ACTA SCIENTIARUM POLONORUM
Acta Sci. Pol. Hortorum Cultus, 18(6) 2019, 119–127
https://czasopisma.up.lublin.pl/index.php/asphc ISSN 1644-0692 e-ISSN 2545-1405 DOI: 10.24326/asphc.2019.6.12
ORIGINAL PAPER
Accepted: 10.04.2019

ABUNDANCE AND COMMUNITY STRUCTURE OF AMMONIA OXIDIZING ARCHAEA AND BACTERIA IN RESPONSE TO PEANUT GROWTH UNDER CONTROLLED CONDITION IN SHANDONG, CHINA

Chao Huang[1,2]✉, Nianfang Xu[3], Zaiqiu Fu[3], Botong Sun[1,2], Shengbo You[1,2], Deyuan Ma[1,2], Jinhui Yu[1,2]

[1] Biotech Research Center, Shandong Academy of Agricultural Sciences, Ji'nan, 250100, China
[2] Shandong Provincial Key Laboratory of Crop Genetic Improvement, Ecology and Physiology, Ji'nan, 250100, China
[3] Agricultural and Sideline Raw Materials Research Institute on Light Industry of Shandong, Gaomi, 261500, China

ABSTRACT

Based on a three-year field experiment under controlled condition in Ji'nan, China, the effects of peanut growth on the variation in the abundance and community structure of ammonia oxidizing bacteria (AOB) and archaea (AOA) before and after peanut growth were investigated through quantitative PCR and cluster analysis of terminal-restriction fragment length polymorphism. Our results show that the community composition of AOA and AOB was greatly affected by the peanut growth leading to the decreased abundance of AOA and increased abundance of AOB. Furthermore, AOA and AOB community structures varied before and after peanut growth. Phylogenetic analysis indicated that all AOA and AOB community sequences were clustered into the uncultured group. Altogether, the results suggested that the abundance of AOA and AOB in soil and their community compositions can be greatly affected by the peanut growth.

Key words: archaea, bacteria, peanut, community structure

INTRODUCTION

Arachis hypogaea Linn. is a kind of important oilseed crop. There are affluent fat, protein, carbohydrate, and other nutrient substances in peanut seeds. It has a different mechanism to interact with soil bacterial with respect to other leguminous plant, similar to dalbergioid clade [Lavin et al. 2001]. Due to the higher rate of nitrification conferred by its special nodule, peanut was categorized into a separate group of legume-rhizobia symbiosis [Bal et al. 1989]. And different from most legumes in tropical and temperate region, the lipid bodies were in close contact with the peribacteroid membrane in peanut root nodules [Abu-baker and Bal 1991]. It is also found that peanut root cell surface proteins can inhibit the attachment of microbial [Dardanelli et al. 2003]. Too many clues lead us to the conclusion: peanut has a different mechanism to attach/interact microbial community and can alter the structure of community specially.

With regard to the importance of soil microorganisms in the functions of ecosystem and acquisition of plant nutrient, the soil resistance and resilience can be readily affected due to the variation of microbial com-

✉ cauhch@hotmail.com

munity compositions after crop growth. For peanut, the continuous cropping can decrease the production of peanut. The change of microbial community may account for this kind of decrease partly.

The conversion of ammonia oxidation from ammonia to nitrite is important to crop growth. Distinguishingly the legume plants have the nodules to help them establish a different way. Ammonia oxidizing bacteria (AOB) have been usually considered dominantly responsible for ammonia oxidation. It was revealed by Venter et al. [2004] that ammonia monooxygenase (amoA), a kind of ammonia oxidation gene, was present in archaea. However, the physiology and metabolic pathways of AOA and AOB may be greatly different [Walker et al. 2010]. Moreover, significantly differentiated ammonia oxidation kinetics in AOA and AOB strains under liquid culture was also observed [Martens-Habbena et al. 2009]. In conclusion, this study aimed to investigate the variation of the abundance and community structure of AOA and AOB related to peanut growth.

MATERIALS AND METHODS

Experimental design. This study was carried out from 2012 to 2014 in Ji'nan, Shandong province, China (36°42'56.25"N, 117°05'09.08"E). Huayu22, a local variety of *Arachis hypogaea* Linn., was planted in April and harvested in September. Pot culture experiments were conducted each year, 60 replicates in CK and 60 replicates in treatment separately. The pot diameter was 0.27 meter and 0.3 meter high. The composition of soil is local soil loam and sand: local soil : sand = 3 : 1, without any known history of cropping. The soil has been mixed well before planting. In every pot two seedlings were planted. All the pots were separated in a closed zone. During the process, only local underground water was applied to the plants, without any fertilizers and pesticides.

