



Review

Microhabitat drive microbial anabolism to promote carbon sequestration during composting

Zimin Wei^a, Taha Ahmed Mohamed^{a,b}, Li Zhao^a, Zechen Zhu^a, Yue Zhao^a, Junqiu Wu^{a,*}

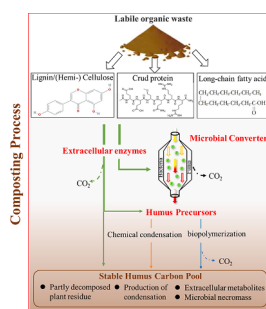
^a College of Life Science, Northeast Agricultural University, Harbin 150030, China

^b Soil, Water and Environment Research Institute, Agricultural Research Center, Giza, Egypt

HIGHLIGHTS

- Microbial metabolism drives the transformation of organic matter in composting.
- Microhabitat factors directly affect microbial metabolism.
- Regulating composting parameters may realize carbon fixation with high efficiency.
- Utilize functional materials could stabilize formed humus components.

GRAPHICAL ABSTRACT



ARTICLE INFO

Keywords:

Composting
Humus formation
Humus stabilization
Carbon sequestration
Microhabitat regulating

ABSTRACT

Transforming organic waste into stable carbon by composting is an eco-friendly way. However, the complex environment, huge microbial community and complicated metabolic of composting have limited the directional transformation of organic carbon, which is also not conducive to the fixation of organic carbon. Therefore, this review is based on the formation of humus, a stable by-product of composting, to expound how to promote carbon fixation by increasing the yield of humus. Firstly, we have clarified the transformation regularity of organic matter during composting. Meanwhile, the microhabitat factors affecting microbial catabolism and anabolism were deeply analyzed, in order to provide a theoretical basis for the micro habitat regulation of directional transformation of organic matter during composting. Given that, a method to adjust the directional humification and stabilization of organic carbon has been proposed. Hoping the rapid reduction and efficient stabilization of organic waste can be realized according to this method.

1. Introduction:

Organic solid waste (OSW) transformation has become an important topic in recent years owing to its mass discarding and improper disposal, including developing and developed countries (Angulo-Mosquera et al.,

2021; Liu et al., 2017). Generally, compost is one of the best ways to management organic waste C, for it avoids secondary pollution caused by arbitrarily discard and incinerate (Neri et al., 2018). Compost can also rapidly and efficiently transform OSW into positive end-product which is beneficial to improve soil fertility, repair environmental

* Corresponding author at: College of Life Science, Northeast Agricultural University, Harbin 150030, China.

E-mail addresses: wujunqiu1990@126.com, wujunqiu@neau.edu.cn (J. Wu).

<https://doi.org/10.1016/j.biortech.2021.126577>

Received 31 October 2021; Received in revised form 10 December 2021; Accepted 11 December 2021

Available online 16 December 2021

0960-8524/© 2021 Elsevier Ltd. All rights reserved.

pollution, and even be widely utilized in pharmaceutical and cosmetic fields (Awasthi et al., 2021; Chen et al., 2022). Because organic carbon (C) transformation in composting is ultimately the consequence of microbial growth and activity (Witzgall et al., 2021), understanding C release and fixation in compost demands improved knowledge of how microbial physiology regulates the process controlling organic C degrading, transforming, CO₂ releasing and humification.

Microorganisms perform two contrary roles in transforming organic C during composting: promoting release of CO₂ into the atmosphere by catabolism or fixing C into compounds that with high humification degree and not easy to be degraded by metabolism (Kallenbach et al., 2016; Liang et al., 2017). To date, researches has focused on the role of microhabitat in regulating humification with less attention paid to anabolism to generate products that can be sequestered (Cotrufo et al., 2015; Liang et al., 2017). This has stimulated research considering the direct incorporation of microbial residues (cellular components from both living and senesced biomass) into the stable organic C pool (Benner, 2011; Ludwig et al., 2015; Miltner et al., 2012; Schaeffer et al., 2015). Recent studies with the main purpose of research on humification is to promote compost maturity by improving microbial activities through regulating microhabitats (aeration, charcoal); while for the purpose of C sequestration, research needs to control carbon emissions based on promoting compost maturity (Awasthi et al., 2020a). High microbial activities are contributed to C transformation and sequestration, but it also leads to huge amount of C be transformed into CO₂, causing organic C loss (Kone & Yao, 2021). During composting, microbe with high active state will promote CO₂ emission accounts for 1.81% of the organic matter (Lu et al., 2018). Calculated according to the composting plant with an annual treatment capacity of 100,000 tons, the cumulative emission of CO₂ is as high as 1810 tons, which causing a huge waste of organic matter. Nevertheless, the less release of CO₂ may reflect low microorganism activities, which might delay the humification process. Therefore, any attempt to manage compost for promoting C sequestration will require an understanding of how to manage microbial-derived C in compost by reducing CO₂ emission. Actually, reducing the release of CO₂ is to reduce the utilization of formed small molecular organic matter by microorganisms. To regulate microbial metabolism to decompose macromolecular organic matter and provide precursor compounds for the formation of stable organic matter such as hums during composting.

To this end, we cite microbial carbon pump (MCP, it was first proposed in marine system and used for reference by soil science (Jiao et al., 2010; Liang et al., 2017) as a conceptual framework for understanding the role of microbial processes in regulating organic waste C dynamics. This framework breaks the balance between organic carbon decomposition and formation (Liang et al., 2017). It highlights the effect of microenvironment on microbial assimilation in the production of stable organic compounds. Here, we focus on the role of microbial metabolism in compost C dynamics, particularly the contributions of microbial anabolism to stable C storage. We first discuss evolving views on metabolic controls of compost microorganism in organic waste C turnover. We then discuss the influencing factors that control microbial metabolism relating to C sequestration during composting. Finally, we propose a way to regulate the parameters to advance C storage by reducing C release during composting.

2. Transformation of organic carbon during composting

Composting is a process of transforming organic waste into mature products by microbial hydrolysis, microbial synthesis and chemical synthesis (Rebollido et al., 2008; Chen et al., 2020; Zhou et al., 2021). Among them, the microbial metabolism is the basis in driving organic C transformation during composting. Conversions in organic C mainly process three stages: degradation, release of CO₂ and C sequestration.

