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Changes of microbial population structure related to lignin degradation during lignocellulosic waste composting

Dan-Lian Huang [a,b], Guang-Ming Zeng [a,b,*], Chong-Ling Feng [a,b], Shuang Hu [a,b], Cui Lai [a], Mei-Hua Zhao [a], Feng-Feng Su [a,b], Lin Tang [a,b], Hong-Liang Liu [a]

[a] College of Environmental Science and Engineering, Hunan University, Changsha 410082, China
[b] Key Laboratory of Environmental Biology and Pollution Control (Hunan University), Ministry of Education, Changsha 410082, China

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ABSTRACT

Microbial populations and their relationship to bioconversion during lignocellulosic waste composting were studied by quinone profiling. Nine quinones were observed in the initial composting materials, and 15 quinones were found in compost after 50 days of composting. The quinone species Q-9(H2), Q-10 and Q-10(H2) which are indicative of certain fungi appeared at the thermophilic stage but disappeared at the cooling stage. Q-10, indicative of certain fungi, and MK-7, characteristic of certain bacteria, were the predominant quinones during the thermophilic stage and were correlated with lignin degradation at the thermophilic stage. The highest lignin degradation ratio (26%) and good cellulose degradation were found at the cooling stage and were correlated with quinones Q-9, MK-7 and long-chain menaquinones attributed to mesophilic fungi, bacteria and actinomycetes, respectively. The present findings will improve the understandings of microbial dynamics and roles in composting, which could provide useful references for development of composting technology.

1. Introduction

Lignin, the second most abundant renewable resource on the earth is difficult to degrade (Huang et al., 2006; Pérez et al., 2002) and also slows biodegradation of cellulose and hemicellulose in lignocellulosic plant materials because it acts as a physical barrier protecting the carbohydrates. Large quantities of lignocellulosic wastes are generated by the logging industry and agriculture. These wastes are valuable for soil erosion control and soil nutrient replenishment, but harm the environment if applied without proper treatment such as composting (Bustamante et al., 2008; Huang et al., 2008; McMahon et al., 2008). The degradation and transformation of lignocellulosic waste is attributed to the metabolism of indigenous microorganisms during composting. Different microbial population dominate at various stages of composting, and have distinct roles in degradation of organic matter (Belyaeva and Haynes, 2009; Raut et al., 2008).

Such microbial communities have been studied by culture-dependent methods, but culture-independent approaches have become more prominent and include genetic methods, phospholipid fatty acids (PLFA) analysis and quinone profile method (Kurisu et al., 2002; Lorenz et al., 2006; Puglisi et al., 2005; Vivas et al., 2009). Since most of the microorganisms contain one major quinone species as biomarker in their membranes, the mole fractions of quinones should reflect the dominant microbial community, and the quinone profile should reveal taxonomic diversity of community (Hiraishi et al., 2003; Hu et al., 1999). Quinone profiling has been used to characterize microbial populations in wastewater, natural aquatic system and soil (Hasanudin et al., 2004; Hu et al., 2001; Katayama et al., 2001), and it is sensitive enough to detect temporal changes in microbial population structure during composting (Hiraishi et al., 2000; Tang et al., 2003).

Since lignocellulolytic microbial populations play important roles in the successful operation of composting (Pérez et al., 2002; Zeng et al., 2007), we investigated microbial population structure and dynamics by quinone profiling at various stages of lignocellulosic waste composting. The relationships between lignocellulolytic microbial community and lignin degradation were also studied to evaluate the roles of lignocellulolytic microorganisms in lignocellulosic waste composting.

2. Methods

2.1. Materials preparation

Wheat straw, root vegetable residues, bran and soil were collected from a suburb of Changsha, China. Wheat straw and root

* Corresponding author. Address: College of Environmental Science and Engineering, Hunan University, Changsha 410082, China. Tel.: +86 731 88822754; fax: +86 731 88823701.
E-mail address: zgming@hnu.cn (G.-M. Zeng).