Soil sampling. In 2014, at pod-maturing stage of peanut (September), the soil samples were collected from peanut growing field and the pots under the controlled environment. All soil samples were taken in a depth of 5 cm using a soil probe (1.5 cm in diameter). Three randomly selected replicates in every pot were combined to form a homogenous sample. 15 samples were collected from CK and peanut growth pots separately. After collection, the samples were mixed with blender before stored at 4°C and were used for further analysis as soon as possible.

Soil chemical properties. The experiment was executed in 2014. PNR, and the pH of the soils, water content, soil ammonium, soil nitrate, were measured following the methods described by Chen et al. [2014]. The levels of nitrogen, available organic matter, phosphorus, potassium, Olsen-P were tested following the protocols from the University of Minnesota [Protocol… 2014], which is popularly used in the world.

DNA extraction and quantitative PCR (qPCR). DNA extraction from the soil material for each sample was performed using PowerSoil DNA kits (MoBio, USA). The quality and quantity of the extracted genomic DNA were determined by OD(A260/A280). The quantity of amoA genes of AOA and AOB was determined by qPCR according to the former literature [Rotthauwe et al. 1997, Francis et al. 2005]. The qPCR assays were carried out in an ABI 7500 Real-Time PCR system with the same procedure. The PCR amplification efficiency for AOA or AOB ranged from 90 to100% and r2 was 0.99.

Terminal restriction fragment length polymorphism (T-RFLP) analysis. In the T-RFLP analysis, qPCR assays were conducted with the primer pairs as described above, difference existed in FAM-labelled forward primer. The PCR reactions and the qPCR assays followed the same conditions. The next steps follows the common procedures referred to Prakash et al. [Prakash et al. 2014].

Cloning and sequence analysis. The primer pairs for the qPCR were also used to construct two clone libraries from the treatment soils and control in September. Ligation of purified PCR products into Promega pGEM-T Easy Vector and their transformation into Escherichia coli JM109 from Takara were conducted with the methods described in the manufacturer's instructions. Thirty-four AOA and eighteen AOB positive clones from CK soil clone library, and sixteen AOA and twelve AOB positive ones from peanut-growth soil clone library were randomly selected and sequenced. Homology analysis of all these sequences was performed using the software DNAMAN with version 6.0.3.48 (Lynnon Biosoft). Operational taxonomy units (OTUs) were defined whey they shared 99% similarity. Phylogenetic analysis with the representative and BLAST-identified related se-

quences of each OTU were performed by the construction of neighbor-joining tree with 1000 bootstrap replicates using the software MEGA (version 6.0) [Tamura et al. 2007].

Statistical method. Variance homogeneity was assumed by log-transformation of the copy numbers of amoA gene, and two independent sample tests were conducted if the test sig was >0.05; if the variance homogeneity test sig was <0.05, then the rank sum test (Mann-Whitney U) was used. There was a significant difference between treatments if $P < 0.05$ for the independent sample t-test and the rank sum test (Mann-Whitney U); for $P < 0.01$ there was highly significant difference, and for $P > 0.05$ there was no-significant difference for test results. The software SPSS (version 16.0, SPSS Inc., Chicago, IL, USA) was used for statistical analysis.

RESULTS

Soil chemical properties. Soil property can be changed by plant growth, usually by root secretion, rhizosphere microbial community. The related properties can be found in Table 1 ($P < 0.001$).

Potential nitrification rates (PNR). It was observed that the rates of potential nitrification decreased from 0.424191 to 0.226978 mg NO^{2-}-N g^{-1} soil h^{-1} after peanut growth.

Abundance of AOA and AOB. The copies of archaeal amoA ranged from $1.95 \cdot 10^9$ to $3.94 \cdot 10^8$ copies g^{-1} soil between control and peanut growth soils. There exists significant difference in AOA abundance ($P < 0.001$). The abundance of AOB was lower than that of AOA and ranged from $4.15 \cdot 10^5$ to $7.84 \cdot 10^6$ copies g^{-1} soil. The obvious difference also exists ($P < 0.001$) (Fig. 1).

Community structures of AOA and AOB. After peanut growth, we found the communities of AOA and AOB are almost totally different, we avoid any statistical comparison analysis in such extreme case as it is meaningless.

Phylogeny of AOA and AOB. Randomly selected 34 AOA and 18 amoA gene clones from the control soils, and 16 AOA and 12 AOB amoA gene clones from the peanut growth soils were sequenced. Phylogenetic analysis revealed that all amoA gene sequences of AOA and AOB belonged to uncultured archaea and bacteria, respectively (Fig. 2 and Fig. 3). The result indicates that there is a great part of soil microbe community which remains being investigated. And the great complexity of soil microbe community makes us confirm the further knowledge about soil microbe community.