2.1. Degradation of organic waste

OSW, including garden waste, such as agricultural straw, lawn waste, fruit and vegetable waste, municipal solid waste, livestock manure, kitchen waste, can be classified into lignin-like, cellulose-like, protein-like and fat-like materials (Zhao et al., 2019). During composting, the non-structural compounds derived from OSW will be incorporated into microbial biomass firstly (Cotrufo et al., 2015). The protein, fat, lignin and cellulose will be degraded in order afterwards (Liu et al., 2015). Actually, there are no clear boundaries among the degradation of protein, fat compounds, lignin and cellulose. In the initial stage of composting, microorganisms will degrade the non-structural compounds like labile protein-like or fat-like compounds in disorder for adapting the environment by releasing protease and lipase with the production such as ammonia, hydrogen sulfide and organic acids (Shao et al., 2014; Voberkova et al., 2017). With the composting proceed, microbial biomass and activity are gradually stabilizing, the degradation is also gradually taking cellulose, hemicellulose, lignin, and any other refractory organic C as the main objective (Zhao et al., 2017). These refractory organic carbons will be degraded by extracellular enzymes, including endoglucanases, cellobiohydrolases, β -glucosaccharase, lignin peroxidase and manganese peroxidase (Feng et al., 2011; Payne et al., 2015), into polysaccharide, polyphenols or some monomer molecule which provide substrates for microbial activity and organic C transformation. Of course, partly undecomposed residues will deposit in the compost pile and not readily assimilate by microorganism (Liang et al., 2017). The degradation of organic matter will continue throughout the composting process, which will be detrimental to the retention of organic C in compost. Researches showed that the microbial metabolite and necromass are difficult to be reused by microorganisms (Cotrufo et al., 2015; Jiao et al., 2010). Therefore, increasing microbial biomass and metabolites are the main ways to promote organic C sequestration during composting. Significant knowledge gaps regarding microorganism mediated C preservation in composts include our comprehensive understanding of C loss, C conversation pathways and C retention forms hinders our ability to promote C sequestration during composting.

2.2. Release of carbon dioxide

Reducing CO₂ emission is one of the main ways to enhance organic C sequestration by regulating microbial metabolism (Hu et al., 2019). It is necessary to clearly understand pathways of CO₂ release at first. It can be categorized two major pathways by which microorganisms influence CO₂ emission: *ex vivo* (extracellular) degradation, in which extracellular enzymes attack and transform organic waste to labile organic C that can readily assimilated by microorganisms; and *in vivo* turnover of organic C via dauntingly complicated metabolism pathway. In the *ex vivo* degradation, CO₂ release is the result of extracellular hydrolysis of organic matter, which is the key steps for deposition of microbial-derived C and should not be restricted by any external force. Therefore, regulating microbial metabolism to limit CO₂ release maybe an effective way to promote C fixation. Decarboxylation reactions are the basic pathway for producing CO₂, which can be regulated by the feedback of NADH, ATP and other inhibitors (Jones et al., 2016; Weusthuis et al., 2011). *In vivo* turnover, fatty acid α -oxidation, amino acids decarboxylation, conversion of pyruvate to acetyl-CoA and tricarboxylic acid cycle (TCA) are the main ways of CO₂ production during composting. Among them, TCA is the core path for receiving end products of these pathways and providing intermediates for other anabolisms. Theoretically, inhibition of TCA can reduce CO₂ released by microbe. However, TCA as the basic pathway of cellular respiration, it is bound to inhibit microbial activity if its metabolism is blocked. Therefore, can we find a way to reduce CO₂ emission by improving the microbial anabolism?

2.3. Microbial carbon pump in composting

MCP is a comprehensive concept involving environment, nutrient source, physiology, molecule and gene interactions for refractory C synthesis and storage of related C in composting systems (Jiao et al., 2010). Factors affecting microorganisms to *in situ* synthesize refractory C are generally referred to microhabitats here. Therefore, the MCP is used as the theoretical support to discuss how to promote the transformation of degradable substances into refractory C by adjusting the microhabitats. During composting, anabolism of aromatic compounds can contribute to improve C stability and promote organic C sequestration. In the microbial anabolism, shikimic acid and acetic acid-malonic acid pathway are the main ways to synthesize lignin-like compounds (Stevenson, 1994; Tan, 2014). On the other hand, increasing microbial biomass is another way to promote organic C sequestration, because of the refractory property of microbial structure substances, such as chitin, amino sugar, lipopolysaccharide, are different to be degraded by microorganism again (Cheng et al., 2017). During composting, readily alkane compounds will be transformed into aromatic substances through the above pathways, and the productions are mainly stored as humus (Stevenson, 1994). Humus as one of the most important by-products of composting, improving its yield and aromatic structure has been focus of current studies about organic waste composting (Piccolo et al., 2019; Rodriguez et al., 2016). Therefore, this study aims to promote the contribution of microbial anabolism to carbon fixation by regulating composting microenvironment based on a thorough understanding of microbial anabolism and its influencing factors (Fig. 1).

3. The influencing factors of carbon metabolism

Microorganisms are the main drivers of C flow in composting and play critical roles in the C balance through the decomposition and anabolism of organic waste of different origin. Here, we review the main factors affecting mineralization and assimilation of organic matter. It appears to be an important step to understand both the C flow and the mechanism controlling the sequestration of C during composting (Fig. 1).

3.1. Factors affecting CO₂ release

In vivo, many factors including substrate patterns, microhabitat and the existence of minerals can drive CO₂ release. Commonly, readily assimilated substrates of glucose, hemicellulose and even the fungal biomass can promote CO₂ release significantly (Lopez-Mondejar et al.,

2018). On the other hand, the existence of clay, mineral or metallic oxide can protect organic C from microbial mineralization to CO₂ (Johnson et al., 2015; Lalonde et al., 2012; Ma et al., 2018). However, during composting, the most important factor affecting CO₂ release is the microhabitat in which microorganisms live, including aeration rate, moisture, pH, temperature and any others environmental factors. During aerobic composting, appropriate aeration rate is the key to ensure oxygen concentration and maintain the high activity of microorganisms (Gao et al., 2010). Moreover, suitable moisture (commonly 60–65%) combines with good dissolved oxygen can reduce the waste of organic C in the form of CO₂ (Chen et al., 2020). Because even under adverse conditions, microorganisms still maintain basic breathing, released CO₂ is almost equal to the desirable microhabitat and the microbial activity and diversity are also limited under water shortage conditions (Whitman et al., 2016). In addition, tricarboxylic acid cycle as a major source to produce CO₂ *in vivo*, which can be regulated by some regulatory factors during composting (Wang et al., 2019). Adenosine triphosphate and nicotinamide adenine dinucleotide as the direct energy and reducing power are like “two sides of a coin”. They may not only enhance the C flux, but their high concentration may also slow the metabolism rate by the feedback inhibition (Causey et al., 2004; Shima et al., 2008; Zhou et al., 2009). However, the adenosine triphosphate and nicotinamide adenine dinucleotide can only promote CO₂ production, while the malonic acid, a succinic acid substrate analogue, is effective in inhibiting the release of CO₂.