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vegetable residues were air-dried and cut into pieces about 20 mm in size. Bran was used to adjust the initial carbon-to-nitrogen (C/N) ratio of composting. Soil was air-dried and ground to pass through a 2-mm nylon screen and added to provide indigenous microorganisms and some necessary nutriments. Wheat straw, root vegetable residues, bran and soil were mixed thoroughly to obtain a mixture with an organic matter content of 62.2% (dry weight), and a C/N ratio of about 31:1. The water content was 65% and the initial content of lignocellulose was 47.3% (dry weight).

2.2. Composting and sampling

The composting mixture was packed loosely in an open box (76 × 55 × 45 cm; with a 70% filling level) under indoor conditions. The pile was turned once every three days in the first 2 weeks and then once every six days afterwards. The composting experiment was performed in three replicates (done simultaneously), and each lasted 50 days. Nine sub-samples were periodically taken from the top, middle and bottom depths in the different sections of pile (left, middle and right), respectively. The nine sub-samples were combined for the analyses. The temperatures in the above nine sampling positions were monitored, and the mean value was considered as the temperature of compost pile. The standard errors of means of temperature were below 0.4 (n = 9).

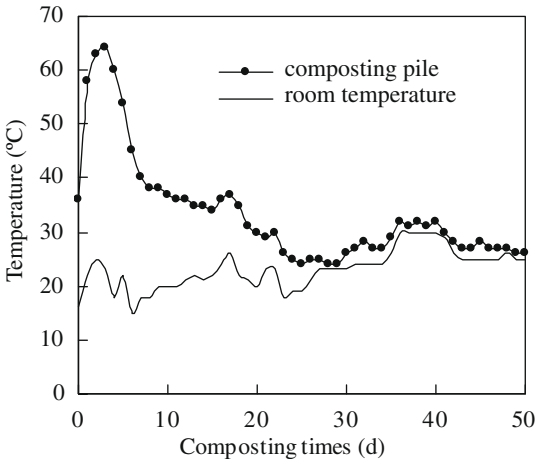

Fig. 1. Changes in temperature of compost pile.

2.3. Analytical methods

Temperature, water, lignocellulose component and quinone content were analyzed in triplicate. The temperature of compost pile and environment were monitored daily. The moisture content of samples was determined by oven-drying at 105 °C for 24 h.

Neutral detergent fiber (NDF), acid detergent fiber (ADF) and acid detergent lignin (ADL) were determined according to Soest et al. (1991) by Foss Fibertec 2010 (Sweden). Hemicellulose was estimated as the difference between NDF and ADF. Cellulose was estimated as the difference between ADF and ADL. Lignin content was estimated as the difference between ADL and ash content.

Respiratory quinones were analyzed according to previously described methods (Jeon et al., 2003; Song and Katayama, 2005). Compost sample was extracted three times with a chloroform–methanol mixture (2:1, v/v). The extract was mixed with 30 ml of NaCl–$CaCl_2$ (10% w/v NaCl, 1% w/v $CaCl_2$) solution and re-extracted with 20 ml n-hexane and 10 ml ultrapure water. The menaquinones in the n-hexane extract were eluted with 20 ml of a 2% (v/v) diethylether–hexane mixture in two Sep-Pak Plus Silica cartridge (Waters, Japan) joined in series. Then the ubiquinones were eluted with 20 ml of a 10% (v/v) diethylether–hexane mixture and analyzed with a high performance liquid chromatograph (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). Menaquinone and ubiquinone samples were monitored at 270 and 275 nm, respectively. Quinone species were identified according to retention time and UV absorption spectrum. The content of each quinone was calculated from the peak area based on the mole absorption coefficients. Ubiquinones (Qs) and menaquinone (MKs) with n isoprene units in their side chains are designated as Q-n and MK-n, respectively. Partially hydrogenated Qs and MKs are expressed as Q-n(Hx) and MK-n(Hx), where x shows the number of hydrogen atoms saturating the side chain (Jeon et al., 2003).