Table 1. **Comparison of results between control and peanut cultured soil**

Soil property	Control	Peanut culture
PNR	0.0041	0.0022**
PH	7.76	7.88**
Water content (%)	22.78	22.94
Organic (g/kg)	15.33	15.19**
N	47.19	44.26**
K	140.7	127.9**
P	160.33	127.45**
NH_4^+-N	14.3	13.7**
NO_3-N	25.898	22.496**
Olsen-P	24.96	19.90**
AOA (*10^9)	1.87	3.86**
AOB (*10^5)	3.99	7.99**

** Means that there exists a significant difference between control and peanut-growth group

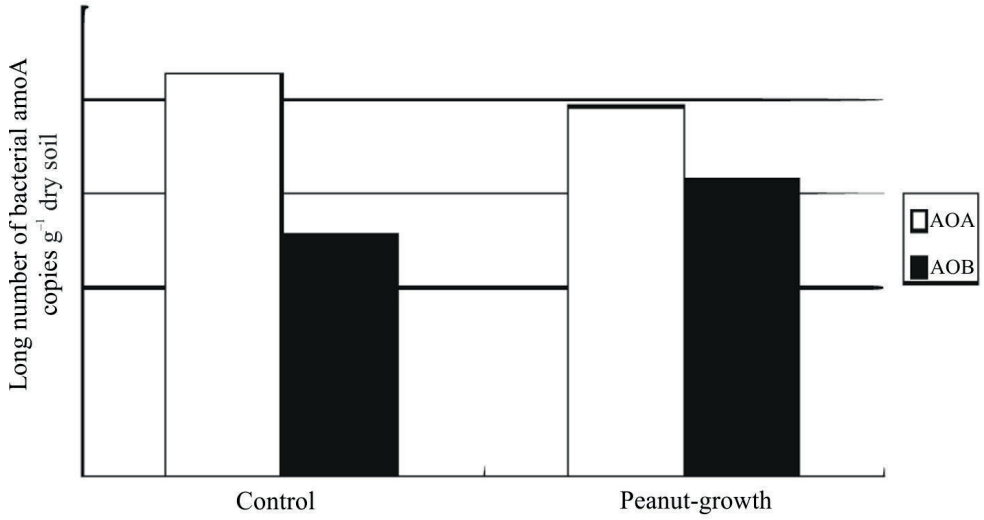

Fig. 1. Log number of bacterial amoA copies g^{-1} dry soil between control and peanut-growth

DISCUSSION

Effects of peanut growth on PNR and abundance of AOA and AOB. Former researchers have found that in different soil circumstance, the responses of AOB and AOA communities to environment changes are different. Such research usually focuses on the PH value of the soil and its fertilization [He et al. 2007, Yao et al. 2011, Zhang et al. 2012]. However, much more efforts should be done to investigate the AOB and AOA communities responding to the plant growth as the microbe communities shift differently even to different genotypes of the same plant [Bulgarelli et al. 2012].

Our study revealed that the number of AOA were much higher than AOB, which is consistent with other reports and it seems that this phenomena is popular in general soils in spite that there still exists controversy [Wu et al. 2011]. However, there is still a lot of work on the AOA physiology and habitat preferences remaining undone considering the complexity of microbe community and the great domain of unexplored microbe community. Martens-Habbena et al. [2009] reported that the affinity of bacterial ammonia monooxygenase (AMO) for substrate was lower than archaeal. The differences of substrate affinity between AOA and AOB may allow them to prefer different ecological niches. Therefore, the relative higher NH^{+}_{4}-N concentrations in the soil can provide an unfavorable environment for AOA growth [Chen 2014]. In similar studies AOA also indicated preference to low ammonia substrate and its growth was inhibited by high ammonium variations [Verhamme et al. 2011].

In our result, PNR decreased after peanut growth. As PNR is usually related with soil fertility status we can consider that after peanut growth soil loses some fertility. This result is correspondent to field investigation: continuous cropping decreases peanut production [Sun Xiu Shan et al. 2001]. Some other papers had reported that allelopathy can inhibit nitrification [Moore and Waid 1971, Kholdebarin 1994]. In fact, in our lab we have unpublished data that microbe community can affect peanut production greatly in spite that there exists allelopathy. So, we understand that in our experiment PNR is affected by allelopathy, but mostly by microbe community.