3.2. Factors related to microbial anabolism

Microbial anabolism including “vegetative growth” and “reproductive growth”, both contribute to C sequestration, but they are also affected by environmental factors at the same time (Glassman et al., 2018). The fixed factor is composting period which promoting microbial transformation between two metabolic modes with other factors remain unchanged. At the initial period of composting, the easily degradable plant materials are firstly utilized for microbial cell growth, that is vegetative growth (Palaniveloo et al., 2020). Driven by the time turnover, they will use sufficient nutrition to enter the reproductive growth stage. Microorganisms thus promote the C fixation into microbial biomass in an iterative process of cell generation, growth and death. In addition, the microhabitat factors (pH, temperature, moisture, physicochemical property, types of substrates and so on) as the variable factors can regulate the anabolism of microorganism in the whole composting process (Wang et al., 2019). Especially the composting temperature which is not conducive to microbial survival in its highest

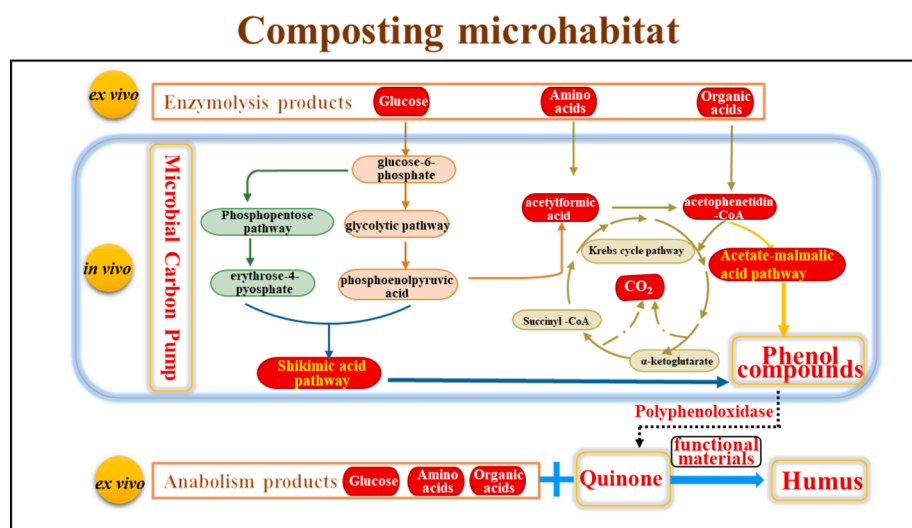


Fig. 1. Microbial metabolism affected by micro habitat during organic wastes composting.

level (~70 °C) (Zhang et al., 2016). However, thermotolerant microorganisms remain active, providing sustainable energy by driving C conversion, even though this period is in the extreme water shortage environment. In order to survive in harsh environment, microorganisms will slow down anabolism for maintain basic respiration (Wang et al., 2019). Moreover, the change of pH from low to high caused by the production of organic acid and humus formation in compost also pushes the microbial metabolism from synthesis to decomposition (Malik et al., 2018). Comprehensively speaking, long term and stable microenvironment is conducive to the anabolism of microorganisms. Nevertheless, in view of the high temperature is the essential factor to kill the pathogens derived from the organic waste, which have limited the above process. Therefore, in the changing composting environment, microorganisms with prominent anabolism may become an important research object for the purpose of carbon sequestration. It can highlight their dominant role in composting through micro environment regulation.

4. Regulating the process parameters of carbon transformation

4.1. Physicochemical regulator

Physicochemical regulators including temperature, pH, C/N, aeration rate, moisture, ammoniacal nitrogen and nitrate nitrogen can not only adjust C transformation, but also the basic parameters to maintain composting process. Commonly, regulating the initial C/N is about 25 ~ 30 and maintaining the moisture at 60–70% in composting process is beneficial to ensure the success of composting (Proietti et al., 2016; Silva et al., 2014). In addition, regulating the aeration rate is contribute to accelerate the maturity of composting products (Gao et al., 2010; Yuan et al., 2016). It is meaningful for reducing organic solid waste pollution. Moreover, reasonable control of aeration can also affect the structure of humus during composting (Gao et al., 2010; Wu et al., 2019). The structure of humus may directly affect its utilization: humus with high aromatic components can be applied in contaminated soil as a soil remediation agent, while the humus with more alkanes fraction may make a stronger contribution in improving soil fertility (Wu et al., 2019). Applying the humus to environment according to the structure and composition will effectively improve the utilization efficiency of compost products and environmental governance. This kind of classified application is called the resource utilization of humus by different components. When compost products are used as organic fertilizers, C/N, ammoniacal nitrogen and ammonia reflux can promote the available nitrogen and phosphorus content in compost products (Wang et al., 2020b). However, the composting process regulated by microhabitat factors is realized by changing microbial metabolism, whether it is to shape the structure of humus or to improve the nutrient content of compost products. The activity of culturable and unculturable microorganisms in compost can be fully mobilized by regulating composting microhabitat factors (Wei et al., 2021). This provides the possibility for the regulation of microbial anabolism by microenvironment factors. In addition to environmental factors, microbial activity is also affected by other microorganisms or its related regulators.

4.2. Biological regulators

During composting, microbial inoculation involved in promoting recalcitrant components degradation (Wu et al., 2022), limiting carbon emission (Awasthi et al., 2020a), enhancing nitrogen fixation (Zhang et al., 2016), boosting compost start-up in low temperature (Xie et al., 2021), controlling pollution of organic waste by composting (Chen et al., 2019), and so on. In the study of organic carbon fixation, the effects of microbial inoculation on organic matter transformation are mainly considered. The research on promoting recalcitrant components hydrolysis by microbial inoculation has still attracted much attention, especially for the degradation of lignocellulose (Cortes-Tolalpa et al., 2016; Fernandez-Bayo et al., 2019). Even that, the mosaic structure of

lignin and cellulose still limits the metabolic intensity and enzyme activity of microorganisms (Sitarz et al., 2016). Additionally, the complexity and drastic changes of composting environment also affect the effect of inoculant. Therefore, both the functional and environmental tolerance should be considered when inoculating microorganisms for the purpose of promoting lignocellulose degradation. Recently, preliminary progress has been made in microbially promoting lignin cellulose hydrolysis in composting. Meanwhile, the small molecular products after hydrolysis have also attracted attention, because the active inoculation may mineralize them as energy, which will cause organic carbon loss (Razanamalala et al., 2018). Accordingly, microbial assimilation of small molecular organic matter is also very important during composting with inoculation. But unfortunately, little studies focused on the microbial anabolism. Stable composting system is conducive to microbial anabolism which synthesis of metabolites through primary and secondary metabolism and even the necromass (Liang et al., 2017; Ni et al., 2021). During the period of drastic changes in the composting environment, no matter the exogenous or indigenous microbe, high microbial activity and diversity promote the formation of a large number of small molecules compounds that are both energy and humus precursors (Tan, 2014). Thereafter, limiting microbial activity and promoting the polymerization of precursor compounds may be conducive to the immobilization of organic carbon in the form of humus. On the other hand, during composting with the purpose of nitrogen fixation, it was unexpectedly found that the effect of exogenous nitrogen fixing bacteria on carbon fixation was also significant (Wang et al., 2020a). Because ammonia is fixed in the composting system in the form of ammonia nitrogen which can polymerize with reducing sugars, polyphenols, and any other precursors (Stevenson, 1994; Tan, 2014). Similarly, phosphorus regulating bacteria are also beneficial to humus formation. Accordingly, functional bacterial agents that enhance the content of nutrients may indirectly promote carbon fixation. Inoculation of microorganisms related to carbon transformation has also achieved certain progress in promoting organic carbon fixation (Wu et al., 2020). However, the research is still at the level of enzyme activity, microbial community or organic matter concentration (Ni et al., 2021), few studies focus on microbial anabolism. While, there are abundant studies on microbial agents combined with functional materials to promote organic carbon immobilization.