2.4. Statistical analysis

Data are the means of three replicates, and the standard deviations were used to analyze experimental data. The standard errors of means were below 1.2% (n = 3). Statistical analyses were performed using the software package SPSS 13.0 for Windows (SPSS, Germany). These tests included (i) one-way analysis of variance (ANOVA) used for testing difference among degradation ratios of lignocellulose components at different stages of composting, and for comparing the mole fraction of quinone species at day 0 with

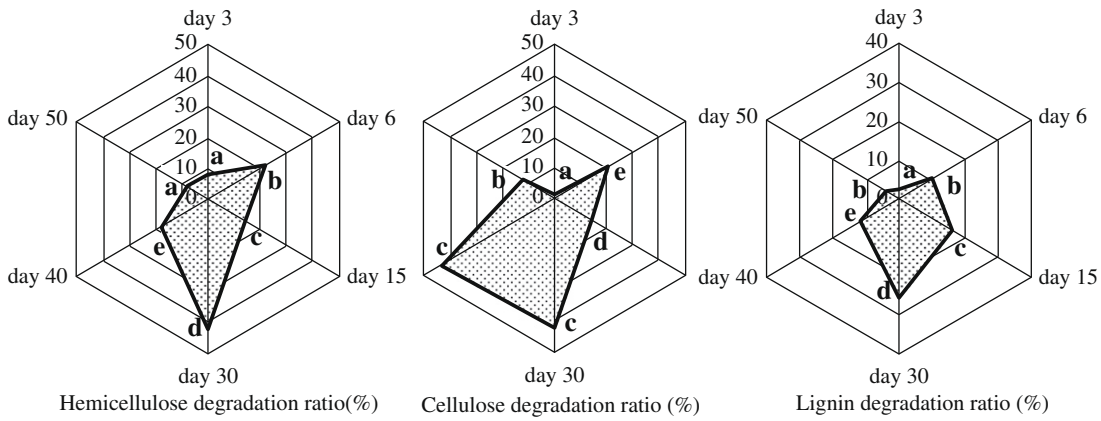

Fig. 2. Degradation of lignocellulose components during the composting process. Results are mean values of triplicate, and the standard deviations are below 2% (n = 3). Different letters in each figure indicate significant differences according to one-way analysis of variance (P < 0.05).

that at day 50, (ii) correlation analyses used to determine the relationships among microorganisms, and relationships between lignocellulose degradation ratio and the content of quinones, respectively and (iii) a principal component analysis (PCA) for the changes in different quinone species.

3. Results and discussion

3.1. Temperature evolution of the compost pile

Since temperature evolution is related to microbial biomass and biological reactions, it is one of the main parameters used to monitor the composting process (Bustamante et al., 2008). Fig. 1 shows a typical composting temperature trend, including the mesophilic stage (before day 1), the thermophilic stage (>50 °C, days 1–5), the cooling stage (days 6–30) and the maturation stage (days 31–50). The temperature increased rapidly and reached a peak on day 3. This might be attributed to the abundant and active indigenous microorganisms in the raw composting materials. After 5 days, the temperature decreased quickly since most of the easily degradable organic matter had been metabolized.

3.2. Degradation of hemicellulose, cellulose and lignin

The degradation ratios of hemicellulose, cellulose and lignin increased significantly ($P < 0.05$) on day 3, and decreased significantly ($P < 0.05$) after day 30 (Fig. 2). High degradation of cellulose was observed between days 3 and 15; however, hemicellulose was mainly transformed between days 3 and 30 except for the early cooling stage (days 6–15). The reason for this phenomenon might be that the hemicellulose-degrading thermophilic microorganisms were dying and the colonization by mesophilic microorganisms was slow during the early cooling stage. Most of the lignin was degraded during the late phase of the thermophilic stage (days 3–5) and the cooling stage (days 6–30). Recalcitrant lignin is chemically bonded with hemicellulose, and the lignin–carbohydrate complexes enwrap cellulose. This intricate association constitutes accessibility barriers to hemicellulose and cellulose degradation (Pérez et al., 2002). The degradation of hemicellulose and cellulose was positively correlated with lignin degradation ($P = 0.017$ and 0.047, respectively) during composting.