There are many former reports that bacteria abundance decreases after peanut growth [Feng Haisheng et al. 1993]. We also confirmed this result many times (unpublished data). However, we found that abundance of AOB increased after peanut growth. So, we can arrive at the conclusion: after peanut growth, bac-

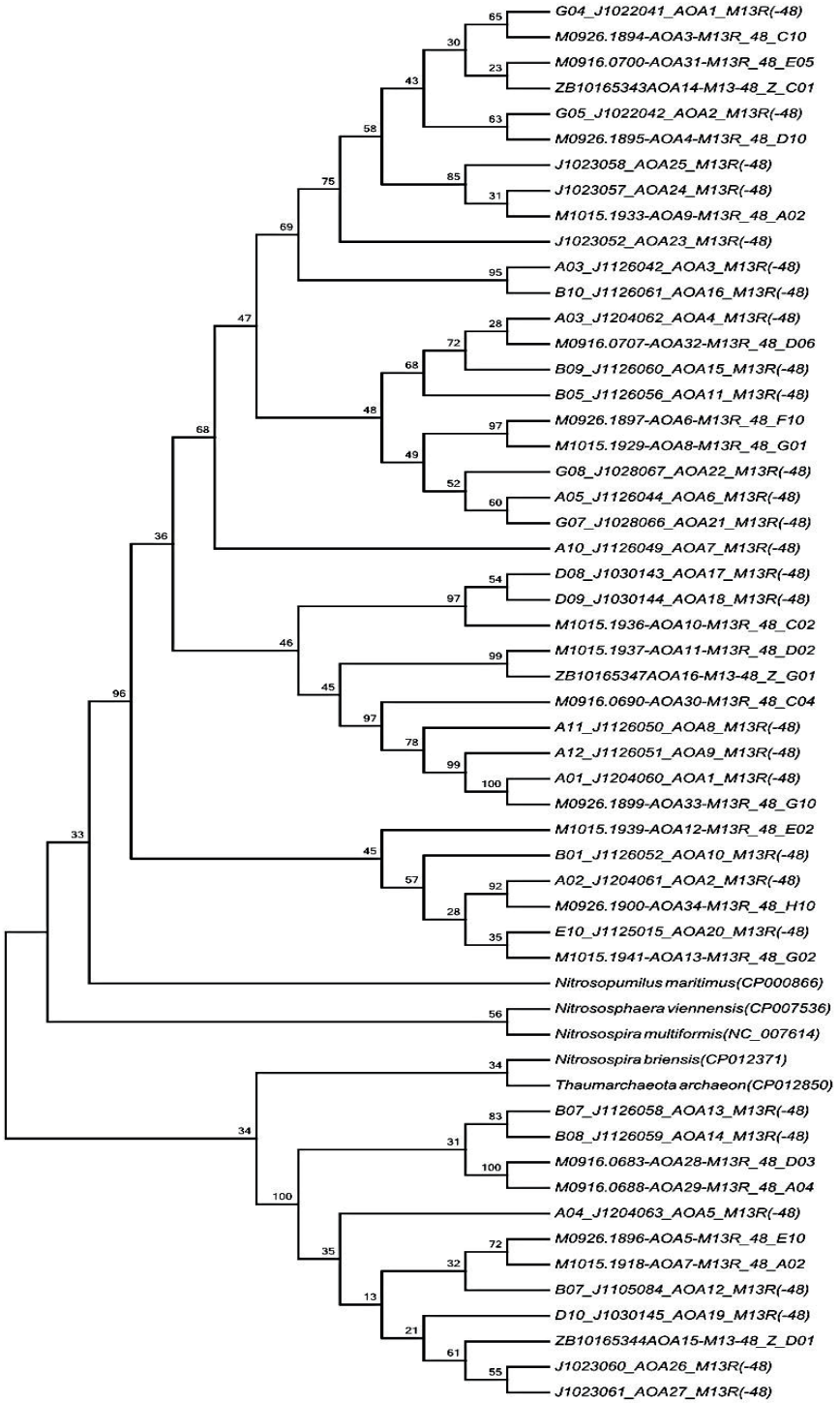

Fig. 2. Neighbor-joining phylogenetic tree of AOA amoA gene sequences retrieved from the clone library of the soil taken in a peanut pot and the NCBI gene bank. Filled Bootstrap values are indicated at branch points

