https://doi.org/10.26651/allelo.j/2020-50-1-1276 0971-4693/94 Euro 20.00
*Allelopathy Journal* 50 (1) : 85-94 (May, 2020) *International Allelopathy Foundation* 2020
Tables : 1 , Figs : 2

# Effects of selected root exudates components on soil *Pseudomonas* spp. community structures and abundances

S.C. Tan[1#]; J.Y. Liu[1,2#]; M. Khashi u Rahman[1]; C.L. Ma[1]; F.Z. Wu[1] and X.G. Zhou[1]*
Key Laboratory of Biology and Genetic Improvement of Horticultural Crops
(Northeast Region), Ministry of Agriculture and Rural Affairs,
Northeast Agricultural University, Harbin, China
E-mail: zxg2025@163.com; xingangzhou@yahoo.com

**(Received in revised form: April 6, 2020)**

## ABSTRACT

Plant-microbes interactions in soil are mainly driven by plant root exudates. However, how different compounds present in root exudates can affect the specific soil microbial communities has not been well studied yet. We studied the glucose, succinic, *p*-hydroxybenzoic, *p*-coumaric and glutamic acids on soil *Pseudomonas* spp. communality in a microcosm experiment. Soils were treated with these selected root exudates (20 µg carbon/g soil), and *Pseudomonas* spp. community structure and abundance were estimated by PCR-denaturing gradient gel electrophoresis and quantitative PCR, respectively. All treatments increased the abundance of *Pseudomonas* spp. community and this increase was highest in the glutamic acid treatment. Moreover, all treatments changed the *Pseudomonas* spp. community structure. All treatments, except glucose, decreased the community diversity of *Pseudomonas* spp. Our findings suggested that various organic compounds found in plant root exudates differed in their abilities to influence the soil *Pseudomonas* spp. community.

**Keywords:** Amino acid, microcosm experiment, organic acid, *Pseudomonas* spp., sugar

## INTRODUCTION

Plant roots exude a variety of organic compounds (organic acids, amino acids and sugars) as root exudates, into the soil (2). Root exudates play important roles in plant-plant and plant-microbe interactions (2,14,15,17,18,26). For example, one plant species can inhibit the growth of another species through its root exudates, a phenomenon known as allelopathy (12). These plant-microbe interactions can have strong influence on the overall performance of plants (34,39). Soil microorganisms use the root secreted components as substrates to meet their energy needs, resulting in their increased microbial biomass and activity around the roots, the so-called rhizosphere effect (2,10,21,36,41). Moreover, root exudates can act as signaling molecules for numerous microbial species in rhizosphere (1). For example, Stringlis *et al.* (30) showed that *Arabidopsis thaliana* could shape its root microbiome by releasing a phenolic compound, scopoletin.

*Pseudomonas* spp. are ubiquitous bacteria in terrestrial ecosystems and frequently found in association with plants (19). Some species in *Pseudomonas* spp. play major roles in nutrients mobilization, plant growth promotion and plant protection, hence, these are important in agriculture (9,19). It is known that microbial community composition in plant rhizosphere differed from the bulk soil (13,20,23). Evidences also suggested that, through

*Correspondence Authors, #Co-first authors, [1] Department of Horticulture, Northeast Agricultural University, Harbin, China. [2] Jilin Academy of Agricultural Sciences, Jilin, China.

root exudation, plants can select beneficial microorganisms in the rhizosphere to deter the pathogenic microorganisms and attracting the mutualistic ones (27,30). Previous studies have shown that artificially applied root exudates can change the soil microbial communities (1,4,22,28,29,42,44). Badri *et al.* (1) showed that phenolic compounds predominantly modulates the soil microbiome. However, few studies have focused on the influences of different root exudates compounds on specific bacterial communities, such as *Pseudomonas* spp.

Plant root exudates contains (i). sugars (glucose and fructose), (ii). organic acids (citric, malic and succinic acids, and phenolic acids) and (iii). amino acids (serine, glutamic acid aspartic acid) (16,25,34). Generally, phenolic acids, (*p*-hydroxybenzoic and *p*-coumaric acids) are phytotoxic to plant growth, such as cucumber (*Cucumis sativus* L.) (25,37). The phenolic acids also changes the rhizosphere bacterial community and thereby affects the plant growth (14,40,42). This study aimed to investigate how selected sugar (glucose), organic acid (succinic acid), two phenolics (*p*-hydroxybenzoic and *p*-coumaric acids) and amino acid (glutamic acid) affected the *Pseudomonas* spp. community.

