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ORIGINAL PAPER

Microbial community succession and lignocellulose degradation during agricultural waste composting

Hongyan Yu · Guangming Zeng · Hongli Huang · Xingmei Xi · Renyou Wang · Danlian Huang · Guohe Huang · Jianbing Li

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Abstract The changes of microbial community during agricultural waste composting were successfully studied by quinone profiles. Mesophilic bacteria indicated by MK-7 and mesophilic fungi containing Q-9 as major quinone were predominant and seemed to be important during the initial stage of composting. *Actinobacteria* indicated by a series of partially saturated and long-chain menaquinones were preponderant during the thermophilic period. While *Actinobacteria*, fungi and some bacteria, especially those microbes containing MK-7(H4) found in Gram-positive bacteria with a low G+C content or *Actinobacteria* were found cooperate during the latter maturating period. Since lignocellulsoe is abundant in the agricultural wastes and its degradation is essential for the operation of composting, it's important to establish the correlation between the quinone profiles changes and lignocellulose degradation. The microbes containing Q-9 or Q-10(H2) as major quinone were found to be the most important hemicellulose and cellulose degrading microorganisms during composting. While the microorganisms containing Q-9(H2) as major quinone and many thermophilic *Actinobacteria* were believed to be responsible for lignin degradation during agricultural waste composting.

Keywords Agricultural waste · Composting · Lignocellulose · Microbial community · Quinone profile

H. Yu · G. Zeng · H. Huang · X. Xi · R. Wang · D. Huang · G. Huang · J. Li
College of Environmental Science and Engineering, Hunan University, Changsha 410082, China

G. Zeng (✉) · G. Huang
Faculty of Engineering, University of Regina, Regina, SK, Canada S4S 0A2
e-mail: zgming@hnu.cn

Introduction

Composting is a process involving a complex ecosystem with many interacting factors, in which biodegradable organic wastes are stabilized and converted by the action of some microorganisms under controlled conditions (Tang et al. 2004; Khalil et al. 2001). Microorganisms are the essential factors for the successful operation of composting. In order to effectively control the composting process, it's necessary to understand the microbial community structure and its change, especially its special role in decomposition of organic matters (Beffa et al. 1996).

Temperature is a primary factor to bring microbial community succession during composting. A typical composting process goes through a series of phases, including a rapid temperature

increase, sustained high temperatures and a gradual cooling of the composting mass. Different microbial communities dominate during these various composting phases, and each adapted to a particular environment (Halet et al. 2006).

Compost microbes are tremendously diverse and their ecologies are extremely complex. Methods used to research the microbial community succession include traditional plate-count method (Hassen et al. 2001; Boulter et al. 2002), community level physiological profiles (CLPPs) (Laine et al. 1997; Mondini and Insam 2003), phospholipid fatty acid (PLFA) analysis (Herrmann and Shann 1997; Klamer and Bååth 1998; Steger et al. 2005), molecular technologies (Dees and Ghiorse 2001; Green et al. 2004; Franke-Whittle et al. 2005) and quinone profile method (Tang et al. 2004). It is well known that less than 10% of bacteria existing in ecosystems could be culturable when using plating culture techniques. Clearly, the conventional approaches are not suitable for the analysis of microbial community structure in many ecosystems (Hu et al. 1999). Different advantages and limitations were found by using the other methods. Quinone profile method entails direct analysis of respiratory quinones in cell membranes to quantitatively reveal community profiles according to quinone molecular types (Kurisu et al. 2002). It is superior to molecular technologies because it correlates quantitatively to the microbial biomass. It also gives more information on taxonomy compared with the PLFA method, because most of the microorganisms contain a major quinone species (Tang et al. 2004). Quinone profile method is widely used in different ecosystems including soil (Song and Katayama 2005), activated sludge (Lin et al. 2003) and bioreactor (Nozawa et al. 1998; Hu et al. 1999; Okunuki et al. 2004). The method was also used in composting. Tang et al. (2003) detected the microbial community structure in various compost products. Quinone profiles and physico-chemical properties were measured to characterize the microbial community structure during a 14-day thermophilic composting of cattle manure mixed with rice straw as a bulking agent by Tang et al. (2004).

