Lignocellulolytic Microorganisms in Cereal Crop Residue Decomposition

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The global escalation in cereal production, essential to meet growing population demands, simultaneously augments the generation of cereal crop residues, estimated annually at approximately 3107 × 10^6 Mg/year. Among different crop residue management approaches, returning them to the soil can be essential for various ecological benefits, including nutrient recycling and soil carbon sequestration. However, the recalcitrant characteristics of cereal crop residues pose significant challenges in their management, particularly in the decomposition rate. Microorganisms employ a range of mechanisms, such as the utilization of different enzymes that work in combination, to initiate oxidative attacks on plant litter. Consequently, this serves to reduce the recalcitrance of the lignocellulosic material, hence facilitating subsequent action by depolymerizing enzymes. Both fungi and bacteria have received increased attention for their ability to secrete a diverse range of lignocellulolytic enzymes.

cereal crop residue decomposition fungi bacteria actinobacteria

1. Introduction

The definition of crop residue has transformed in the last few decades, reflecting shifts in agricultural practices, technological progress, and a deeper understanding of its role in promoting sustainable agriculture and the environment. Earlier, the main focus of the definition was centered on the vegetative remnants left in fields after harvesting the main crop. It was frequently considered as waste and required removal from the field in order to facilitate preparation for the following planting season, particularly since it was viewed as an impediment to conventional tillage practices [1]. In contrast, modern agriculture redefines crop residue as a plant material deliberately retained in the fields, aligned with conservation agriculture practices. Furthermore, redefinition has expanded to reflect its potential impacts on carbon sequestration, and climate change mitigation, and is an important resource for the generation of bioenergy and the establishment of a circular economy [2][3][4]. Northern Europe, including Nordic countries, the UK, Ireland, and Baltic states plays a significant role in cereal grain production encompassing wheat, barley, maize, oats, and rye within the European Union [5][6].

It is well-known that incorporating or retaining cereal crop residue on the soil surface has numerous advantages in improving soil quality. Hence, the large-scale removal of crop residues from fields might have a detrimental impact on soil quality and productivity [7][8] by lowering total nitrogen (N) levels and soil organic carbon (C) [9][10], enhancing wind and water erosion [11], and decreasing soil microbial activity [12]. Furthermore, it is important to acknowledge the influence of C, N, cellulose, lignin, and polyphenols on the rate at which nutrients are released from agricultural residues. These decomposition products have a significant impact on the absorption rate of nutrients by crops [13]. The different approaches of cereal crop residue utilization include livestock fodder, compost, biogas, biochar or biofuel production and incorporation into the field. Among these approaches, incorporation is considered to be a better option since it manages a large quantity of residue while improving soil health [14][15].

The soil microbial community plays a crucial role in crop residue decomposition, carbon processes, and nutrient cycle in the soil. To break down crop residue components effectively, a collaborative effort of various hydrolytic and oxidative enzyme families is essential. These enzymes are produced by lignocellulose-degrading microorganisms and work together in a coordinated manner to carry out multiple oxidative, hydrolytic, and non-hydrolytic activities. In essence, they function as a synergistic cocktail with complementary actions to achieve the breakdown process [16][17][18].

Microorganisms employ a range of mechanisms, such as the utilization of different enzymes that work in combination, to initiate oxidative attacks on plant litter. Consequently, this serves to reduce the recalcitrance of the lignocellulosic material, hence facilitating subsequent action by depolymerizing enzymes [19]. In recent years, both fungi and bacteria have received increased attention for their ability to secrete a diverse range of lignocellulolytic enzymes.

2. Lignocellulolytic Activity of Fungi

Fungi are well known for their pivotal role in the soil microbiota, particularly in relation to the process of plant residue breakdown in the soil. Being filamentous by nature, fungi have an advantage in the breakdown of lignocellulosic material since they can create spores fast and prolifically and are assisted by a wide range of enzymes that have complementary catalytic activities [20]. The extracellular enzymatic system consists of hydrolytic enzymes that are involved in the breakdown of polysaccharides, as well as oxidative enzymes that are responsible for causing the deterioration of lignin and the opening of phenyl rings. Within the realm of lignocellulose breakdown, there are three particular groups of fungi, namely soft-rot, brown-rot, and white-rot fungi, each of which demonstrates diverse impacts and degradation techniques [21][22]. Likewise, it was reported that the decomposition process of plant residue in natural ecosystems is greatly aided by the presence of the *Basidiomycota* group [23].