## MATERIALS AND METHODS

### Microcosm experiment

A microcosm experiment was done during September to October 2016. The soil was collected from the undisturbed upper soil layer (0-15 cm) of open field in Experimental Station, Northeast Agricultural University, Harbin, China (45°41'N, 126°37'E, mean height above sea level: 127.95 m, annual precipitation: 524.5 mm, maximum and minimum temperature: 36.7 °C, -37.7 °C). The soil was sandy loam, organic matter: 3.67 %, inorganic N: 89.02 mg/kg, Olsen P: 63.36 mg/kg, available K: 119.15 mg/kg, EC (1:2.5, w/v): 0.33 mS/cm and pH (1:2.5, w/v): 7.78.

The Microcosm experiment was done in flasks containing 60 g fresh soils. To stabilize the soil microbial communities, the soils (soil water content of about 50 % water holding capacity) were pre-incubated at 20 °C in dark for 5-days. Then, $NH_4NO_3$ solution was added to these soils at 450 µg N/g soil, to avoid potential microbial growth limitation due nitrogen deficiency (29). The organic compounds (Glucose, succinic acid, *p*-hydroxybenzoic acid, *p*-coumaric acid and glutamic acid) were added into the soil periodically as described before (29). These compounds were added 5-times into soil at 20 µg C/g soil every two days. All organic compounds used were purchased from Solarbio Life Science Company, Beijing, China. Soil treated with distilled water served as control. After each addition all added solutions were uniformly mixed with soil to avoid concentration gradients. Each treatment had 5-flasks and were replicated thrice. The solution pH was adjusted to 7.0 with 0.1 M NaOH because the soil pH is major factor that regulates the soil microbial communities (8). Flasks containing treated soils were sealed with Parafilm (Bemis Company, Inc., Wisconsin, USA) and incubated at 20 °C in dark. Water contents of soil samples were maintained at 50 % water holding capacity.

### Soil DNA extraction

One day after the final application of organic compounds, 10 g fresh soil was

collected from each flask and soils from five flasks in each replicate were mixed to make a composite sample. Total soil DNA was extracted with the PowerSoil DNA Isolation Kit (MO BIO Laboratories, Carlsbad, USA) as per the manufacturer's instructions.

**Polymerase chain reaction (PCR)-denaturing gradient gel electrophoresis (DGGE) analysis**

The nested PCR protocols were used to amplify the *Pseudomonas* spp. partial 16S rDNA gene with primer set of PsF/PsR (9) in the first and second round of PCR as per (43).

DGGE analysis was done on 6 % (w/v) acrylamide gel with 30-70 % and 45-65 % denatured gradients (urea and formamide) for *Pseudomonas* spp. communities. The gel was run in a 1×TAE (Tris-acetate-EDTA) buffer for 12 h under conditions of 60 °C and 80 V with a DCode universal mutation detection system (Bio-Rad Lab, LA, USA). After electrophoresis, the gel was stained in 1:3300 (v/v) GelRed (Biotium, USA) nucleic acid staining solution for 20 min. DGGE profiles were photographed with an AlphaImager HP imaging system (Alpha Innotech Crop., CA, USA) under UV light.

**Quantitative PCR assay**

Soil *Pseudomonas* spp. community abundances were estimated by quantitative PCR assays with primer sets of PsF/PsR (9) as per (39). Standard curves were made with 10-folds dilution series of plasmids containing 16S rRNA genes from soil samples. Sterilized water was used as negative control to replace the template. All amplifications were done in triplicate. The products specificity was confirmed by melting curve analysis and agarose gel electrophoresis. The threshold cycle (*Ct*) values obtained for each sample were compared with the standard curve to determine the initial copy number of the target gene.

**Statistical analysis**

Banding patterns of the DGGE profiles were analyzed using Quantity One V4.5 (Bio-Rad Lab, LA, USA). Principal component analysis (PCA) was used to compare the banding patterns between samples with normalized data using Canoco for Windows 4.5 software (Plant Research International, Wageningen, the Netherlands). Analysis of similarities (ANOSIM) was used to test for the overall effects of treatments on microbial community structures with normalized data using the Vegan package in 'R' (Version 3.3.1). Bray-Curtis distance among treatments was calculated using the Vegan package in 'R' (Version 3.3.1). The microbial community diversity indices, including number of bands, Shannon-Wiener index and evenness index, were calculated as described before (38). Data was analyzed following analysis of variance (ANOVA) and mean comparison between treatments was performed based on the Tukey's honestly significant difference (HSD) test at 0.05 probability level.