4.3. Functional material adjustment

In this review, the functional materials mainly point to the exogenous materials which were added to promote the composting process. The most common functional material is biochar, which has been studied in regulating composting system, accelerating composting maturity, controlling heavy metal pollution in waste and improving humification of composting products (Chen et al., 2020; Godlewska et al., 2017). In the respect of carbon sequestration, the effect of common biochar (without modification and not used in combination with other materials) on composting mainly promoted the humification, while the organic carbon fixation needs to be further detected (Guo et al., 2020). Because the ordinary biochar mainly be regarded as bulking agent to increase the porosity of composting (Yin et al., 2021). However, modified biochar, high biochar concentration or biochar combined with other functional materials can efficiently promote carbon fixation (Awasthi et al., 2020b; Li et al., 2020; Qu et al., 2020). Before the beginning of composting, addition of regulator to promote composting humification is the most common application of functional materials, include the metallic oxide, mineral, humus precursors, modified biochar or others, which have been studied for decades years (Li et al., 2020; Qi et al., 2012; Wu et al., 2022). While the research reports on promoting the directional transformation of organic components to form stable humus are increasing in recent years. During the single material composting, the formation efficiency of humus is often limited due to the haploid type of humus precursor. Therefore,

researches that added amino acids or reducing sugars as functional precursors into straw or chicken manure composting have been conducted to promote humus formation (Wu et al., 2022; Zheng et al., 2021). Additionally, benzoic acid has also been utilized as aromatic skeleton of humus to improve carbon stabilization (Zhang et al., 2018). On the other hand, metallic oxide (e.g., manganese (IV), iron (III), aluminum and silicon oxide) can catalyze humus precursors polymerization by abiotic process to form humus (Jokic et al., 2004; Qi et al., 2012; Zhang et al., 2017). In earlier years, this chemical catalysis was mainly achieved under sterile conditions (Hardie et al., 2009; Jokic et al., 2004; Song et al., 2021). In recent years, it has been proved in composting practice that their promoting effects on humus formation depends on the material source, especially for manganese dioxide (MnO_2) (Wu et al., 2020). If there are abundant reducing sugars, MnO_2 will effectively exert its chemical catalytic properties and promote the formation of humus (Wu et al., 2020). Otherwise, MnO_2 will act as bioactive activator to drive OC degradation (Qi et al., 2021; Wu et al., 2020). Overall, the application of multi-functional materials should be targeted according to the material type in order to obtain high-efficiency carbon sequestration.

5. Future perspectives of the retention of organic matter

At the later stage of composting, the humus, plant residue, and some unpolymerized microbial necromass (for the broken cytoplasmic membrane, structural protein and any other metabolic intermediates) and extracellular metabolites are composed of the stable carbon of composting products. However, the persistence of microbial activity must degrade the stable organic carbon of compost, including macromolecular humus. Therefore, while preventing carbon loss, it is also necessary to prevent the formed stable carbon from being further degraded by microbe.

5.1. Reduce organic carbon loss by regulating microbial anabolism

Microbial anabolism can be predicted by the results of 16S rRNA gene (Qi et al., 2020). While the most common way is through multi omics to conduct comprehensive research (Hultman et al., 2015; Shahab et al., 2020; Chen et al., 2021). The locally anaerobic of composting will lead to denitrification, which can hydrolyze aromatic compounds by carboxylation (Shi et al., 2020b; Xu et al., 2015). Given humus is a complex macromolecule with aromatic compounds as the core structure, it has great potential to be hydrolyzed by denitrification (Stevenson, 1994). Moreover, study have confirmed that denitrification does reduce the content of humus during composting (Shi et al., 2020a). For solving this issue, the process of dissimilatory nitrate reduction to ammonium

(DNRA) is attracting widespread concern, which utilized the same substrates and enzymes with denitrification (Caceres et al., 2018; Kraft et al., 2014; Ribeiro et al., 2018). In view of the ammonium is also the precursors of humus, regulating denitrification turn to DNRA is a win-win way to promote carbon stabilization. On the other hand, microbial anabolism and catabolism reached a balance at the stably later stage of composting, which also presents the balance between priming effect and entombing effect (Liang et al., 2017). Breaking this balance may also achieve the promotion of carbon fixation (Fig. 2), because microbial anabolism contributes greatly to the formation of soil organic carbon (Kallenbach et al., 2016). But the related studies are insufficient, especially in the composting system. The complex composting environment and microbial communities result in metabolic diversity, which limit the in-depth study of metabolic direction adjustment (Qi et al., 2021), including to confirm the boundary between “reproductive” growth and “vegetative” growth. Reproductive and vegetative growth is a couple concept cited from botany. The vigorous reproductive growth of microorganisms in the early stage of composting provides the possibility for the hydrolysis of organic matter and the increase of composting temperature. But the persistence of this growth state is not conducive to the sequestration of organic matter. At the later stage of composting, vegetative growth is dominant and contributes to organic carbon fixation. However, vegetative growth is the basis of reproductive growth, and reproductive growth is a necessary condition for vegetative growth. They restrict and compete with each other. No research has revealed the two metabolic transformation conditions and their effects on organic carbon fixation during composting. Therefore, it is necessary to explore the influencing factors of microbial metabolism in the composting process in order to better adjust the metabolic direction according to different composting purposes.

5.2. Preservation by functional materials

Metal oxides and minerals can act as functional materials to interact with organic components to form protection and prevent them from being degraded by microorganisms (Johnson et al., 2015; Wiesmeier et al., 2019). For metal oxides, they can combine with organic matter by ion adsorption or chemical interactions, and then form a metal layer on the surface of organic matter (Cloy et al., 2014). The structure of composted products is rich in oxygen-containing functional groups, for example the carboxyl group, phenolic hydroxyl group, alcohol hydroxyl group, benzoquinonyl and any others (Stevenson, 1994). These groups will ionize into negative status, which easy to combine with positively charged metal ions. And it has been confirmed that the metal layer has a significantly protective effect on protecting organic matter (Johnson et al., 2015). However, metal oxides applied must be controlled under

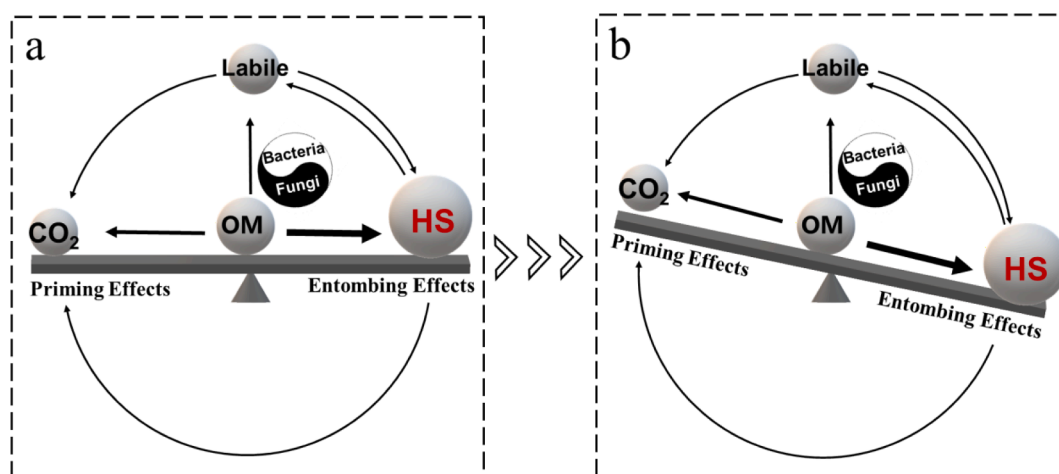


Fig. 2. Promoting humic substance formation by breaking the balance of priming effects and entombing effects (OM: organic matter; HS: humic substance).

pollutant concentration to avoid secondary pollution. Given the threaten of heavy metal pollution, minerals may be the eco-friendly materials for organic carbon stabilization. For minerals, the principle of its combination with organic matter is similar to that of metal oxide (Barre et al., 2014). But the adsorption mechanism between minerals and organic matter is more diversity, including Van der Waals force and ion adsorption (Araujo et al., 2017). But the adsorption efficiency between them has not been compared. Illite, montmorillonite, clay minerals, chitosan and their modified materials are the stabilizers which attract more attention at present. Heat-pretreatment, acid-base treatment, cation replacement and organic reagent washing are the common pre-treatment ways for modifying these functional materials (Pan et al., 2021). They can effectively increase the specific surface area or activate the surface adsorption center. Recently, research has primarily tested and verified the addition of illite and montmorillonite can positively promote carbon sequestration (Pan et al., 2021).