However, much less is known about the interrelationship between the microbial community succession and lignocellulose degradation, especially with regard to composting of agricultural waste. In the agricultural waste composting, lignocellulose accounts for the major part of biomass, and consequently, its degradation is essential for the operation of composting (Tuomela et al. 2000; Dixon and Langer 2006). The main objective of this study was to obtain more useful information about the correlation between microbial communtiy succession detected through quinone profile and lignocellulsoe degradation, which will help us find out some characters of microbial community responsible for lignocellulose degradation.

Materials and methods

Composting materials

The typical agricultural organic wastes from Changsha suburb were selected as composting materials. Rice straw, which was dried and cut to 10–20 mm lengths before use, was used as organic materials difficult to be decomposed. Several kinds of vegetables cut to 10–20 mm lengths were used as easy metabolizing materials. Bran was used to adjust the initial C/N ratio of composting.

Composting conditions

An experimental composting system was set up in this study. The compost was packed loosely in an open wooden box that was kept inside an incubator to maintain the temperature at 30°C. All the materials were fully mixed with an initial C/N ratio of about 30 and lignocellulose content of 50.31% (dry weight). The moisture content was maintained at about 60%. The compost in the box was turned by hand twice a week in first 2 weeks and then once a week afterwards. Two same piles were set up in this work. Each sample of approximately 20 g was made by mixing five subsamples taken from five points of pile 1. Each subsample was a mixture of grab samples taken from the top to the bottom of the pile at each sampling point. In order to calculate accurate losses of linocellulose, the same quantity of

compost was taken from pile 2 and supplemented into pile 1 after it was sampled.

Analytical methods

The temperature in the center of the composting material was monitored every day. The moisture content was determined after drying at 105°C for 24 h. Neutral detergent fiber (NDF), acid detergent fiber (ADF) and acid detergent lignin (ADL) were determined in accordance with the procedures outlined by Van Soest et al. (1991). Hemicellulose was estimated as the difference between NDF and ADF. Cellulose was estimated as the difference between ADF and ADL. Lignin was estimated as the difference between ADL and ash content.

The respiratory quinone profile analysis was performed by the method described by Tang et al. (2004) and Hasanudin et al. (2004). Quinones were first extracted from the compost samples by a mixture of chloroform–methanol (2:1, v/v), and then re-extracted by hexane and NaCl–$CaCl_2$ solution. The quinones in *n*-hexane were then purified using solid extraction cartridge (Sep-Pak® Plus Silica, Waters). The types and concentrations of quinones were determined with HPLC equipped with a reverse phase column (Zorbax-C18, 4.6 mm × 150 mm × 5 μm, Agilent) and a diode-array detector (1100 Series, Agilent). A mixture of methanol and di-isopropyl ether (9:2, v/v) was used as the mobile phase at a flow rate of 1.0 ml min^{-1}. The temperature of the column oven was maintained at 35°C. The quinone species were identified according to the retention time and the UV spectrum. The linear relationship between the logarithm of the retention times of quinones and the equivalent number of isoprenoid unit (ENIU) was also used to identify the quinone type. In some cases liquid chromatograph-mass spectrometry was used to confirm the results. Ubiquinones (Qs) and menaquinones (MKs) with *n* isoprenoid units as well as the number *x* of hydrogen atoms in the hydrogenation of side-chain double bonds are designated as Q–*n*(H*x*) and MK–*n*(H*x*), respectively. Q-10 and vitamin K1 (Sigma) were used as the quantitative standards for ubiquinone and menaquinone, respectively. The quinone profiles were averaged with three repeats of every compost sample.

Statistical analysis

Since the total quinone content (TQ) correlates with the biomass and the quinone diversity index (DQ) value corresponds to the diversity of the microbial community, TQ and DQ were calculated according to Tang et al. (2004). The difference between microbial community structures (quinone profiles) of different compost samples was quantified with dissimilarity index (*D*) defined by the equation of Hiraishi et al. (1991).

Cluster analysis through software package SPSS 13.0 was used to identify natural groupings among compost samples and quinone species, respectively. The microbial community change of compost samples was evaluated with reference to the dissimilarity (*D*).