3.3. Microbial population structure and dynamics

The quinone profile, expressed as the mole fraction of each quinone species, is usually used to quantify microbial population structure (Hiraishi et al., 2003). The quinone profiles analysis showed a continuous change in microbial population structure during composting (Fig. 3). Nine quinone species were detected in the raw composting materials, and MK-5 accounted for the largest mole fraction, followed by Q-9 and Q-8. After three days, Q-9(H2), Q-10 or Q-10(H2) increased rapidly, MK-5, Q-8, and Q-9 decreased quickly. MK-5 has previously been observed in some sulfate-reducing bacteria (White et al., 2005), but it is not known which microorganism produce this compound in compost. Q-8 has been found in the β-subclass of *Proteobacteria* (such as *Nitrosomonas* spp., *Rhodospirillaceae* spp. and *Chromatiaceae* spp.) (Imhoff, 2006; Lim et al., 2004). Q-9 might be indicative of lignin degraders such as *Aspergillus niger*, *Aspergillus japonicus* and most *Penicillium* strains (Matsuda et al., 1992; Paterson and Buddie, 2008). The decrease in Q-9 could indicate a diminishing presence of mesophilic lignin-degrading fungi during the thermophilic stage. Since Q-9(H2) has previously been found in the hemicellulose-degrading fungus *Aureobasidium pullulans* and Q-10(H2) in the majority of *Talaromyces* species with cellulose-degrading ability (Christov and Prior, 1996; Yaguchi et al., 1996), the appearance of Q-9(H2) and Q-10(H2), these fungi may have also played key

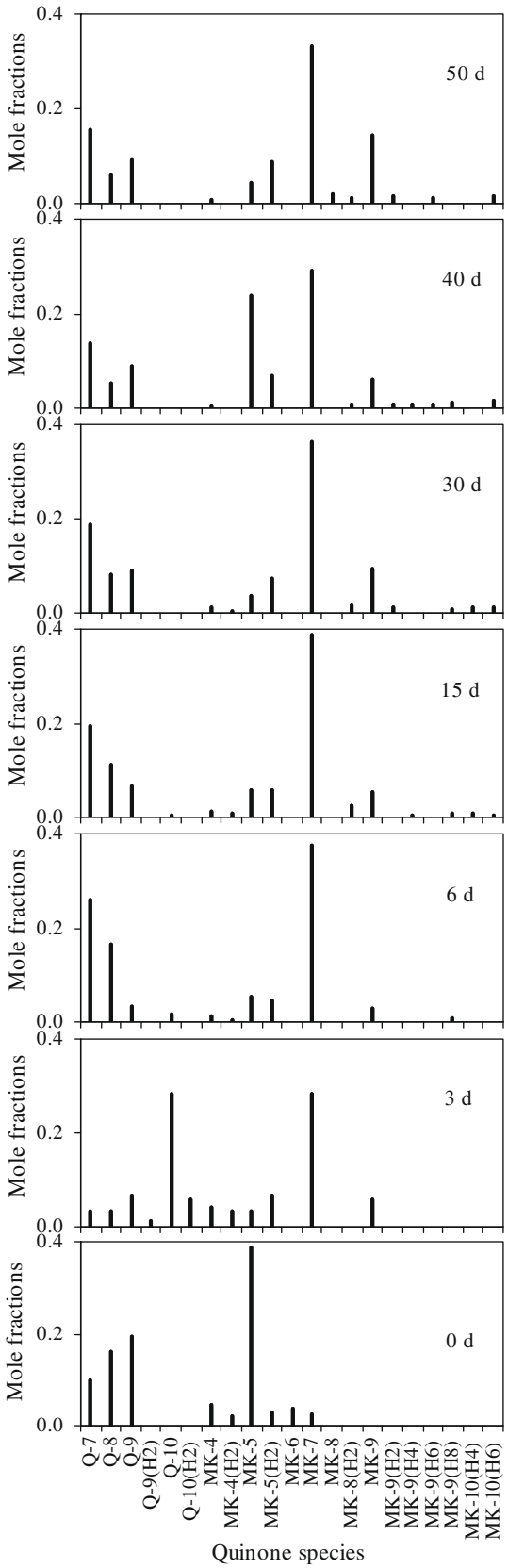

Fig. 3. Mole fractions of quinine species at different times (0, 3, 6, 15, 30 and 50 days) in composting. Results are mean values of triplicate, and the standard deviations are below 1% ($n = 3$).