6. Conclusion

How to achieve efficient fixation of organic C while rapid transformation is always a restrictive problem for OSW composting. This review focus on how to increase C sequestration by promoting humus formation and stabilization. During composting, organic C will be hydrolyzed into humus precursors, with the mineralization of organic matter by microorganisms, which leads to organic C loss. Therefore, we cited the concept of MCP to decrease CO₂ release and enhance microbial anabolism to promote C fixation, including regulation of the microhabitat of composting and immobilization of organic C with functional materials.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work is funded by the National Key Research and Development Project (No. 2019YFC1906403), National Natural Science Foundation of China (No. 51878132; No. 52000021; No. 51978131; No. 51778116).

References

- Angulo-Mosquera, L.S., Alvarado-Alvarado, A.A., Rivas-Arrieta, M.J., Cattaneo, C.R., Rene, E.R., Garcia-Depraet, O., 2021. Production of solid biofuels from organic waste in developing countries: A review from sustainability and economic feasibility perspectives. In: *Science of the Total Environment*, p. 795.
- Araujo, B.R., Romao, L.P.C., Doumer, M.E., Mangrich, A.S., 2017. Evaluation of the interactions between chitosan and humics in media for the controlled release of nitrogen fertilizer. *J. Environ. Manage.* 190, 122–131.
- Awasthi, M.K., Duan, Y.M., Awasthi, S.K., Liu, T., Zhang, Z., 2020a. Effect of biochar and bacterial inoculum additions on cow dung composting. *Bioresour. Technol.* 297.
- Awasthi, M.K., Duan, Y., Awasthi, S.K., Liu, T., Zhang, Z., 2020b. Influence of bamboo biochar on mitigating greenhouse gas emissions and nitrogen loss during poultry manure composting. *Bioresour. Technol.* 303, 122952.
- Awasthi, M.K., Ferreira, J.A., Sirohi, R., Sarsaiya, S., Khoshnevisan, B., Baladi, S., Sindhu, R., Binod, P., Pandey, A., Juneja, A., Kumar, D., Zhang, Z.Q., Taherzadeh, M. J., 2021. A critical review on the development stage of biorefinery systems towards the management of apple processing-derived waste. *Renew. Sustain. Energy Rev.* 143.
- Barre, P., Fernandez-Ugalde, O., Virto, I., Velde, B., Chenu, C., 2014. Impact of phyllosilicate mineralogy on organic carbon stabilization in soils: incomplete knowledge and exciting prospects. *Geoderma* 235, 382–395.
- Benner, R., 2011. Biosequestration of carbon by heterotrophic microorganisms. *Nat. Rev. Microbiol.* 9 (1).
- Caceres, R., Malinska, K., Marfa, O., 2018. Nitrification within composting: A review. *Waste Manage.* 72, 119–137.
- Causey, T.B., Shanmugam, K.T., Yomano, L.P., Ingram, L.O., 2004. Engineering *Escherichia coli* for efficient conversion of glucose to pyruvate. *PNAS* 101 (8), 2235–2240.
- Chen, S.C., Budhraj, R., Adrian, L., Calabrese, F., Stryhanyuk, H., Musat, N., Richnow, H.H., Duan, G.L., Zhu, Y.G., Musat, F., 2021. Novel clades of soil biphenyl degraders revealed by integrating isotope probing, multi-omics, and single-cell analyses. *The ISME Journal* 1–14.
- Chen, H.Y., Awasthi, S.K., Liu, T., Duan, Y.M., Ren, X.N., Zhang, Z.Q., Pandey, A., Awasthi, M.K., 2020. Effects of microbial culture and chicken manure biochar on compost maturity and greenhouse gas emissions during chicken manure composting. *J. Hazard. Mater.* 389.
- Chen, Y.R., Chen, Y.N., Li, Y.P., Wu, Y.X., Zeng, Z.P., Xu, R., Wang, S., Li, H., Zhang, J.C., 2019. Changes of heavy metal fractions during co-composting of agricultural waste and river sediment with inoculation of *Phanerochaete chrysosporium*. *J. Hazard. Mater.* 378.
- Chen, X., Du, Z., Guo, T., Wu, J., Wang, B., Wei, Z., Jia, L., Kang, K., 2022. Effects of heavy metals stress on chicken manures composting via the perspective of microbial community feedback. *Environmen. Pollut.* 294, 118624.
- Cheng, L., Zhang, N.F., Yuan, M.T., Xiao, J., Qin, Y.J., Deng, Y., Tu, Q.C., Xue, K., Van Nostrand, J.D., Wu, L.Y., He, Z.L., Zhou, X.H., Leigh, M.B., Konstantinidis, K.T., Schuur, E.A.G., Luo, Y.Q., Tiedje, J.M., Zhou, J.Z., 2017. Warming enhances old organic carbon decomposition through altering functional microbial communities. *ISME J.* 11 (8), 1825–1835.
- Cloy, J.M., Wilson, C.A., Graham, M.C., 2014. Stabilization of Organic Carbon via Chemical Interactions with Fe and Al Oxides in Gley Soils. *Soil Sci.* 179 (12), 547–560.
- Cortes-Tolalpa, L., Jimenez, D.J., Brossi, M.J.D., Salles, J.F., van Elsas, J.D., 2016. Different inocula produce distinctive microbial consortia with similar lignocellulose degradation capacity. *Appl. Microbiol. Biotechnol.* 100 (17), 7713–7725.
- Cotrufo, M.F., Soong, J.L., Horton, A.J., Campbell, E.E., Haddix, M.L., Wall, D.H., Parton, A.J., 2015. Formation of soil organic matter via biochemical and physical pathways of litter mass loss. *Nat. Geosci.* 8 (10), 776–779.
- Feng, C.L., Zeng, G.M., Huang, D.L., Hu, S., Zhao, M.H., Lai, C., Huang, C., Wei, Z., Li, N. J., 2011. Effect of ligninolytic enzymes on lignin degradation and carbon utilization during lignocellulosic waste composting. *Process Biochem.* 46 (7), 1515–1520.
- Fernandez-Bayo, J.D., Hestmark, K.V., Claypool, J.T., Harrold, D.R., Randall, T.E., Achmon, Y., Stapleton, J.J., Simmons, C.W., VanderGheynst, J.S., 2019. The initial soil microbiota impacts the potential for lignocellulose degradation during soil solarization. *J. Appl. Microbiol.* 126 (6), 1729–1741.
- Gao, M.C., Li, B., Yu, A., Liang, F.Y., Yang, L.J., Sun, Y.X., 2010. The effect of aeration rate on forced-aeration composting of chicken manure and sawdust. *Bioresour. Technol.* 101 (6), 1899–1903.
- Glassman, S.L., Weihe, C., Li, J.H., Albright, M.B.N., Looby, C.L., Martiny, A.C., Treseder, K.K., Allison, S.D., Martiny, J.B.H., 2018. Decomposition responses to climate depend on microbial community composition. *PNAS* 115 (47), 11994–11999.
- Godlewski, P., Schmidt, H.P., Ok, Y.S., Oleszczuk, P., 2017. Biochar for composting improvement and contaminants reduction. A review. *Bioresour. Technol.* 246, 193–202.
- Guo, X.X., Liu, H.T., Zhang, J., 2020. The role of biochar in organic waste composting and soil improvement: a review. *Waste Manage.* 102, 884–899.
- Hardie, A.G., Dynes, J.J., Kozak, L.M., Huang, P.M., 2009. The role of glucose in abiotic humification pathways as catalyzed by birnessite. *Journal of Molecular Catalysis a-Chemical* 308 (1–2), 114–126.
- Hu, G., Li, Y., Ye, C., Liu, L., Chen, X., 2019. Engineering Microorganisms for Enhanced CO₂ Sequestration. *Trends Biotechnol.* 37 (5), 532–547.
- Hultman, J., Waldrop, M.P., Mackelprang, R., David, M.M., McFarland, J., Blazewicz, S. J., Jansson, J.K., 2015. Multi-omics of permafrost, active layer and thermokarst bog soil microbiomes. *Nature* 521 (7551), 208–212.
- Jiao, N., Herndl, G.J., Hansell, D.A., Benner, R., Kattner, G., Wilhelm, S.W., Kirchman, D. L., Weinbauer, M.G., Luo, T.W., Chen, F., Azam, F., 2010. Microbial production of recalcitrant dissolved organic matter: long-term carbon storage in the global ocean. *Nat. Rev. Microbiol.* 8 (8), 593–599.
- Johnson, K., Purvis, G., Lopez-Capel, E., Peacock, C., Gray, N., Wagner, T., Marz, C., Bowen, L., Ojeda, J., Finlay, N., Robertson, S., Worrall, F., Greenwell, C., 2015. Towards a mechanistic understanding of carbon stabilization in manganese oxides. *Nature. Communications* 6.
- Jokic, A., Wang, M.C., Liu, C., Frenkel, A.I., Huang, P.M., 2004. Integration of the polyphenol and Maillard reactions into a unified abiotic pathway for humification in nature: the role of delta-MnO(2). *Org. Geochem.* 35 (6), 747–762.
- Jones, S.W., Fast, A.G., Carlson, E.D., Wiedel, C.A., Au, J., Antoniewicz, M.R., Papoutsakis, E.T., Tracy, B.P., 2016. CO₂ fixation by anaerobic non-photosynthetic mixotrophy for improved carbon conversion. *Nat. Commun.* 7, 12800.
- Kallenbach, C.M., Frey, S.D., Grandy, A.S., 2016. Direct evidence for microbial-derived soil organic matter formation and its ecophysiological controls. *Nat. Commun.* 7, 13630.
- Kone, A.W., Yao, M.K., 2021. Soil microbial functioning and organic carbon storage: can complex timber tree stands mimic natural forests? *J. Environ. Manage.* 283.
- Kraft, B., Tegetmeyer, H.E., Sharma, R., Klotz, M.G., Ferdelman, T.G., Hettich, R.L., Geelhoed, J.S., Strous, M., 2014. The environmental controls that govern the end product of bacterial nitrate respiration. *Science* 345 (6197), 676–679.
- Lalonde, K., Mucci, A., Ouellet, A., Gelinas, Y., 2012. Preservation of organic matter in sediments promoted by iron. *Nature* 483 (7388), 198–200.
- Li, H., Zhang, T., Tsang, D.C., Li, G., 2020. Effects of external additives: Biochar, bentonite, phosphate, on co-composting for swine manure and corn straw. *Chemosphere* 248, 125927.
- Liang, C., Schimel, J.P., Jastrow, J.D., 2017. The importance of anabolism in microbial control over soil carbon storage. *Nat. Microbiol.* 2, 17105.