Results and discussion

Lignocellulose degradation during composting

Figure 1 shows temperature changes during composting. Temperature increased rapidly and reached the maximum on day 3 when the composting went into thermophilic phase. Until day 12, the composting temperature began to fall. Representative samples from different composting phases (day 2 as initial stage, day 3–11 as thermophilic phase, day 12–20 as temperature falling phase, day 0–20 as first fermentation phase and day 21–45 as second fermentation phase i.e.,

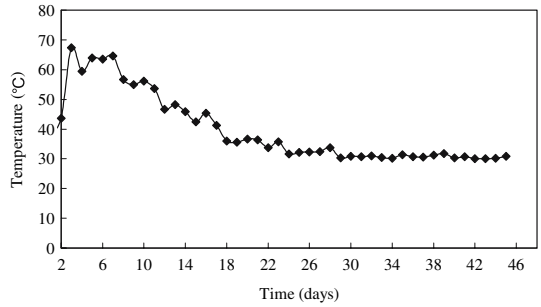

Fig. 1 Temperature changes during composting

maturing phase) were obtained according to the temperature change.

Lignocellulose is mainly composed of a mixture of cellulose (ca. 40%), hemicellulose (ca. 20–30%), and lignin (ca. 20–30%) (Tuomela et al. 2000). Lignocellulose was gradually degraded during composting as shown in Fig. 2. The decomposing trend of hemicellulose was found to be resembled with that of cellulose. They were partially degraded during the initial stage of composting. Then the degrading ratio was almost unaltered due to the high temperature followed by the large decomposition during the temperature falling phase and initial stage of the second fermentation. Since enough researches confirmed that many mesophile fungi are responsible for cellulose and hemicellulose metabolization during composting, these results were believed to be reasonable. Lignin is a highly branched, irregular three-dimensional organic polymer, which provides plant strength and resistance to microbial degradation (Kapat and Dey 2000; Tuomela et al. 2000). Its degradation was quite different from that of cellulose or hemicellulose. Lignin was slightly decomposed during the initial stage of composting. When the temperature was lower than the maximum value during thermophilic phase, lignin was greatly degraded until the temperature began to fall. Waksman et al. (1939) found that the highest degradation of lignin occurred at 50°C during horse manure and straw compost. According to the study of Tomati et al. (1995), 70% of lignin was degraded during 35 days when the temperature of the compost was kept at 50°C. During the later maturating phase, lignin was again degraded with the degrading ratio increasing from 20.25% (day 28) to 24.89% (day 45).

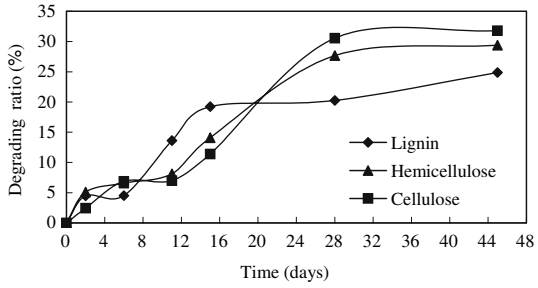

Fig. 2 Changes of lignocellulose components degrading ratio during composting

Changes in microbial biomass and diversity

Figure 3 shows the temporal changes of TQ and DQ during the agricultural waste composting. Since the linear relationship between TQ and the soil microbial biomass was established by Saitou et al. (1999), TQ was usually used as the indicator of microbial biomass. TQ value increased rapidly and reached a peak on day 2 followed by the fast decline along with the high temperature. When the temperature was under 60°C, TQ value became stable and just slightly fluctuated. The changing trend of microbial biomass resembled what has been found by Tiquia et al. (1996) during spent pig-manure sawdust litter composting using different methods.

DQ is an indicator of taxonomic diversity of microorganism because many microorganisms contain one major quinone species (Song and Katayama 2005). In this work, DQ values increased during the composting process reaching a value of approximately 16 after 15 days of composting. This suggests that the microbial community complexity increased rapidly and that the 15-day incubation period was long enough to induce similar levels of microbial diversity. The change of TQ and DQ indicated that the microbial

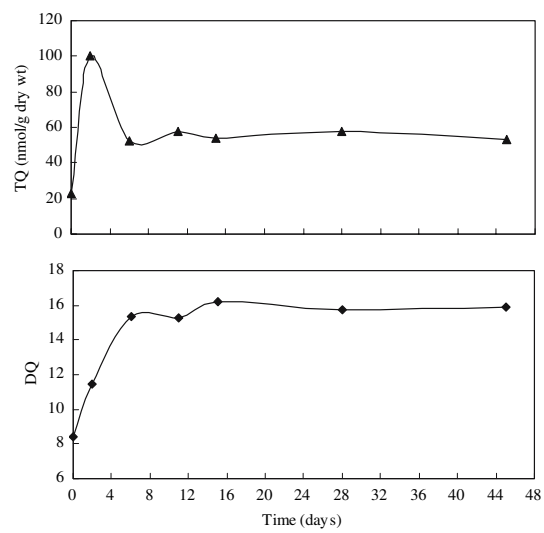

Fig. 3 Changes in TQ and DQ during composting

community developed successively and became more complex with the composting duration.