White-rot fungi utilize a diverse range of carbohydrate-active enzymes (CAZymes) that specifically target cellulose, hemicellulose, and pectin [24][25]. Furthermore, they use lignin-modifying enzymes belonging to the AA2 family and include class-II heme peroxidases including lignin peroxidases, versatile peroxidases, and manganese peroxidases [26][27]. These enzymes, along with auxiliary CAZyme oxidoreductases, catalyze oxidative reactions that effectively degrade the complex lignin polymers in plant residue [26][28]. White-rot fungi, belonging to the *Basidiomycota* phylum, have a particular ability to metabolize lignin as their primary source of energy [29]. Furthermore, there has been significant research conducted on the examination of lignocellulosic pretreatment methods, specifically focusing on two distinct classifications: selective and non-selective delignifiers of fungal species of the *Basidiomycota* phylum. The primary focus of selective delignifiers is to specifically target heteropolymeric lignin while scarcely affecting cellulose and hemicellulose components [29][30][31]. The aforementioned attribute renders them more appealing for scientific investigation, as they demonstrate a greater output of lignin-free cellulosic biomass in comparison to non-selective delignifiers. These are mostly responsible for the simultaneous degradation of lignocellulosic biomass structural components [32][33][34]. Several species of white-rot fungi have notable potential in the breakdown of lignin. *Phanerochaete chrysosporium* [28][35] and *Trametes versicolor* [36][37] have been the subject of much research due to their significant biological pretreatment capabilities. These organisms are commonly used as model organisms to gain insights into the process of lignin breakdown. Moreover, *Ganoderma lucidum* [38][39] and *Phlebia* spp. [40][41][42] have also been acknowledged for their ability to produce lignin-degrading enzymes, which enhances their potential to be viable candidates for diverse applications in the area. Xu and colleagues [43] obtained promising results, investigating the efficacy of white-root fungus *Inonotus obliquus* pretreatment for the first time in producing lignocellulolytic enzymes induced by wheat straw, rice straw, and maize stover biomass. The fungus process resulted in the highest lignin loss of 72%, 39%, and 47% within 12 days for wheat straw, rice straw, and corn stover, respectively.

Another essential group of fungi in the degradation of plant residue are brown-rot fungi, which are involved in the breakdown of crop residue. Similarly to forest ecosystems, brown-rot fungi adopt a selective decay strategy that primarily targets the degradation of cellulose and hemicellulose, while mostly modifying lignin rather than completely degrading it [44][45]. In comparison with white-rot fungi, brown-rot fungi do not possess genes for class-II peroxidases. As a result, the breakdown of polysaccharides of plant cell walls mostly occurs via non-enzymatic Fenton reactions, which are produced outside the fungal hyphae [19][46]. In the Hermosilla and colleague study, wheat straw pretreatment by the brown-rot fungus *Gloeophyllum trabeum* resulted in 11.3% weight loss after 40 days, and increased glucose recovery [47]. Another comparative investigation of lignocellulosic biomass degradation revealed that brown-rot fungi *Fomitopsis pinicola* exhibited the highest level of maize stalk mass reduction by 38% at 16 weeks among the species examined. Importantly, the observed effect was preceded by a substantial lag phase, a characteristic that was conspicuously lacking in the degradation patterns reported concerning other species [48]. It is worth noticing that the research on the ability of brown-rot fungi to degrade lignocellulosic biomass, particularly those derived from agricultural ecosystems, is relatively limited.

The significant contributions of lignocellulolytic fungi, particularly white-rot and brown-rot fungi, in the context of sustainable crop residue management, are of utmost importance and should not be underestimated. Initially, they utilize a diverse array of enzymes, efficiently breaking down complex lignocellulosic structures. Moreover, these fungi employ distinct mechanisms, such as selective degradation and the Fenton reaction, to enhance and accelerate the process. The comprehensive nature of this method highlights the essential contribution of these organisms in the natural processes of carbon and nitrogen recycling, hence playing a crucial role in the preservation of ecological equilibrium. In assessing the utilization of fungi for the decomposition of crop residue, it is important to take into account several factors. First and foremost, species specificity is of utmost importance, since different fungi exhibit varying levels of effectiveness and preference for different types of residues. Furthermore, it is essential to verify that the selected fungi do not cause diseases in crops and have positive effects on soil health. Therefore, it is crucial to carry out experimental studies or trials in order to evaluate the efficacy and safety of these fungi in certain agroecosystems, thereby guaranteeing an informed and appropriate strategy in terms of sustainable crop residue management.