- Liu, D.M., Li, M.X., Xi, B.D., Zhao, Y., Wei, Z.M., Song, C.H., Zhu, C.W., 2015. Metaproteomics reveals major microbial players and their biodegradation functions in a large-scale aerobic composting plant. *Microb. Biotechnol.* 8 (6), 950–960.
- Liu, Y.L., Xing, P.X., Liu, J.G., 2017. Environmental performance evaluation of different municipal solid waste management scenarios in China. *Resour. Conserv. Recycl.* 125, 98–106.
- Lopez-Mondejar, R., Brabcova, V., Stursova, M., Davidova, A., Jansa, J., Cajthaml, T., Baldrian, P., 2018. Decomposer food web in a deciduous forest shows high share of generalist microorganisms and importance of microbial biomass recycling. *ISME J.* 12 (7), 1768–1778.
- Lu, Q., Zhao, Y., Gao, X., Wu, J., Zhou, H., Tang, P., Wei, Z., 2018. Effect of tricarboxylic acid cycle regulator on carbon retention and organic component transformation during food waste composting. *Bioresour. Technol.* 256, 128–136.
- Ludwig, M., Achtenhagen, J., Miltner, A., Eckhardt, K.U., Leinweber, P., Emmerling, C., Thiele-Bruhn, S., 2015. Microbial contribution to SOM quantity and quality in density fractions of temperate arable soils. *Soil Biol. Biochem.* 81, 311–322.
- Ma, T., Zhu, S.S., Wang, Z.H., Chen, D.M., Dai, G.H., Feng, B.W., Su, X.Y., Hu, H.F., Li, K. H., Han, W.X., Liang, C., Bai, Y.F., Feng, X.J., 2018. Divergent accumulation of microbial necromass and plant lignin components in grassland soils. *Nat. Commun.* 9.
- Malik, A.A., Puissant, J., Buckeridge, K.M., Goodall, T., Jehmlich, N., Chowdhury, S., Gweon, H.S., Peyton, J.M., Mason, K.E., van Agtmaal, M., Bland, A., Clark, I.M., Whitaker, J., Pywell, R.F., Ostle, N., Gleixner, G., Griffiths, R.I., 2018. Land use driven change in soil pH affects microbial carbon cycling processes. *Nat. Commun.* 9.
- Miltner, A., Bombach, P., Schmidt-Brucken, B., Kastner, M., 2012. SOM genesis: microbial biomass as a significant source. *Biogeochemistry* 111 (1–3), 41–55.
- Neri, E., Passarini, F., Cespi, D., Zoffoli, F., Vassura, I., 2018. Sustainability of a bio-waste treatment plant: Impact evolution resulting from technological improvements. *J. Cleaner Prod.* 171, 1006–1019.
- Ni, H.W., Jing, X.Y., Xiao, X., Zhang, N., Wang, X.Y., Sui, Y.Y., Sun, B., Liang, Y.T., 2021. Microbial metabolism and necromass mediated fertilization effect on soil organic carbon after long-term community incubation in different climates. *ISME J.* 15 (9), 2561–2573.
- Palaniveloo, K., Amran, M.A., Norhashim, N.A., Mohamad-Fauzi, N., Peng-Hui, F., Hui-Wen, L., Kai-Lin, Y., Jiale, L., Chian-Yee, M.G., Jing-Yi, L., Gunasekaran, B., Razak, S. A., 2020. Food Waste Composting and Microbial Community Structure Profiling. *Processes* 8 (6).
- Pan, C.N., Zhao, Y., Zhao, L., Wu, J.Q., Zhang, X., Xie, X.Y., Kang, K.J., Jia, L.M., 2021. Modified montmorillonite and illite adjusted the preference of biotic and abiotic pathways of humus formation during chicken manure composting. *Bioresour. Technol.* 319.
- Payne, C.M., Knott, B.C., Mayes, H.B., Hansson, H., Himmel, M.E., Sandgren, M., Stahlberg, J., Beckham, G.T., 2015. Fungal Cellulases. *Chem. Rev.* 115 (3), 1308–1448.
- Piccolo, A., Spaccini, R., De Martino, A., Scognamiglio, F., di Meo, V., 2019. Soil washing with solutions of humic substances from manure compost removes heavy metal contaminants as a function of humic molecular composition. *Chemosphere* 225, 150–156.
- Proietti, P., Calisti, R., Gigliotti, G., Nasini, L., Regni, L., Marchini, A., 2016. Composting optimization: Integrating cost analysis with the physical-chemical properties of materials to be composted. *J. Cleaner Prod.* 137, 1086–1099.
- Qi, G., Yue, D., Fukushima, M., Fukuchi, S., Nishimoto, R., Nie, Y., 2012. Enhanced humification by carbonated basic oxygen furnace steel slag-II. Process characterization and the role of inorganic components in the formation of humic-like substances. *Bioresour. Technol.* 114, 637–643.
- Qi, H., Zhang, A., Du, Z., Wu, J., Chen, X., Zhang, X., Zhao, Y., Wei, Z., Xie, X., Li, Y., Ye, M., 2021. delta-MnO₂ changed the structure of humic-like acid during co-composting of chicken manure and rice straw. *Waste. Manag.* 128, 16–24.
- Qi, H., Zhao, Y., Zhao, X., Yang, T., Dang, Q., Wu, J., Lv, P., Wang, H., Wei, Z., 2020. Effect of manganese dioxide on the formation of humin during different agricultural organic wastes compostable environments: It is meaningful carbon sequestration. *Bioresour. Technol.* 299, 122596.
- Qu, J., Zhang, L., Zhang, X., Gao, L., Tian, Y., 2020. Biochar combined with gypsum reduces both nitrogen and carbon losses during agricultural waste composting and enhances overall compost quality by regulating microbial activities and functions. *Bioresour. Technol.* 314, 123781.
- Razanamalala, K., Razafimbelo, T., Maron, P.A., Ranjard, L., Chemidlin, N., Lelievre, M., Dequiedt, S., Ramarosoan, V.H., Marsden, C., Becquer, T., Trap, J., Blanchart, E., Bernard, L., 2018. Soil microbial diversity drives the priming effect along climate gradients: a case study in Madagascar. *ISME J.* 12 (2), 451–462.
- Rebolledo, R., Martinez, J., Aguilera, Y., Melchor, K., Koerner, I., Stegmann, R., 2008. Microbial Populations during Composting Process of Organic Fraction of Municipal Solid Waste. *Appl. Ecol. Environ. Res.* 6 (3), 61–67.
- Ribeiro, H., de Sousa, T., Santos, J.P., Sousa, A.G.G., Teixeira, C., Monteiro, M.R., Salgado, P., Mucha, A.P., Almeida, C.M.R., Torgo, L., Magalhaes, C., 2018. Potential of dissimilatory nitrate reduction pathways in polycyclic aromatic hydrocarbon degradation. *Chemosphere* 199, 54–67.
- Rodriguez, F.J., Schlenger, P., Garcia-Valverde, M., 2016. Monitoring changes in the structure and properties of humic substances following ozonation using UV-Vis, FTIR and H-1 NMR techniques. *Sci. Total Environ.* 541, 623–637.
- Schaeffer, A., Nannipieri, P., Kastner, M., Schmidt, B., Botterweck, J., 2015. From humic substances to soil organic matter-microbial contributions. In honour of Konrad Haider and James P. Martin for their outstanding research contribution to soil science. *J. Soils Sediments* 15 (9), 1865–1881.
