydroxybenzoic acid, vanillic acid and ferulic acid under laboratory conditions, and the degradation rates were 58.20%, 98.38% and 97.88%, respectively [44]. The above studies showed that the strains that could degrade autotoxins were screened from the continuous cropping soil of plants, and most of these strains were fungi or bacteria. In this study, four strains of autotoxin-degrading bacteria that could efficiently degrade various phenolic acids were screened from the continuous cropping soil of muskmelon and muskmelon plants. This was consistent with the results of previous studies, that many strains could efficiently degrade a variety of phenolic acids with a broad substrate spectrum. Compared with the previous studies, it was found that many autotoxins of plants were the same, such as salicylic acid, cinnamic acid, ferulic acid, gallic acid, etc. Therefore, the four strains of autotoxin-degrading bacteria in this study

may be able to alleviate the continuous cropping obstacles of other plants, which needs to be further verified.

Studies have shown that phenolic acids usually undergo biochemical reactions such as decarboxylation, oxidation and hydroxylation under the degradation of microorganisms. The substituents on the benzene ring in the molecular structure are easily degraded and converted. These reactions usually lead to the degradation of macromolecular phenolic acids into small molecular phenolic acids or other small molecular organic compounds containing benzene rings [3].

Studies showed that bacteria with the ability to degrade p-hydroxybenzoic acid could significantly improve growth indexes such as the root length, leaf area, plant height and dry weight of strawberry seedlings [45]. An autotoxin-degrading strain was isolated from sludge, which could alleviate the toxic effects of phenylacrylic acid on cucumber growth by hydroponic and soil culture experiments [46]. A strain of actinomycetes was screened, which could effectively alleviate the toxic effects of ferulic acid on the growth of watermelon seedlings [47]. In the pot experiment of our study, the plant height, root length, fresh weight and dry weight of muskmelon seedlings inoculated with four autotoxin-degrading bacteria were significantly better than the control group without inoculation. In the present study, four strains of autotoxin-degrading bacteria could not only alleviate the toxic effects of phenolic acids on plants, but also promote the growth of muskmelon seedlings, which was similar to the previously reported growth-promoting effects of autotoxin-degrading bacteria on other crops.

Pseudomonas sp. is one of the preferred strains for plant rhizosphere control and growth promotion [48]. The strains of this genus have the effects of promoting plant growth, inhibiting pathogenic microorganisms and degrading autotoxins. The strains of *Pseudomonas* sp. are prominent in the degradation of autotoxins. The degradation rates of p-hydroxybenzoic acid, cinnamic acid, syringic acid, benzoic acid and ferulic acid by *Pseudomonas putida*, which was screened from peanut rhizosphere soil, were 99.85%, 17.44%, 90.04%, 98.69% and 38.89%, respectively [49]. *P. putida*, which was screened from cucumber rhizosphere soil, could degrade p-hydroxybenzoic acid [50]. In this study, *Pseudomonas* sp. strain H16 could promote the growth of muskmelon seedlings, which was consistent with the growth-promoting effects of some strains in *Pseudomonas oryzihabitans* [51].

Burkholderia sp. is a kind of beneficial microorganism that has been found in recent years to have growth-promoting effects on plant rhizosphere soil [52–54]. *Burkholderia* sp. could promote sugarcane growth through biological nitrogen fixation [55]. In this study, *Burkholderia* sp. strain T58, *Burkholderia* sp. strain T79 and *Burkholderia* sp. strain T15 could promote the growth of muskmelon seedlings, which was similar to the results of previous studies on *Burkholderia* sp. YZU-S230 [56], *Burkholderia tropica* MTo-293 [57], and *Burkholderia* sp. [58], which could promote the growth of different crops.

Previous studies showed that phenolic acids could inhibit the growth of muskmelon plants [27]. Therefore, the growth of muskmelon was promoted in this study, which might be due to the growth-promoting effects of autotoxin-degrading bacteria and the reduction in phenolic acids in the soil.

5. Conclusions

In this study, four strains of autotoxin-degrading bacteria that could efficiently degrade various phenolic acids were screened from the continuous cropping soil of muskmelon and muskmelon plants. After 21 days of culture under laboratory conditions, four strains of autotoxin-degrading bacteria had significant degradation effects on various phenolic acids. The results of the pot experiment showed that four strains of autotoxin-degrading bacteria could alleviate the toxic effects of phenolic acids on muskmelon and promote the growth of muskmelon seedlings. The four strains demonstrated good degradation ability for various phenolic acids in the soil environment. The four strains of autotoxin-degrading bacteria had a relatively stable ability to degrade phenolic acids after subculture. The results of this

study can provide a relevant theoretical basis for using autotoxin-degrading bacteria to alleviate continuous cropping obstacles of muskmelon.

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Conflicts of Interest: The authors declare no conflict of interest.

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