## RESULTS AND DISCUSSION

**Soil *Pseudomonas* spp. community structure**

DGGE analyses showed that all exogenously added organic compounds changed

the soil *Pseudomonas* spp. community structure. DGGE profiles of soil *Pseudomonas* spp. community were similar in triplicate samples of each treatment but differed among the treatments (Fig 1A). Treatments of succinic acid, *p*-hydroxybenzoic acid, *p*-coumaric acid and glutamic acid had lower number of bands, Shannon-Wiener index and evenness index than treatments of water and glucose ($p$ <0.05) (Table 1). PCA analysis of soil *Pseudomonas* spp. community and DGGE banding patterns clearly separated all treatments from each other. The first two axes together accounted for 65.5 % of the total variation (Fig 1B).

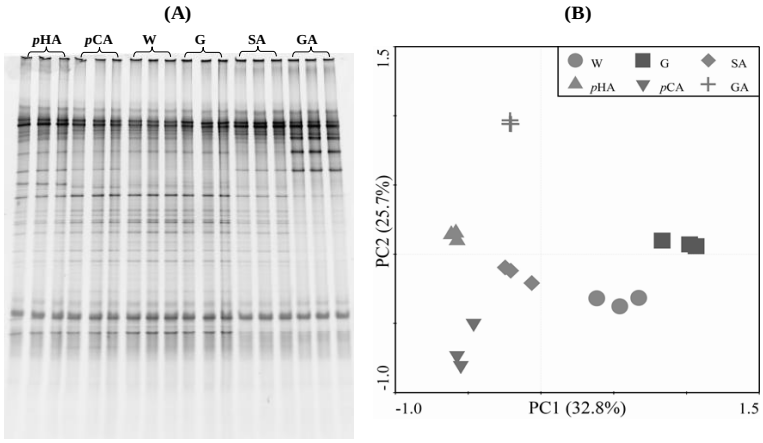


Figure 1. PCR-DGGE profile (a) and PCA analysis (b) of soil *Pseudomonas* spp. community
*W, G, SA, *p*HA, *p*CA and GA represent soils treated with water, glucose, succinic acid, *p*-hydroxybenzoic acid, *p*-coumaric acid and glutamic acid, respectively. PCR-DGGE: Polymerase chain reaction-denaturing gradient gel electrophoresis. PC: Principal component. PCA: Principal component analysis.

Table 1. Effects of root exudates selected components on soil *Pseudomonas* spp. community diversity

| Treatment | Number of bands | Shannon-Wiener | Evenness |
|---|---|---|---|
| Water | 28.33±0.58 a | 3.18±0.05 a | 0.92±0.01 a |
| Glucose | 28.67±0.58 a | 3.20±0.04 a | 0.92±0.01 a |
| Succinic acid | 25.67±0.58 b | 2.99±0.02 b | 0.86±0.01 b |
| *p*-Hydroxybenzoic acid | 18.00±0.00 c | 2.64±0.04 c | 0.76±0.01 c |
| *p*-Coumaric acid | 24.67±0.58 b | 2.99±0.05 b | 0.86±0.01 b |
| Glutamic acid | 16.00±0.00 d | 2.42±0.01 d | 0.70±0.00 d |

Notes: Values with different letters were significantly different between treatments ($p$<0.05, Tukey's HSD test).

ANOSIM analysis also confirmed that soil *Pseudomonas* spp. community structure significantly differed among the treatments ($R$ =0.999, $p$ =0.001). The Bray-Curtis distance between the treatment of water and glucose was smaller than between water and treatments of succinic acid, *p*-hydroxybenzoic acid, *p*-coumaric acid and glutamic acid ($p$

<0.05) (Fig 2A). Moreover, the Bray-Curtis distance between the treatment of water and glutamic acid was larger than that of water and organic compounds treatments ($p$ <0.05).