- Shahab, R.L., Brethauer, S., Davey, M.P., Smith, A.G., Vignolini, S., Luterbacher, J.S., Studer, M.H., 2020. A heterogeneous microbial consortium producing short-chain fatty acids from lignocellulose. *Science* 369 (6507).
- Shao, L.M., Zhang, C.Y., Wu, D., Lu, F., Li, T.S., He, P.J., 2014. Effects of bulking agent addition on odorous compounds emissions during composting of OFMSW. *Waste Manage.* 34 (8), 1381–1390.
- Shi, M., Zhao, X., Zhu, L., Wu, J., Mohamed, T.A., Zhang, X., Chen, X., Zhao, Y., Wei, Z., 2020a. Elucidating the negative effect of denitrification on aromatic humic substance formation during sludge aerobic fermentation. *J. Hazard Mater.* 388, 122086.
- Shi, M.Z., Zhao, Y., Zhu, L.J., Song, X.Y., Tang, Y., Qi, H.S., Cao, H.J., Wei, Z.M., 2020b. Denitrification during composting: Biochemistry, implication and perspective. *International Biodeterioration & Biodegradation*, p. 153.
- Shima, J., Ando, A., Takagi, H., 2008. Possible roles of vacuolar H⁺-ATPase and mitochondrial function in tolerance to air-drying stress revealed by genome-wide screening of *Saccharomyces cerevisiae* deletion strains. *Yeast* 25 (3), 179–190.
- Silva, M.E.F., de Lemos, L.T., Nunes, O.C., Cunha-Queda, A.C., 2014. Influence of the composition of the initial mixtures on the chemical composition, physicochemical properties and humic-like substances content of composts. *Waste Manage.* 34 (1), 21–27.
- Sitarz, A.K., Mikkelsen, J.D., Meyer, A.S., 2016. Structure, functionality and tuning up of laccases for lignocellulose and other industrial applications. *Crit. Rev. Biotechnol.* 36 (1), 70–86.
- Song, C., Li, W., Cai, F., Liu, G., Chen, C., 2021. Anaerobic and Microaerobic Pretreatment for Improving Methane Production From Paper Waste in Anaerobic Digestion. *Front Microbiol.* 12, 688290.
- Stevenson, F.J., 1994. *Humic Chemistry: Genesis, composition. Reactions*, John Wiley and Sons, New York.
- Tan, K.H., 2014. *Humic Matter in Soil and the Environment: Principles and Controversies*. CRC Press.
- Voberkova, S., Vaverkova, M.D., Adamcova, D., 2017. Enzyme Production During Composting of Aliphatic-Aromatic Copolyesters in Organic Wastes. *Environ. Eng. Sci.* 34 (3), 177–184.
- Wang, L.Q., Zhao, Y., Ge, J.P., Zhu, L.J., Wei, Z.M., Wu, J.Q., Zhang, Z.C., Pan, C.N., 2019. Effect of tricarboxylic acid cycle regulators on the formation of humic substance during composting: The performance in labile and refractory materials. *Bioresour. Technol.* 292.
- Wang, R.X., Zhao, Y., Xie, X.Y., Mohamed, T.A., Zhu, L.J., Tang, Y., Chen, Y.F., Wei, Z.M., 2020a. Role of NH₃ recycling on nitrogen fractions during sludge composting. *Bioresour. Technol.* 295.
- Wang, Y., Liu, W., Wang, X., Yang, R., Wu, Z., Wang, H., Wang, L., Hu, Z., Guo, S., Zhang, H., Lin, J., Fu, C., 2020b. MiR156 regulates anthocyanin biosynthesis through SPL targets and other microRNAs in poplar. *Hortic Res.* 7 (1), 118.
- Wei, X., Liu, Y., Luo, Y., Shen, Z., Wang, S., Li, M., Zhang, L., 2021. Effect of organosolv extraction on the structure and antioxidant activity of eucalyptus kraft lignin. *Int. J. Biol. Macromol.* 187, 462–470.
- Weusthuis, R.A., Lamot, I., van der Oost, J., Sanders, J.P., 2011. Microbial production of bulk chemicals: development of anaerobic processes. *Trends Biotechnol.* 29 (4), 153–158.
- Whitman, T., Pepe-Ranney, C., Enders, A., Koehli, C., Campbell, A., Buckley, D.H., Lehmann, J., 2016. Dynamics of microbial community composition and soil organic carbon mineralization in soil following addition of pyrogenic and fresh organic matter. *ISME J.* 10 (12), 2918–2930.
- Wiesmeier, M., Urbanski, L., Hobbey, E., Lang, B., von Lutzow, M., Marin-Spiotta, E., van Wesemael, B., Rabot, E., Liess, M., Garcia-Franco, N., Wollschläger, U., Vogel, H.J., Kogel-Knabner, I., 2019. Soil organic carbon storage as a key function of soils - A review of drivers and indicators at various scales. *Geoderma* 333, 149–162.
- Witzgall, K., Vidal, A., Schubert, D.I., Hoschen, C., Schweizer, S.A., Buegger, F., Pouteau, V., Chenu, C., Mueller, C.W., 2021. Particulate organic matter as a functional soil component for persistent soil organic carbon. *Nat. Commun.* 12 (1).
- Wu, D., Qu, F., Li, D., Zhao, Y., Li, X., Niu, S., Zhao, M., Qi, H., Wei, Z., Song, C., 2022. Effect of Fenton pretreatment and bacterial inoculation on cellulose-degrading genes and fungal communities during rice straw composting. *Sci. Tol. Environ.* 806, 151376.
- Wu, J.Q., Wei, Z.M., Zhu, Z.C., Zhao, Y., Jia, L.M., Lv, P., 2020. Humus formation driven by ammonia-oxidizing bacteria during mixed materials composting. *Bioresour. Technol.* 311.
- Wu, J.Q., Zhao, Y., Yu, H.M., Wei, D., Yang, T.X., Wei, Z.M., Lu, Q., Zhang, X., 2019. Effects of aeration rates on the structural changes in humic substance during co-composting of digestates and chicken manure. *Sci. Total Environ.* 658, 510–520.
- Xie, X.Y., Wang, Y.H., Wei, Z.M., Zhang, Y.T., Zhang, C., Zhang, S.B., Yang, H.Y., Zhang, X., Zhao, Y., 2021. Continuous insulation strategy of organic waste composting in cold region: Based on cold-adapted consortium. *Bioresour. Technol.* 335.
- Xu, M., He, Z., Zhang, Q., Liu, J., Guo, J., Sun, G., Zhou, J., 2015. Responses of Aromatic-Degrading Microbial Communities to Elevated Nitrate in Sediments. *Environ Sci Technol.* 49 (20), 12422–12431.
- Yin, Y., Yang, C., Li, M., Zheng, Y., Ge, C., Gu, J., Chen, R., 2021. Research progress and prospects for using biochar to mitigate greenhouse gas emissions during composting: A review. *Sci. Total Environ.* 149294.
- Yuan, J., Chadwick, D., Zhang, D.F., Li, G.X., Chen, S.L., Luo, W.H., Du, L.L., He, S.Z., Peng, S.P., 2016. Effects of aeration rate on maturity and gaseous emissions during sewage sludge composting. *Waste Manage.* 56, 403–410.
- Zhang, Y., Zhao, Y., Chen, Y.N., Lu, Q., Li, M.X., Wang, X.Q., Wei, Y.Q., Xie, X.Y., Wei, Z. M., 2016. A regulating method for reducing nitrogen loss based on enriched ammonia-oxidizing bacteria during composting. *Bioresour. Technol.* 221, 276–283.