Table 1
Pearson correlation coefficients among quinone species during composting.

	Q-7	Q-8	Q-9	MK-5(H2)	MK-7	MK-8(H2)	MK-9	MK-9(H2)	MK-9(H4)	MK-9(H6)	MK-9(H8)	MK-10(H4)	MK-10(H6)
Q-7	1												
Q-8	0.519	1											
Q-9	−0.443	0.272	1										
MK-5(H2)	0.001	−0.796*	−0.436	1									
MK-7	0.565	−0.318	−0.402	0.627	1								
MK-8(H2)	0.358	−0.209	−0.213	0.462	0.538	1							
MK-9	0.043	−0.666	−0.296	0.964**	0.536	0.477	1						
MK-9(H2)	0.118	−0.508	−0.005	0.824*	0.294	0.399	0.873*	1					
MK-9(H4)	−0.041	−0.357	−0.148	0.332	0.271	0.346	0.170	0.441	1				
MK-9(H6)	−0.029	−0.453	−0.059	0.682	0.264	0.311	0.717	0.892**	0.375	1			
MK-9(H8)	0.610	0.033	−0.425	0.095	0.505	0.333	−0.047	0.144	0.798*	0.004	1		
MK-10(H4)	0.497	−0.001	−0.257	0.234	0.525	0.728	0.236	0.219	0.322	−0.114	0.603	1	
MK-10(H6)	0.169	−0.528	−0.062	0.769*	0.341	0.466	0.749	0.943**	0.713	0.739	0.413	0.318	1

* Correlation is significant at the 0.05 level (two-tailed).
** Correlation is significant at the 0.01 level (two-tailed).

roles in hemicellulose and cellulose degradation during the thermophilic stage in this study.

Q-10 and MK-7 were dominant quinones on day 3. Q-10 has previously been found in the thermotolerant, lignin-degrading fungus *Aspergillus fumigatus* (Matsuda et al., 1992). MK-7 is considered an indicator of Gram-positive lignocellulose-degrading bacteria with a low G + C content (e.g. *Bacillus* spp., *Clostridium thermocellum* and *Clostridium cellulolyticum*), as well as members of the Cytophaga–Flavobacterium cluster (*Flavobacterium* spp.) and δ- and ε-subclass *Proteobacteria* (Collins and Jones, 1981; Hu et al., 1999) and this quinone species is thus likely derived from thermophilic *Bacillus* spp. and *C. thermocellum* and some mesophilic bacteria during the thermophilic stage. The predominance of Q-10 and MK-7 indicate that the fungi and bacteria producing these quinones are likely the most important lignin-degrading microorganisms during the thermophilic stage of lignocellulosic waste composting.

At the cooling stage, the number of quinone species increased to about 17 from 12 at the thermophilic stage (Fig. 3). Many long-chain menaquinones including MK-8(H2), MK-9(H2), MK-9(H4), MK-9(H6), MK-9(H8), MK-10(H4) and MK-10(H6) appeared, while Q-9(H2), Q-10 and Q-10(H2) decreased. Q-7, contained in some bacteria (such as *Shewanella* sp.), and Q-8, MK-5 and MK-5(H2), found in sulfate-reducing bacteria (Suzuki et al., 2007), increased during the early cooling stage. These bacteria appear to transform organic matter other than lignocellulose, and might also be important for the composting process. The long-chain menaquinones could represent several actinomycete genera (e.g. *Nocardia* spp., *Mycobacterium* spp., *Cellulomonas* spp., *Streptomyces* spp. and *Micromonospora* spp.), and these actinomycetes are able to decompose lignocellulose effectively in composting (Tang et al., 2004).