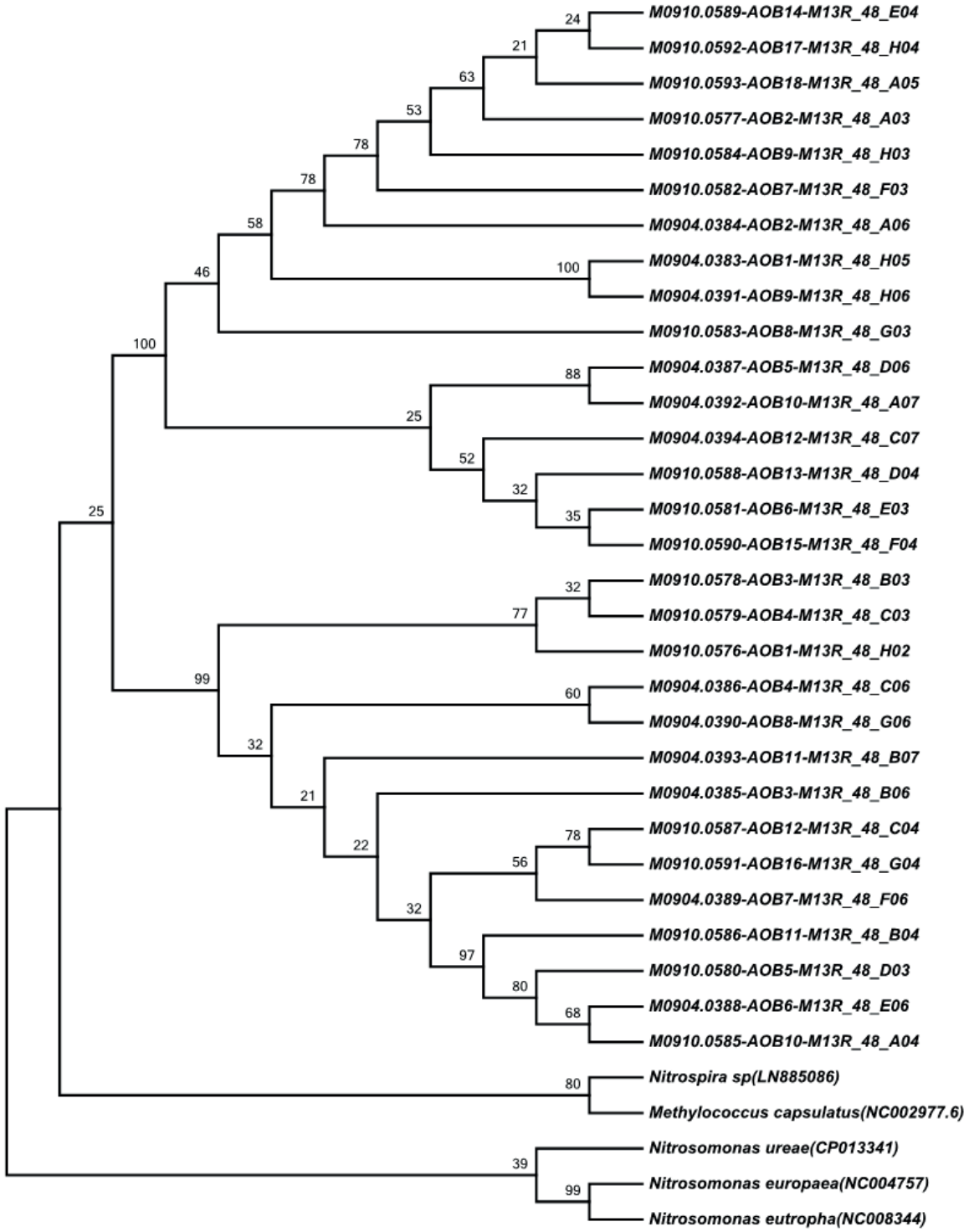

Fig. 3. Neighbor-joining phylogenetic tree of AOB amoA gene sequences retrieved from the clone library of the soil taken in peanut pot and the NCBI gene bank. Filled Bootstrap values are indicated at branch points

teria abundance decreases, in the meanwhile the abundance of AOB increases, which means the bacteria community shifts a lot.

For archaea, there is not a lot data about its quantity change after peanut growth. As we found that the abundance of AOA decreases greatly we can reasonably conclude that PNR decrease mainly affected by archaea, not bacteria. Similar result has been reported by other researchers [Yao et al. 2011]. Controversy views about AOA or AOB as the substantial community in the soils responsible for ammonia oxidation were reported [Zhang et al. 2012]. In our experiment, we can think that the abundance of AOA decreases mainly because of stable (relatively lower than fertilized soil) N availability and peanut root exudates, at the same time the abundance of AOB increases also mainly because of the effect of peanut exudates. The correlation between AOA and PNR in such case should be supposed to be largely attributed to peanut root executes and the ammonia substrate availability.

After peanut growth, the relative lower NH_4^+-N concentrations in soil with lower PNR leads us to the conclusion: the lower PNR is mainly affected by microbe community, especially by Archaeal.

It was reported that the activity of ammonia oxidizers is sensitive to water stress due to the substrate limitation and dehydration under water stress [Stark and Firestone 1995]. There are also some data indicating that PNR can be affected by the climate, such as: temperature, etc. [Stark and Firestone 1995, Sher et al. 2013]. For such reason we picked up the samples at the same time for CK and peanut-planted soil avoiding the affection from the climate.