Changes in microbial community structure

Figure 4 shows the changes in mole fractions of quinone species during composting. The ubiquinone dominated during the initial stage and its concentration changed along with the temperature shift, which means most of the microorganisms containing ubiquinone as their major quinone could not tolerate high temperature. The initial composting material contained 10 quinone species, then the species increased from 13 during the initial stage of composting to 18 or so after 6 days' incubation. The distribution of quinone species during later maturating phase (day 45) obviously became more even. These results indicated that the microbial community became more complex with the composting process as confirmed by the DQ changing.

Expect the appearance of some new quinone species, such as MK-7(H2), MK-7(H4) and MK-8(H4), the quinone profiles were similar between composting material and initial composting stage. MK-7 and Q-9 predominated during the initial stage of composting followed by Q-8, Q-10, Q-7, Q-10 (H2) and Q-10 (H4). MK-7 is found in Gram-positive bacteria with a low G+C content, as well as δ- and ε-subclass *Proteobacteria* and members of the Cytophaga-Flavobacterium cluster (Tang et al. 2004). It was also found predominated during thermophilic composting of manure by Tang et al. (2004). Katayama et al. (1998) confirmed that MK-7 existed in the final mature compost. Since MK-7 concentration was still high during thermophilic phase, it is always considered that thermophilic *Bacillus* spp. containing MK-7 are the main species of microorganism in compost operated at a high temperature (Tang et al. 2004). The presence of Q-9 found in γ-subclass of *Proteobacteria* and fungi, Q-8 found in β-subclass of *Proteobacteria* (such as *Comamonas* sp. and *Pseudomonasy* sp.), Q-10 found in α-subclass of *Proteobacteria*, Q-10 (H2) and Q-10 (H4) found in fungi and Q-7 found in some bacteria (e.g., *Shewanella* sp., *Pasteurella* sp., *Haemophilus* sp., and so on) indicated that bacteria and fungi were the most important microorganisms during the initial stage of composting (Katayama et al. 2001).

During the thermophilic phase, the concentration of Q-9, Q-10, Q-10 (H2) and Q-10 (H4) (found in some fungi, such as *Chaetomium* sp. and *Botrytis* sp.) decreased (Data in Japan Collection of Microorganisms; World Data Center for Microorganisms, 1995). While many partially saturated and long-chain menaquinones including MK-8(H2), MK-8(H4), MK-9(H2), MK-9(H4), MK-9(H6), MK-9(H8), MK-9(H10), MK-10(H4) and MK-10(H6) appeared and gradually increased