The gradual increase in Q-9 and MK-9 until day 50 suggests a corresponding increase in lignocellulolytic fungi and actinomycetes (Hiraishi et al., 2003). MK-7 was dominant until the later maturation stage, which might be due to the increase in mesophilic bacteria (such as *C. cellulolyticum* and *Flavobacterium* spp.). Deguchi et al. (1997) confirmed that most of *Flavobacterium* strains could degrade cellulose and low molecular weight lignin fragments. Overall, the quinone profile suggests that the high lignin degradation ratio observed during the cooling stage was due to the cooperation of some fungi, actinomycetes and high numbers of bacteria.

From days 30 to 50 (maturation stage), no obvious changes in quinone species and content were observed. The long-chain menaquinones increased slightly, whereas the predominant quinones decreased slightly. The distribution of quinone species became more even and stable suggesting a slow microbial population succession and a more stable microbial composition during the maturation stage. Furthermore, significant differences ($P < 0.05$) were found between the mole fractions of Q-7, Q-8, Q-9, MK-4, MK-4(H2), MK-5, MK-5(H2), MK-6, MK-7, MK-8, MK-8(H2), MK-9, MK-9(H2), MK-9(H6) and MK-10(H6) on days 0 and 50. This finding indicates that microbial population composition varied significantly after 50 days of composting.

3.4. Relationship among different microorganisms

Correlation coefficients among quinone species were obtained to reveal microbial interactions during lignocellulosic waste composting (Table 1). MK-9(H2) positively correlated with MK-9, MK-9(H6) and MK-10(H6) respectively, which suggests coexistence and possibly even cooperativity among the corresponding microorganisms. Significant positive correlation was also suggested for the bacteria indicated by MK-5(H2) and the ligninolytic actinomycetes containing MK-9 or MK-9(H2) as major quinone.

3.5. Relationship between lignocellulose degradation and lignocellulolytic microorganisms

Principal component analysis (PCA) of the changes in different quinone species was performed. The cumulative contribution rate of the two principal components (PC1 and PC2) reached 64.2%, which accounted for the main information of the changes in microbial community structure. The relationships between each of the two principal components and the loading variables can be seen from the loading plot (Fig. 4). Several quinone species indicative of ligninolytic microorganisms, such as Q-9, MK-7, MK-8(H2), MK-9, MK-9(H2), MK-9(H6), MK-9(H8) and MK-10(H6), showed high PC1 loading scores. PC2 was found with high loading scores for Q-9(H2), Q-10 and Q-10(H2). Since these three ubiquinones increased rapidly with a rise in temperature of the compost pile and then decreased quickly at higher temperatures, their appearance and disappearance could be regarded as a milestone in microbial population succession.

The correlations between lignocellulose degradation and lignocellulolytic microorganisms were analyzed (Figs. 5 and 6). No obvious relationship was found between hemicellulose degradation and any of the quinones. A remarkable linear correlation between lignin degradation ratio and MK-10(H4) content was found. *Micromonospora* strains containing MK-10(H4) as major quinone have been found to be responsible for lignin and cellulose degradation

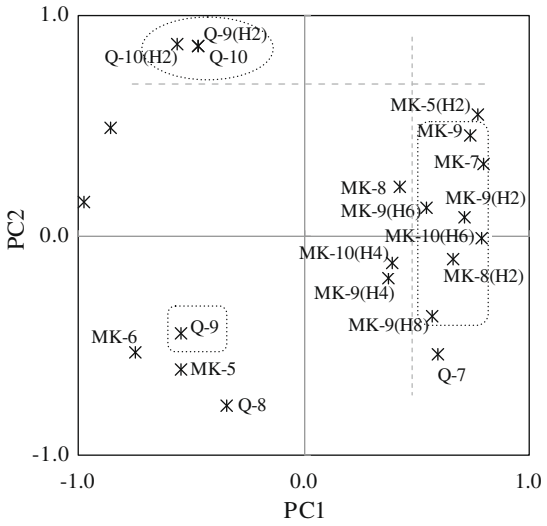

Fig. 4. Loading plot from principal component analysis (PCA) of different quinone species.