Some evidences indicate that AOA can also use organic carbon, which makes them more metabolically versatile and heterotrophs or mixotrophs [Walker et al. 2010]. For AOB, the situation is different. The abundance increase of AOB by high levels of N fertilizers was also reported in many studies [Shen et al. 2008, Di et al. 2009, Chen et al. 2013]. Di et al. [2010] found it prefers high ammonia substrate. So the distinctness of AOA and AOB in soil microcosms could be defined by the ammonia concentration [Verhamme et al. 2011], which may explain a higher AOB abundance in this study.

Reponses of AOA and AOB community structures to peanut growth. As our expectation, AOA and AOB soil communities shifted a lot after peanut growth, which could be a comprehensive effect by several mechanisms: first of all is that exudates from peanut roots promote this kind of shift. In recent years some researches about different plants have shed light to such mechanism [Chu et al. 2007, Chen et al. 2008, Bulgarelli et al. 2012, Lundberg et al. 2012, Ai et al. 2013].

Chu et al. [2007] found differences of amoA genes between the control and treated plots with PK (phosphorus and potassium) in 16 years in agricultural soils with DGGE method. Stability of ammonia oxidizer communities in P-treated plots suggests us to exclude the consideration of correlation between P and structure of AOA.

Different researchers has found that AOB community compositions shift responding to N availability [He et al. 2007, Hynes and Germida 2012]. It was revealed that N fertilization has a great effect on AOB community compositions, but has a slight effect on AOA in alkaline agricultural and neutral grassland soils. However, molecular biology evidences demonstrated that in various acidic soils AOA were more sensitive to various fertilization than AOB [He et al. 2007, Chen et al. 2011]. Therefore, the responding change of community composition of ammonia oxidizers to peanut growth may be determined by the soil type and its pH scale.

For phosphorus and potassium, there are some reports that they cannot significantly affect the population and size of AOB [Chu et al. 2008]. So, in our research we can ignore the affection to AOB from phosphorus and potassium at this time.

Reasonably, seasonal factors such as temperature and soil humidity are also pivotal in determining the compositions of ammonia oxidizers. One of the most important reasons is that different AOA lineages need different circumstance to meet their optimal growth condition. Such experiments have been carried in field and microcosm experiments [Stres et al. 2008, Tourna et al. 2008, Gleeson et al. 2010, Chen et al. 2013].

All AOA and AOB sequences were clustered into the uncultured microbes in this study, indicating that there still exists a great field in soil microbe community remaining unexplored and the complexity in soil circumstance is AOB can also affect PNR, in spite that this kind of affection can be much compensated by AOA.

In conclusion, until now this is the first study to exploit abundance and community composition of ammonia oxidizers after the peanut growth in a controlled circumstance. We clearly demonstrated that peanut growth (peanut root exudates) played a key role in affecting ammonia oxidizing communities. The abundance of ammonia oxidizers changed significantly and AOA and AOB communities varied subtlety, which should be partly responsible for continuous cropping obstacle.

On the other hand, the role of AOA in soil N/C cycling remains unresolved. And the community of Archaeal and bacteria may interact continuously with peanut roots. Our data can enrich our knowledge to such interaction.

CONCLUSION

All in all, our study aims to investigate the community dynamics of the ammonia oxidizers deeply after peanut growth. Our results confirm the former research: AOA and AOB changed a lot after plant growth, and therefore has implications for exploring the continuous cropping obstacle.

REFERENCE

Ai, C., Liang, G., Sun, J., Wang, X., He, P., Zhou, W. (2013). Different roles of rhizosphere effect and long-term fertilization in the activity and community structure of ammonia oxidizers in a calcareous fluvo-aquic soil. Soil Biol. Biochem., 57, 30–42.

Bal, A.K., Hameed, S., Jayaram, S. (1989). Ultrastructural characteristics of the host-symbiont interface in nitrogen-fixing peanut nodules. Protoplasma, 150, 19–26.

Bulgarelli, D., Rott, M., Schlaeppi, K., Ver Loren van Themaat, E., Ahmadinejad, N., Assenza, F., Rauf, P., Huettel, B., Reinhardt, R., Schmelzer, E., Peplies, J., Gloeckner, F.O., Amann, R., Eickhorst, T., Schulze-Lefert, P. (2012). Revealing structure and assembly cues for Arabidopsis root-inhabiting bacterial microbiota. Nature, 488, 91–95.

Chen, X., Zhang, L.-M., Shen, J.-P., Wei, W.-X., He, J.-Z. (2011). Abundance and community structure of ammonia-oxidizing archaea and bacteria in an acid paddy soil. Biol. Fertil. Soils, 47, 323–331.