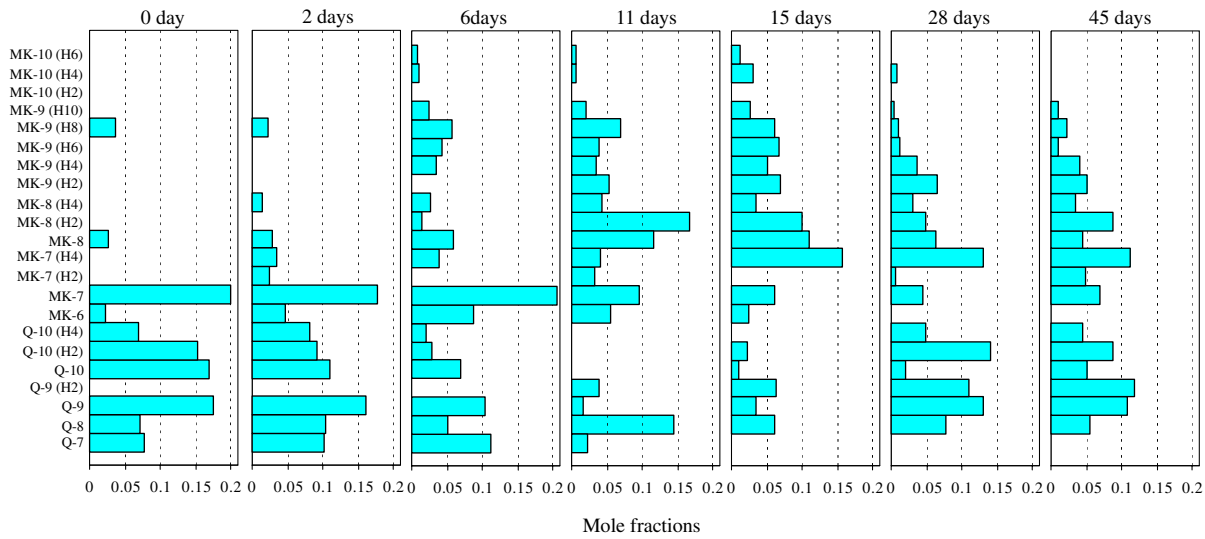

Fig. 4 Changes in mole fractions of quinone species during composting process

until the second fermentation phase. This group of quinone is the indicator of *Actinobacteria*, such as *Nocardia* sp., *Streptomyces* sp. and *Micromonospora* sp. common in composting (Waksman et al. 1939). The obvious increase of MK-8 was found during the thermophilic phase in this work. Because MK-8 is indicative of Gram-positive bacteria with a low G+C content, δ- and ε-subclass *Proteobacteria* and *Actinobacteria*, some of these microorganisms were believed to play role in this composting phase. Since Blanc et al. (1999) found that *Thermus thermophilus* contained MK-8 as the major quinone was dominant during thermophilic composting, *T. thermophilus* might play important role during thermophilic phase of agricultural waste composting.

From day 15, the concentration of MK-7(H4) became the largest until late composting period when most of ubiquinone increased obviously. MK-7(H4) is found in Gram-positive bacteria with a low G+C content (e.g., *Bacillus saliphilus*, *Friedmanniella capsulata*) (Romano et al. 2005; Maszenan et al. 1999) and *Actinobacteria* (e.g., *Cellulomonas*, *Nocardia*, *Noeardiodes*, *Oerskooia*, *Promicromonospora*) (Tang et al. 2004; Jin et al. 1998). These results indicated that Gram-positive bacteria were cooperative with fungi during the later maturating phase.

Dissimilarity index (D) is usually used. The larger the value of D, the more different between the two quinone profiles. $D = 0$ shows that the two quinone profiles are identical. Because of the fluctuations in dissimilarity of quinone profiles extracted from one sample the critical value of D to make a judgement whether two quinone profiles are different or not was important and should be first ascertained. Hu et al. (2001) demonstrated that the critical value of dissimilarity between two quinone profiles of activated sludge was 0.1 for the analytical method used. Fujie et al. (1998) found that dissimilarities greater than 0.2 indicated a statistically significant difference in the quinone profile between two soil samples. While Song and Katayama (2005) obtained that D between subsurface soil samples larger than 21.2% corresponded to $P < 0.05$ and larger than 24.7% to $P < 0.01$, respectively. In this work, 0.2 was used as the critical value in the quinone profiles of composting. The classification of the quinone profiles based on dissimilarity (D) is shown in Fig. 5.

The microbial communities during the initial composting phase (day 0 and day 2) were similar since the quinone profiles formed a cluster at a dissimilarity level of less than 20%. That was to the microbial communities of the second fermentation phase (day 28 and day 45). The quinone profiles between day 11 and 15 were slightly different at a level of 29.4%, and they were distinguished with the cluster of the late maturating phase at the level of 37.5%. While the remarkable change of microbial communities were found between the cluster of the beginning composting (before day 6) and the other profiles. These results quantificationally elucidated the succession of microbial community during the composting.