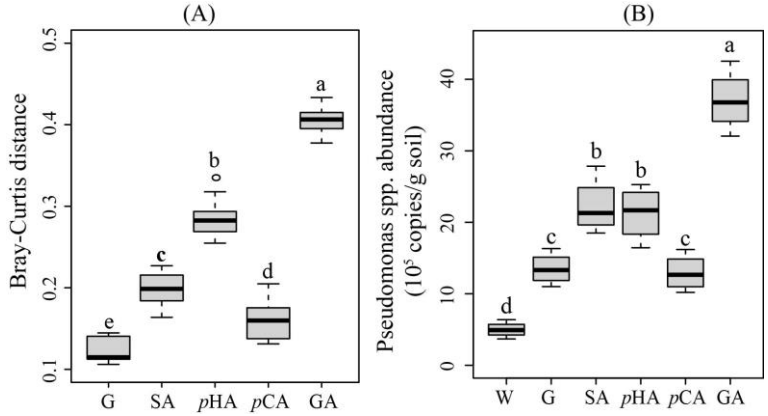


Figure 2. Bray-Curtis distances between control and treatments of organic compounds for *Pseudomonas* spp. community (A) and effects of selected root exudates components on *Pseudomonas* spp. community abundance (B). *W, G, SA, *p*HA, *p*CA and GA represent soils treated with water, glucose, succinic acid, *p*-hydroxybenzoic acid, *p*-coumaric acid and glutamic acid, respectively.

Root exudates can serve as selective agents, through which a plant regulates the microbial community in its surrounding rhizosphere (1,2,5). Previous studies have shown that different organic compounds had variable effects on the soil *Pseudomonas* spp. communities (43). Consistent with previous observations, PCA analysis showed that *Pseudomonas* spp. community structure differed in the soils treated with various organic compounds. Our results also showed that soils treated with various organic compounds harbored different *Pseudomonas* spp. community structures, thereby, different organic compounds varied in their abilities to influence the *Pseudomonas* spp. communities.

**Soil *Pseudomonas* spp. community abundance**

Quantitative PCR showed that all exogenously added organic compounds significantly increased the *Pseudomonas* spp. community abundance ($p$ < 0.05) (Fig 2B). The glutamic acid had the highest abundances of *Pseudomonas* spp. communities, while the succinic acid and *p*-hydroxybenzoic acid had higher abundances of *Pseudomonas* spp. community than glucose and *p*-coumaric acid ($p$ < 0.05).

Among all treatments, the glutamic acid had the highest *Pseudomonas* spp. community abundance. The Bray-Curtis distance between the treatment of water and glutamic acid was larger than between water and other organic compounds. These results suggested that glutamic acid had stronger influence on soil *Pseudomonas* spp. community. Contrarily, organic acid (*e.g.*, citric acid) had a stronger impact on soil bacterial community than sugar (*e.g.*, glucose) and amino acid (*e.g.*, glycine) (7). This was because we used different organic acids and amino acids than above study. Secondly, the

concentration of organic compounds used in our study (20 μg C/g soil every two days) was much lower than in study of Eilers *et al*. (7) (240 μg C/g soil), because soil microbial community's response to organic compounds is concentration-dependent. Thirdly plant root exudation rate was about 1-10 μg C/g root per hour (24,32) and plant root exudates also contained various organic compounds (2) i.e. the exudation rate of an individual compound was even lower. Therefore in our study, each organic compound was added at relative low concentration. Hence, further studies are suggested with more organic compounds to compare the relative effectiveness of organic acid, sugar and amino acid.

The phenolic acids reduces the diversity but increases the abundance of bacterial community in cucumber rhizosphere (35,40,42,43), these results were in accordance with our present study. However, phenolic acids decreased the abundance of *Pseudomonas* spp. community in cucumber rhizosphere, which is in contrast to the observations of our present study. This might be due to the fact that soil samples used in present study (bare soils) and our previous studies (cucumber rhizosphere soil) were different. Phenolic compounds disrupt the plant root cell membrane integrity and increases the ion leakage (3,37) and these changes could affect the rhizosphere microbial communities. Thus, the effects of phenolic compounds on rhizosphere communities were the combined results of direct effects of phenolic compounds and also their indirect effects through regulating the physiological status of plant.

Generally, the microbial community diversity was lower, while microbial community abundance was higher in the rhizosphere than in bulk soils (20,23). Our results showed that, except glucose, all added organic compounds decreased the diversity indices of soil bacterial and *Pseudomonas* spp. communities. The Bray-Curtis distance between the treatment of water and glucose was smaller than between the water and other organic compounds. Therefore, compared with other components of root exudates, glucose has minor role in influencing the bacterial and *Pseudomonas* spp. communities. These results agree with the observations that organic acids cause greater changes in the soil bacterial community than sugars (29).