3. Lignocellulolytic Activity of Bacteria

In addition to fungi, the utilization of bacteria for possible biodegradation processes is beginning to gain recognition due to their extensive functional diversity and versatility [49]. That can be explained by the ability to exhibit rapid growth rates and a remarkable tolerance range in terms of temperature, pH, and salinity, enabling them to adapt to a diverse array of environmental conditions [50][51][52][53]. In addition, some bacteria have the ability to meet their nitrogen needs through the process of biological nitrogen fixation [54]. Moreover, bacterial lignocellulases can produce multi enzymatic complexes, which are more adapted for the elaborate breakdown of biomass [55]. Some of the observations show that bacteria increase abundance in the latter stages of the lignocellulose breakdown process, which can be determined by the predominance of complex and recalcitrant carbon sources [56][57]. However, Arcand and colleagues [58] observed temporal variations in the relative abundance of Gram-positive bacteria depending on treatment, in contrast to a consistent decline in Gram-negative bacteria across different treatments. Concurrently, there was a notable increase in the relative abundance of Actinobacteria over time, a trend that persisted across all treatment conditions. Therefore, it is essential to acknowledge one more time that the abundance of bacteria in soil, specifically during the process of plant residue breakdown, is influenced by a complex combination of biotic and abiotic factors. Including nutrient availability, prevailing environmental conditions, inter-species competition, and synergistic associations, as well as the particular types of crops and their residues. The complex relationship described highlights the subtle features that define soil microbial ecology in agricultural ecosystems.

Bacteria possess distinct species and decomposition mechanisms that are adapted for either aerobic [59] or anaerobic conditions in plant lignocellulose breakdown [60]. During the lignocellulose degradation process, aerobic bacteria commence the breakdown by secreting lignocellulolytic enzymes that are capable of targeting biomass [61]. The bacteria initially engage in the hydrolysis of cellulose, resulting in the production of cellobiose, which is then followed by a stage of fermentation [62]. During this phase, the cellobiose molecule undergoes further hydrolysis reactions, leading to the formation of carbon dioxide, hydrogen, and other organic acids [63]. Within the bacterial community, some aerobes, such as *Cellulomonas*, *Bacillus*, *Pseudomonas*, and *Streptomyces*, etc., are recognized as key players in cellulose degradation, contributing significantly to the process of residue decomposition [64][65][66][67].

Aerobic bacteria have numerous significant benefits over anaerobic bacteria in the context of crop residue breakdown in agricultural settings [68][69]. Firstly, aerobic bacteria exhibit a faster rate of breakdown, which can be attributed to the more effective pathways for energy release in the presence of oxygen. Their high efficiency allows them to rapidly break down complex compounds such as cellulose and lignin [70]. This phenomenon occurs as a result of the wide range of enzymes generated by aerobic bacteria, which efficiently break down recalcitrant plant compounds and facilitate complete mineralization. Finally, the aerobic process improves the availability of nutrients in forms that are easier for plants to absorb. For instance, nitrogen is released in the form of nitrate, which is easily assimilated by plants, in contrast to the ammonium released by anaerobic processes [71][72][73].

In the anaerobic degradation of lignocellulose by bacteria, sugars are transformed into alcohol or acids, leading to the generation of biogas through subsequent anaerobic digestion [74]. This process involves various microorganisms, notably methanogens and acetogens, which are capable of utilizing cellulose. While CO_2 is the primary byproduct of microbial cellulose degradation, methane (CH_4) is also produced under anaerobic conditions [62]. The genus *Clostridium* is well recognized as a highly researched group for anaerobic degradation of lignocellulose, mostly due to its exceptional ability to efficiently breakdown cellulose [75][76]. This particular genus possesses the ability to produce complex enzymes known as cellulosomes, which exhibit a high level of efficiency in the process of breaking down cellulose and hemicellulose [74][77]. Moreover, anaerobic bacteria break down cellulose utilizing complex cellulase systems such polycellulosomes, while aerobic bacteria use a synergistic free cellulase system to utilize cellulose as a carbon and energy source by secreting different types of endo- and exo-acting enzymes.