Relationship between the lignocellulose degradation and the microbial properties

During the agricultural waste composting, six groups of quinone species were obtained based on average linkage cluster as shown in Fig. 6. The correlation between lignocellulose degrading ratio and quinone content (include average quinone content of every group and individual quinone content) was analyzed. Group 1 was MK-7 that mainly existed in the first fermentation of composting, especially in the beginning phase. Since lignocellulose was mainly decomposed after the beginning phase, the microbes containing

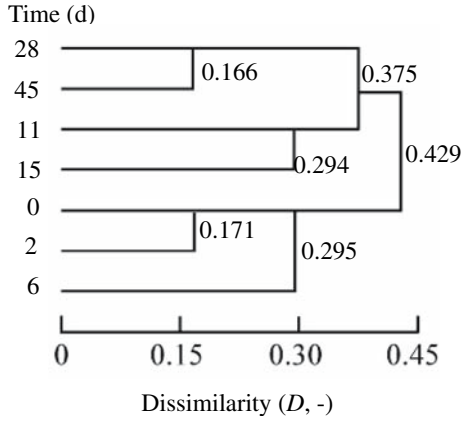

Fig. 5 Classification of the quinone profiles based on dissimilarity (D)

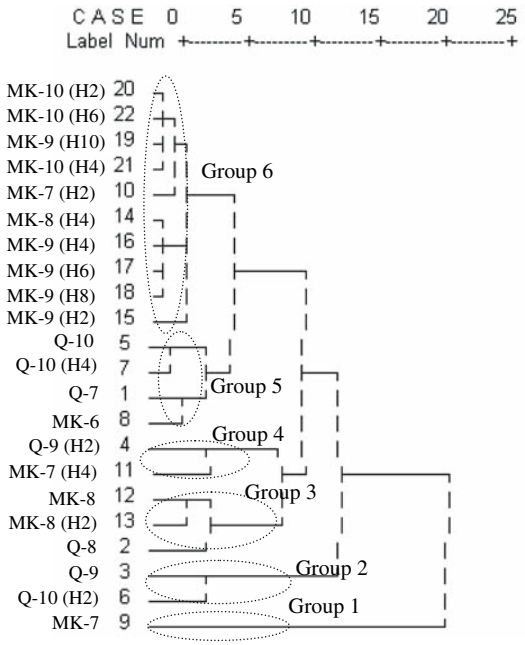

Fig. 6 Grouping of the quinone species based on average linkage cluster

MK-7 as major quinone were believed to be useless in lignocellulose degradation. The correlation analyses indicated that there was no obvious interrelationship between MK-7 content and lignocellulose degrading ratio. Q-9 and Q-10(H2) belong to Group 2 represented those microbes that could not tolerate very high temperature since their concentration decreased rapidly along with the temperature increase. Their concentration after day 11 correlated to the cellulose and hemicellulose degradation (Fig. 7). No obvious relationship was found between their concentration and lignin degradation. These results indicated that microbes containing Q-9 or Q-10(H2) as major quinone might be the most important hemicellulose and cellulose degrading microorganisms during composting since each quinone might derive from more than one bacterium containing non-lignocellulose degrading ability.

The microbes containing Q-8, MK-8 or MK-8(H2) belong to Group 3 as major quinone could tolerate high temperature. No obvious relationship was found between the content of these quinones and lignocellulose degradation, but they were supposed to assist lignin degrading since the content of these quinones were high during the thermophilic phase. *Thermus thermophilus* that contain MK-8 as the major quinone and produce xylose isomerases was found dominant during thermophilic composting (Blanc et al. 1999; Pantazaki et al. 2002; Tang et al. 2004).