- Zhang, Y.C., Yue, D.B., Lu, X.F., Zhao, K.Y., Ma, H., 2017. Role of ferric oxide in abiotic humification enhancement of organic matter. *J. Mater. Cycles Waste Manage.* 19 (1), 585–591.
- Zhang, Z., Zhao, Y., Wang, R., Lu, Q., Wu, J., Zhang, D., Nie, Z., Wei, Z., 2018. Effect of the addition of exogenous precursors on humic substance formation during composting. *Waste. Manag.* 79, 462–471.
- Zhao, X.Y., Tan, W.B., Dang, Q.L., Li, R.F., Xi, B.D., 2019. Enhanced biotic contributions to the dechlorination of pentachlorophenol by humus respiration from different compostable environments. *Chem. Eng. J.* 361, 1565–1575.
- Zhao, Y., Zhao, Y., Zhang, Z.C., Wei, Y.Q., Wang, H., Lu, Q., Li, Y.J., Wei, Z.M., 2017. Effect of thermo-tolerant actinomycetes inoculation on cellulose degradation and the formation of humic substances during composting. *Waste Manage.* 68, 64–73.
- Zheng, G.R., Liu, C.G., Deng, Z., Wei, Z.M., Zhao, Y., Qi, H.S., Xie, X.Y., Wu, D., Zhang, Z.C., Yang, H.Y., 2021. Identifying the role of exogenous amino acids in catalyzing lignocellulosic biomass into humus during straw composting. *Bioresour. Technol.* 340.
- Zhou, J.W., Liu, L.M., Shi, Z.P., Du, G.C., Chen, J., 2009. ATP in current biotechnology: Regulation, applications and perspectives. *Biotechnol. Adv.* 27 (1), 94–101.
- Zhou, Y., Awasthi, S.K., Liu, T., Verma, S., Zhang, Z., Pandey, A., Awasthi, M.K., 2021. Patterns of heavy metal resistant bacterial community succession influenced by biochar amendment during poultry manure composting. *J. Hazard. Mater.* 420, 126562.