## CONCLUSIONS

All exogenously added organic compounds (Glucose, succinic acid, *p*-hydroxybenzoic acid, *p*-coumaric acid and glutamic acid) changed the *Pseudomonas* spp. community structure and increased the abundances of *Pseudomonas* spp.; however, the effects of various organic compounds were different. Among 5-test root exudates components, the glutamic acid was prominent, while glucose and *p*-coumaric acids were least effective. These findings suggested that these compounds stimulated certain *Pseudomonas* spp. taxa, while inhibited others. Further studies are needed to determine the specific phylogenetic information of stimulated or inhibited *Pseudomonas* spp. with more advanced techniques, such as high-throughput sequencing and to illustrate the functional differences of changes in certain soil microbial communities induced by different components of root exudates.

## ACKNOWLEDGEMENTS

This work was supported by the the Natural Science Foundation of Heilongjiang Province (YQ2019C009), National Natural Science Foundation of China (31772361), Longjiang Scholars Program (Q201920) and China Agricultural Research System (CARS-23-B-10).

## REFERENCES

1. Badri, D.V., Chaparro, J.M., Zhang, R., Shen, Q. and Vivanco, J.M. (2013). Application of natural blends of phytochemicals derived from the root exudates of *Arabidopsis* to the soil reveal that phenolic-related compounds predominantly modulate the soil microbiome. *The Journal of Biological Chemistry* **288:** 4502-4512.
2. Bais, H.P., Weir, T.L., Perry, L.G., Gilroy, S. and Vivanco, J.M. (2006). The role of root exudates in rhizosphere interactions with plants and other organisms. *Annul Reviews in Plant Biology* **57:** 233-266.
3. Baziramakenga, R., Leroux, G. and Simard, R. (1995). Effects of benzoic and cinnamic acids on membrane permeability of soybean roots. *Journal of Chemical Ecology* **21:** 1271-1285.
4. Bressan, M., Roncato, M.A., Bellvert, F., Comte, G., el Zahar Haichar, F., Achouak, W. and Berge, O. (2009). Exogenous glucosinolate produced by *Arabidopsis thaliana* has an impact on microbes in the rhizosphere and plant roots. *The ISME Journal* **3:** 1243-1257.
5. Broeckling, C.D., Broz, A.K. Bergelson, J. Manter, D.K. and Vivanco, J.M. (2008). Root exudates regulate soil fungal community composition and diversity. *Applied and Environmental Microbiology* **74:** 738-744.
6. Carrillo, Y., Bell, C., Koyama, A., Canarini, A., Boot, C.M., Allenstein, M. and Pendall, E. (2017). Plant traits, stoichiometry and microbes as drivers of decomposition in the rhizosphere in a temperate grassland. *Journal of Ecology* **105:** 1750-1765.
7. Eilers, K.G., Lauber, C.L., Knight, R. and Fierer, N. (2010). Shifts in bacterial community structure associated with inputs of low molecular weight carbon compounds to soil. *Soil Biology and Biochemistry* **42:** 896-903.
8. Fierer, N. and Jackson, R.B. (2006). The diversity and biogeography of soil bacterial communities. *Proceedings, National Academy of Sciences of United States of America* **103:** 626-631.
9. Garbeva, P., van Veen, J.A. and van Elsas, J.D. (2004). Assessment of the diversity and antagonism towards *Rhizoctonia solani* AG3, of *Pseudomonas* species in soil from different agricultural regimes. *FEMS Microbiology and Ecology* **47:** 51-64.
10. Ge, T., Li, B., Zhu, Z., Hu, Y., Yuan, H., Dorodnikov, M., Jones, D.L., Wu, J. and Kuzyakov, Y. **(2017)**. Rice rhizodeposition and its utilization by microbial groups depends on N fertilization. *Biology and Fertility of Soils* **53:** 37-48.
11. Goldfarb, K.C., Karaoz, U., Hanson, C.A., Santee, C.A., Bradford, M.A., Treseder, K.K., Wallenstein, M.D. and Brodie, E.L. (2011). Differential growth responses of soil bacterial taxa to carbon substrates of varying chemical recalcitrance. *Frontiers in Microbiology* **2:** 00094.
12. Inderjit, Wardle, D.A., Karban, R. and Callaway, R.M. (2011). The ecosystem and evolutionary contexts of allelopathy. *Trends in Ecology & Evolution* **26:** 655- 662.
13. Jia, H.T., Liu, J.Y., Shi, Y.J., Li, D.L., Wu, F.Z. and Zhou, X.G. (2019). Characterization of cucumber rhizosphere bacterial community with high-throughput amplicon sequencing. *Allelopathy Journal* **47:** 103-112.
14. Jin, X. Wu, F. and Zhou, X. (2020). Different toxic effects of ferulic and *p*-hydroxybenzoic acids on cucumber seedlings growth related to their different influences on rhizosphere microbial composition. *Biology and Fertility of Soils* **56:** 125-136
15. Jin, X., Zhang, J. Shi, Y. Wu, F. and Zhou, X. (2019). Green manures of Indian mustard and wild rocket enhance cucumber resistance to Fusarium wilt through modulating rhizosphere bacterial community composition. *Plant and Soil* **441:** 283-300.