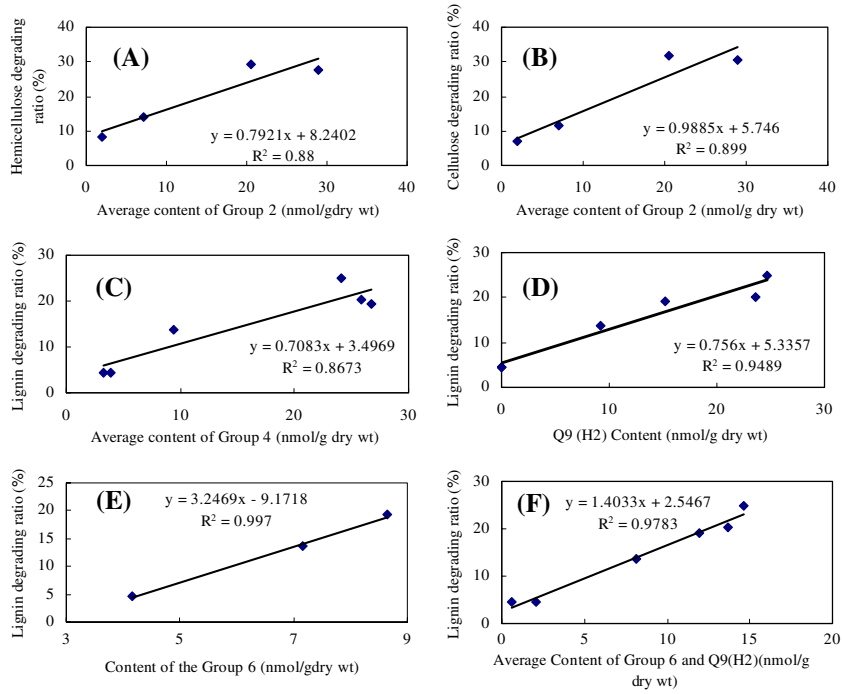

Fig. 7 Relationship between lignocellulose degradation and quinone content. (**A**) hemicellulose degrading ratio and content of Group 2 quinones after 11 days composting, (**B**) cellulose degrading ratio and content of Group 2 quinones after 11 days composting, (**C**) lignin degrading ratio and content of Group 4, (**D**) lignin degrading ratio and content of Q-9(H2), (**E**) lignin degrading ratio and content of Group 6, (**F**) lignin degrading ratio and average content of Group 6 and Q-9(H2)

Group 4 include the quinones MK-7(H4) and Q-9(H2). The former was usually found during composting, while the latter was infrequent. Takizawa et al. (1992) isolated it as a minor ubiquinone component from the fungus *Aureobasidium pullulans*. In this work, the remarkable correlation between lignin degrading ratio and the content of Group 4, especially that of Q-9(H2) was found (Fig. 7). Therefore, the microbes containing Q-9(H2) as major quinone might be the most important lignin degrading microorganisms during agricultural waste composting.

As to Group 5 containing Q-7, Q-10, Q-10(H4) and MK-6 found in mesophilic bacteria and fungi, no obvious correlation was found between their content and lignocellulose degradation. Since their content slightly increased during the second fermentation during composting, these mesophilic microbes existed in that phase might partially transform lignocellulose. *Chaetomium* sp. and *Botrytis* sp. containing Q-10(H4) as well as *Aspergillus fumigatus* containing Q-10 as major quinone were isolated as the fungi with lignin-degrading potential from woody compost (Chamuris et al. 2000).

Those partially saturated and long-chain menaquinones including MK-7(H2), MK-8(H4), MK-9(H2), MK-9(H4), MK-9(H6), MK-9(H8), MK-9(H10), MK-10(H2), MK-10(H4) and MK-10(H6) composed Group 6. During the thermophilic period (from 6 to 15 days), remarkable correlation was established between the average content of Group 6 and lignin degradation (Fig. 7). There was obvious correlation between lignin degrading ratio and individual quinone content of Group 6 except MK-7(H2) during this phase. These results confirmed that *Actinobacteria* might be responsible for lignin degradation during the thermophilic composting period.

Since the microbes containing Q-9(H2) or Group 6 quinones as major quinone were found to be the most important lignin degrading microorganisms, the correlation between their average content and lignin degrading ratio was upbuilt as shown in Fig. 7. Apparently, the correlation was more precise to reflect lignin biodegradation during agricultural waste composting than what is established between Q-9(H2) content and lignin degrading ratio. Thus microorganisms containing Q-9(H2) as major quinone and many thermophilic *Actinobacteria* were believed to be responsible for lignin degradation during agricultural waste composting.

Conclusions

The quinone profile method was successfully applied in monitoring the microbial community succession during agricultural waste composting. The change of TQ, DQ and quinone profiles confirmed that the microbial community developed successively and became more complex with the composting duration. Bacteria indicated by MK-7 and fungi containing Q-9 as major quinone were predominant and seemed to be important during the beginning period of composting. *Actinobacteria* was preponderant during thermophilic stage, while *Actinobacteria*, fungi and some bacteria were found cooperating with each other during the later maturating phase. Furthermore, the changes in quinone profiles were found to be correlated with lignocellulose degradation. The microbes containing Q-9 or Q-10(H2) as major quinone were the most important hemicellulose and cellulose degrading microorganisms during composting. While the microorganisms containing Q-9(H2) as major quinone and many thermophilic *Actinobacteria* were believed to be responsible for lignin degradation during agricultural waste composting.

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