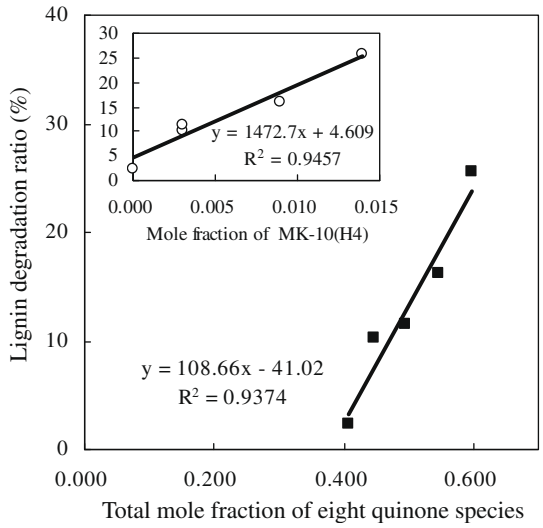

Fig. 5. Relationship between lignin degradation ratio and total mole fraction of eight quinone species including Q-9, MK-7, MK-8(H2), MK-9, MK-9(H2), MK-9(H6), MK-9(H8) and MK-10(H6). The small figure shows the relationship between lignin degradation ratio and MK-10(H4).

(McCarthy and Broda, 1984). No obvious relationship was established between lignin degradation and other single quinone species; however, there was a significant positive correlation between the lignin degradation ratio and the total content of Q-9, MK-7, MK-8(H2), MK-9, MK-9(H2), MK-9(H6), MK-9(H8) and MK-10(H6). The results indicate that the microbial community consisting of mesophilic fungi, actinomycetes and bacteria played a key role in lignin degradation during lignocellulosic waste composting. Tuomela et al. (2000) reported that some of fungi could completely degrade lignin to carbon dioxide and water, whereas actinomycetes and bacteria attacked the lignin molecule mainly by removal of methoxyl groups and breakdown of C_α–C_β linkages.

Except for MK-10(H4) and MK-8(H2), cellulose degradation did not correlate with other quinone species (Fig. 6), but a remarkable correlation between cellulose degradation and the total content of MK-7, MK-8(H2), MK-9, MK-9(H2), MK-9(H6), MK-9(H8) and MK-10(H6) was observed. The reason might be that the ligninolytic bacteria and actinomycetes indicated by these menaquinones can

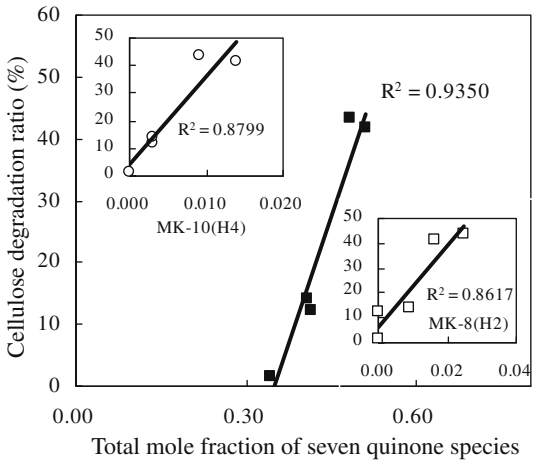

Fig. 6. Relationship between cellulose degradation ratio and total mole fraction of seven quinone species including MK-7, MK-8(H2), MK-9, MK-9(H2), MK-9(H6), MK-9(H8) and MK-10(H6). The two small figures show the relationships among cellulose degradation ratio and MK-10(H4), and MK-8(H2).

produce highly active cellulase (Katayama et al., 2001; Tuomela et al., 2000).

4. Conclusions

Quinone species increased from 9 at day 0 to 15 at day 50, indicating microbial population succession in composting. Fungi indicated by Q-9(H2) or Q-10(H2) were considered to be the most important hemicellulose and cellulose-degrading microorganisms during thermophilic stage, while high-temperature resistant fungi and Gram-positive bacteria were responsible for lignin degradation. However, high lignin degradation at cooling stage might be attributed to the cooperation of mesophilic fungi, actinomycetes and bacteria respectively represented by Q-9, long-chain menaquinones and MK-7. The present findings could be used as references for screening ligninolytic microorganisms and promoting lignocellulose bioconversion in composting by microbial inoculants.

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