16. Kamilova, F., Kravchenko, L.V., Shaposhnikov, A.I., Azarova, T., Makarova, N. and Lugtenberg, B. (2006). Organic acids, sugars, and L-tryptophane in exudates of vegetables growing on stonewool and their effects on activities of rhizosphere bacteria. *Molecular Plant-Microbe Interactions* **19:** 250- 256.
17 Li, H.Y., Zhou, X.G. and Wu, F.Z. (2018). Effects of root exudates from potato onion on *Verticillium dahliae*. *Allelopathy Journal* **43:** 217- 222.
18 Liang, Z.Y., Li, X.Y. Zhang, H. Li, J. Bian, X.J. and Xu, J.C. (2018). Allelopathic effects of Bermuda grass (*Cynodon dactylon* L.) root exudates on seed germination and seedling growth of Tall fescue (*Festuca arundinacea* Schreb). *Allelopathy Journal* **44:** 25- 34.
19. Lugtenberg, B. and Kamilova, F. (2009). Plant-growth-promoting rhizobacteria. *Annual Review of Microbiology* **63:** 541- 556.
20. Lundberg, D.S., Lebeis, S.L., Paredes, S.H., Yourstone, S., Gehring, J., Malfatti, S., Tremblay, J., Engelbrektson, A., Kunin, V. and del Rio, T.G. (2012). Defining the core *Arabidopsis thaliana* root microbiome. Nature **488:** 86- 90.
21. Ma, X.M., Liu, Y., Zarebanadkouki, M., Razavi, B.S., Blagodatskaya, E. and Kuzyakov, Y. (2018). Spatiotemporal patterns of enzyme activities in the rhizosphere: Effects of plant growth and root morphology. *Biology and Fertility of Soils* **54:** 819- 828.
22. Paterson, E., Gebbing, T., Abel, C., Sim, A. and Telfer, G. 2006. Rhizodeposition shapes rhizosphere microbial community structure in organic soil. *New Phytologist* **173:** 600- 610.
23. Peiffer, J.A., Spor, A., Koren, O., Jin, Z., Tringe, S.G., Dangl, J.L., Buckler, E.S. and Ley, R.E. (2013). Diversity and heritability of the maize rhizosphere microbiome under field conditions. *Proceedings, National Academy of Sciences of the United States of America* **110:** 6548- 6553.
24. Phillips, R.P., Finzi, A.C. and Bernhardt, E.S. (2011). Enhanced root exudation induces microbial feedbacks to N cycling in a pine forest under long-term $CO_2$ fumigation. *Ecology Letters* **14:** 187- 194.
25. Pramanik, M.H.R., Nagai, M., Asao, T. and Matsui, Y. (2000). Effects of temperature and photoperiod on phytotoxic root exudates of cucumber (*Cucumis sativus*) in hydroponic culture. *Journal of Chemical Ecology* **26:** 1953- 1967.
26. Premathilake, U., Wathugala, D.L. and Dharmadasa, R.M. (2018). Phytotoxic potential of lemongrass (*Cymbopogon citrates* (DC.) Stapf). *Allelopathy Journal* **44:** 261-268.
27. Rudrappa, T., Czymmek, K.J., Pare, P.W. and Bais, H.P. (2008). Root-secreted malic acid recruits beneficial soil bacteria. *Plant Physiology* **148:** 1547- 1556.
28. Schneckenberger, K., Demin, D. Stahr, K. and Kuzyakov, Y. (2008). Microbial utilization and mineralization of [$^{14}$C] glucose added in six orders of concentration to soil. *Soil Biology and Biochemistry* **40:** 1981-1988.
29. Shi, S., Richardson, A.E., O'Callaghan, M., Deangelis, K.M., Jones, E.E., Stewart, A., Firestone M.K. and Condron L.M. (2011). Effects of selected root exudate components on soil bacterial communities. *FEMS Microbiology Ecology* **77:** 600-610.
30. Stringlis, I.A., Yu, K., Feussner, K., de Jonge, R., van Bentum, S., Van Verk, M.C., Berendsen, R.L., Bakker, P., Feussner I. and Pieterse C.M.J. (2018). MYB72-dependent coumarin exudation shapes root microbiome assembly to promote plant health. *Proceedings, National Academy of Sciences of the United States of America* **115:** E5213-E5222.
31. Sultana, N., Zhao, J., Zheng, Y., Cai, Y.F., Faheem, M., Peng, X.L., Wang, W.D. and Jia, Z.J. (2019). Stable isotope probing of active methane oxidizers in rice field soils from cold regions. *Biology and Fertility of Soils* **55:** 243-250.
32. Trofymow, J.A., Coleman, D.C. and Cambardella, C. (1987). Rates of rhizodeposition and ammonium depletion in the rhizosphere of axenic oat roots. *Plant and Soil* **97:** 333-344.
33. van der Heijden, M.G., Bardgett, R.D. and van Straalen, N.M. (2008). The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecology Letters* 11: 296-310.
34. Vančura, V. and Hovadik, A. (1965). Root exudates of plants: II. Composition of root exudates of some vegetables. *Plant and Soil* **22:** 21-32.
35. Wang, Z., Zhang, J., Wu, F. and Zhou, X. (2018). Changes in rhizosphere microbial communities in potted cucumber seedlings treated with syringic acid. *PloS one* **13:** e0200007.
36. Xia, Z.C., Yu, L., He, Y., Korpelainen, H. and Li, C.Y. (2019) Broadleaf trees mediate chemically the growth of Chinese fir through root exudates. *Biology and Fertility of Soil* **55:** 737-749.