Chen, X.-P., Zhu, Y.-G., Xia, Y., Shen, J.-P., He, J.-Z. (2008). Ammonia-oxidizing archaea: important players in paddy rhizosphere soil? Environ. Microbiol., 10, 1978–1987.

Chen, Y., Xu, Z., Hu, H., Hu, Y., Hao, Z., Jiang, Y., Chen, B. (2013). Responses of ammonia-oxidizing bacteria and archaea to nitrogen fertilization and precipitation increment in a typical temperate steppe in Inner Mongolia. Appl. Soil Ecol., 68, 36–45.

Chen, Y.-L., Hu, H.-W., Han, H.-Y., Du, Y., Wan, S.-Q., Xu, Z.-W., Chen, B.-D. (2014). Abundance and community structure of ammonia-oxidizing archaea and bacteria in response to fertilization and mowing in a temperate steppe in Inner Mongolia. FEMS Microbiol. Ecol., 89, 67–79.

Chu, H., Fujii, T., Morimoto, S., Lin, X., Yagi, K. (2008). Population size and specific nitrification potential of soil ammonia-oxidizing bacteria under long-term fertilizer management. Soil Biol. Biochem., 40, 1960–1963.

Chu, H., Fujii, T., Morimoto, S., Lin, X., Yagi, K., Hu, J., Zhang, J. (2007). Community structure of ammonia-oxidizing bacteria under long-term application of mineral fertilizer and organic manure in a sandy loam soil. Appl. Environ. Microbiol., 73, 485–491.

Dardanelli, M., Angelini, J., Fabra, A. (2003). A calcium-dependent bacterial surface protein is involved in the attachment of rhizobia to peanut roots. Can. J. Microbiol., 49, 399–405.

Di, H.J., Cameron, K.C., Shen, J.P., Winefield, C.S., O'Callaghan, M., Bowatte, S., He, J.Z. (2009). Nitrification driven by bacteria and not archaea in nitrogen-rich grassland soils. Nat. Geosci., 2, 621–624.

Di, H.J., Cameron, K.C., Shen, J.-P., Winefield, C.S., O'Callaghan, M., Bowatte, S., He, J.-Z. (2010). Ammonia-oxidizing bacteria and archaea grow under contrasting soil nitrogen conditions. FEMS Microbiol. Ecol., 72, 386–394.

Feng, H.S, Zhang, S.S, Wan, S.B, Sui, Q.W, Zuo, X.Q. (1993).The variation of nutrient in soil of sequential cropping of peanut and its response to fertilizer. Chinese J. Oil Crop Sci., 2, 55–59.

Francis, C.A., Roberts, K.J., Beman, J.M., Santoro, A.E., Oakley, B.B. (2005). Ubiquity and diversity of ammonia-oxidizing archaea in water columns and sediments of the ocean. Proc. Nat. Acad. Sci. USA, 102, 14683–14688.

Gleeson, D.B., Müller, C., Banerjee, S., Ma, W., Siciliano, S.D., Murphy, D.V. (2010). Response of ammonia oxidizing archaea and bacteria to changing water filled pore space. Soil Biol. Biochem., 42, 1888–1891.

He, J.-Z., Shen, J.-P., Zhang, L.-M., Zhu, Y.-G., Zheng, Y.-M., Xu, M.-G., Di, H. (2007). Quantitative analyses of the abundance and composition of ammonia-oxidizing bacteria and ammonia-oxidizing archaea of a Chinese upland red soil under long-term fertilization practices. Environ. Microbiol., 9, 2364–2374.

Hynes, H.M., Germida, J.J. (2012). Relationship between ammonia oxidizing bacteria and bioavailable nitrogen in harvested forest soils of central Alberta. Soil Biol. Biochem., 46, 18–25.

Kholdebarin, B., Oertli, J.J. (1994). Nitrification: interference by phenolic compounds. J. Plant Nutr., 17, 1827–1837.

Lavin, M., Pennington, R.T., Klitgaard, B.B., Sprent, J.I., de Lima, H.C., Gasson, P.E. (2001). The dalbergioid legumes (Fabaceae): delimitation of a pantropical monophyletic clade. Am. J. Bot., 88, 503–533.

Martens-Habbena, W., Berube, P.M., Urakawa, H., de la Torre, J.R., Stahl, D.A. (2009). Ammonia oxidation kinetics determine niche separation of nitrifying Archaea and Bacteria. Nature, 461, 976–979.

Moore, D.R.E., Waid, J.S. (1971). The influence of washings of living roots on nitrification. Soil Biol. Biochemistry 3, 69–83.

Prakash, O., Pandey, P.K., Kulkarni, G.J., Mahale, K.N., Shouche, Y.S. (2014). Technicalities and glitches of terminal restriction fragment length polymorphism (T-RFLP). Ind. J. Microbiol., 54(3), 255–261.