37. Yu, J.Q. and Matsui, Y. (1997). Effects of root exudates of cucumber (*Cucumis sativus*) and allelochemicals on ion uptake by cucumber seedlings. *Journal of Chemical Ecology* **23:** 817-827.
38. Zhang, J.H., Pan, D.D., Ge, X., Shen, Y.H., Qiao, P.L., Yang, S.Y., Wu, F.Z. and Zhou, X.G. (2018). Effects of syringic acid on *Fusarium* and *Trichoderma* communities in cucumber (*Cucumis sativus* L.) seedling rhizosphere. *Allelopathy Journal* **44:** 181-190.
39. Zhou, X., Liu, J. and Wu, F. (2017). Soil microbial communities in cucumber monoculture and rotation systems and their feedback effects on cucumber seedling growth. *Plant and Soil* **415:** 507-520.
40. Zhou, X., Yu, G. and Wu, F. (2012). Responses of soil microbial communities in the rhizosphere of cucumber (*Cucumis sativus* L.) to exogenously applied *p*-hydroxybenzoic acid. *Journal of Chemical Ecology* **38:** 975-983.
41. Zhou, X.G., Wang, J. Jin, X., Li, D.L., Shi, Y.J. and Wu, F.Z. (2019). Effects of selected cucumber root exudates components on soil *Trichoderma* spp. communities. *Allelopathy Journal* **47:** 257-266.
42. Zhou, X., Zhang, J., Pan, D., Ge, X., Jin, X., Chen, S. and Wu, F. (2018a). *p*-Coumaric can alter the composition of cucumber rhizosphere microbial communities and induce negative plant-microbial interactions. *Biology and Fertility of Soil* **54:** 363-372.
43. Zhou, X.G., Wang, Z.L., Pan, D.D. and Wu, F.Z. (2018b). Effects of vanillin on cucumber (*Cucumis sativus* L.) seedling rhizosphere *Bacillus* and *Pseudomonas* spp. community structures. *Allelopathy Journal* **43:** 255-264.
44. Zwetsloot, M.J., Kessler, A. and Bauerle, T.L. (2018). Phenolic root exudate and tissue compounds vary widely among temperate forest tree species and have contrasting effects on soil microbial respiration. *New Phytologist* **218:** 530-541.