Protocol of soil test. (2014). Available: http://soiltest.cfans.umn.edu/our-methods/ [date of access: 03.04.2014]

Rotthauwe, J.H., Witzel, K.P., Liesack, W. (1997). The ammonia monooxygenase structural gene amoA as a functional marker: molecular fine-scale analysis of natural ammonia-oxidizing populations. Appl. Environ. Microbiol., 63, 4704–4712.

Shen, J.-P., Zhang, L.-M., Zhu, Y.-G., Zhang, J.-B., He, J.-Z. (2008). Abundance and composition of ammonia-oxidizing bacteria and ammonia-oxidizing archaea communities of an alkaline sandy loam. Environ. Microbiol., 10, 1601–1611.

Sher, Y., Zaady, E., Nejidat, A. (2013). Spatial and temporal diversity and abundance of ammonia oxidizers in semi-arid and arid soils: indications for a differential seasonal effect on archaeal and bacterial ammonia oxidizers. FEMS Microbiol. Ecol., 86, 544–556.

Stark, J.M., Firestone, M.K. (1995). Mechanisms for soil moisture effects on activity of nitrifying bacteria. Appl. Environ. Microbiol., 61, 218–221.

Stres, B., Danevčič, T., Pal, L., Fuka, M.M., Resman, L., Leskovec, S., Hacin, J., Stopar, D., Mahne, I., Mandic-Mulec, I. (2008). Influence of temperature and soil water content on bacterial, archaeal and denitrifying microbial communities in drained fen grassland soil microcosms. FEMS Microbiol. Ecol., 66, 110–122.

Sun, X.S., Feng, H.S., Wan, S.B., Zuo, X.Q. (2001). Changes of main microbial strains and enzymes activities in peanut continuous cropping soil and their interactions. Acta Agron. Sin., 1.

Tamura, K., Dudley, J., Nei, M., Kumar, S. (2007). MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) Software Version 4.0. Mol. Biol. Evol., 24, 1596–1599.

Tourna, M., Freitag, T.E., Nicol, G.W., Prosser, J.I. (2008). Growth, activity and temperature responses of ammonia-oxidizing archaea and bacteria in soil microcosms. Environ. Microbiol., 10, 1357–1364.

Venter, J.C., Remington, K., Heidelberg, J.F., Halpern, A.L., Rusch, D., Eisen, J.A., Wu, D., Paulsen, I., Nelson, K.E., Nelson, W., Fouts, D.E., Levy, S., Knap, A.H., Lomas, M.W., Nealson, K., White, O., Peterson, J., Hoffman, J., Parsons, R., Baden-Tillson, H., Pfannkoch, C., Rogers, Y.-H., Smith, H.O. (2004). Environmental genome shotgun sequencing of the Sargasso Sea. Science, 304, 66–74.

Verhamme, D.T., Prosser, J.I., Nicol, G.W. (2011). Ammonia concentration determines differential growth of ammonia-oxidising archaea and bacteria in soil microcosms. ISME J. 5, 1067–1071.

Walker, C.B., de la Torre, J.R., Klotz, M.G., Urakawa, H., Pinel, N., Arp, D.J., Brochier-Armanet, C., Chain, P.S.G., Chan, P.P., Gollabgir, A., Hemp, J., Hügler, M., Karr, E.A., Könneke, M., Shin, M., Lawton, T.J., Lowe, T., Martens-Habbena, W., Sayavedra-Soto, L.A., Lang, D., Sievert, S.M., Rosenzweig, A.C., Manning, G., Stahl, D.A. (2010). Nitrosopumilus maritimus genome reveals unique mechanisms for nitrification and autotrophy in globally distributed marine crenarchaea. Proc. Nat. Acad. Sci., 107, 8818–8823.

Wu, Y., Lu, L., Wang, B., Lin, X., Zhu, J., Cai, Z., Yan, X., Jia, Z. (2011). Long-term field fertilization significantly alters community structure of ammonia-oxidizing bacteria rather than archaea in a paddy soil. Soil. Sci. Soc. Am. J. 75, 1431–1439.

Yao, H., Gao, Y., Nicol, G.W., Campbell, C.D., Prosser, J.I., Zhang, L., Han, W., Singh, B.K. (2011). Links between ammonia oxidizer community structure, abundance, and nitrification potential in acidic soils. Appl. Environ. Microbiol., 77, 4618–4625.

Zhang, L.-M., Hu, H.-W., Shen, J.-P., He, J.-Z. (2012). Ammonia-oxidizing archaea have more important role than ammonia-oxidizing bacteria in ammonia oxidation of strongly acidic soils. ISME J., 6, 1032–1045.