4. Lignocellulolytic Activity of Actinobacteria

Another group of microorganisms that display characteristics that bear resemblance to both bacteria and fungi are actinobacteria. Nevertheless, the resemblance between actinomycetes and fungi is only superficial, and they possess sufficient distinctive characteristics to definitively classify them within the bacterial kingdom [78]. The majority of filamentous actinomycetes that frequently occur belong to the *Streptomyces* and *Micromonospora* families. Usually, actinomycetes are known for their ability to break down complex carbon and nitrogen compounds [79][80]. In soil, organic residues are initially decomposed by bacteria and fungi with actinomycetes subsequently taking over due to their comparatively slower growth and activity rates. Moreover, they have a crucial function in the subsequent decomposition of humus in the soil [81][82]. Actinobacteria communities exhibit a wide range of hydrolytic enzymes, such as β-glucosidase, cellobiohydrolase, ligninase, acetyl xylan esterase, and arabinofuranosidase. These enzymes, along with their associated supramolecular cellulosomes, are crucial for breaking down plant residues [83][84][85].

Additionally, the high C/N ratio in cereal crop residues constrains the nitrogen availability for microbial reproduction. However, the nitrogen-fixing capability of actinobacteria potentially enhances nitrogen availability during cereal residue decomposition driven by microbes [86][87][88]. Notably, this group of microorganisms have the ability to inhibit the growth of other species by producing antibiotics [89]. These ecological and physiological attributes collectively indicate a wide adaptation of actinobacteria communities in crop residue decomposition and soil carbon sequestration.

The key genera engaged in the process of degrading lignocellulose biomass include *Streptomyces*, *Micromonospora*, *Thermobifida*, *Thermomonospora*, *Actinomadura*, *Nocardia*, and others [18][90][91][92][93][94][95][96]. A study on wheat straw biodegradation by *Streptomyces viridosporus* T7A, revealed lignin and hemicellulose removal, carbonyl and methoxyl group modifications, and a significant guaiacyl unit reduction [97]. Another research conducted by Gong and his colleagues on the characterization of maize-straw-degrading actinomycetes revealed that a consortium composed of the three *Streptomyces* spp. showed a decomposition rate of 51.60% after 77 days, significantly reducing the content of recalcitrant components in the maize straw [98]. A metatranscriptomic analysis of compost-derived microbial communities enriched on rice straw under thermophilic and mesophilic conditions showed significant overexpression of enzymes from glycoside hydrolase family 48 and carbohydrate-binding modules families 2 and 33 in the thermophilic community, predominantly expressed by the actinobacteria genus *Micromonospora* [99].

Another study investigated the process of breaking down lignocellulose and specifically focused on the lignin-degrading ability of peroxidase Tfu-1649 secreted by *Thermobifida fusca* BCRC 19214, particularly in synergy with xylanase Tfu-11 substantially enhanced the degradation of lignocellulosic biomass [94].

The efficacy of cereal crop residue breakdown by various microbial inoculants varies depending on parameters such as application rate, timing of inoculation, type of cereal crop residue, etc. The efficiency of the microorganisms was assessed by measuring the percentage of mass loss of residues. The results are summarized in **Table 1**. The secretion of hydrolytic enzymes positions actinomycetes as a principal group among soil microorganisms that are responsible for organic matter decomposition. As decomposers, they are adept at breaking down resilient lignocellulose from crop residues including the most recalcitrant structures such as lignin. Furthermore, the nitrogen-fixing capability of certain species enhances the decomposition of cereal crop residues, which typically have low nitrogen content.

Table 1. Summary of microbial inoculant efficiency for degradation of cereal crop residues.

Microorganism	Residue Type	Method	Days	Mass Loss, %	Enzyme(s) Evaluated	Reference
Trichoderma reesei	Rice straw, bran	Solid-state fermentation	10	51.16	Laccase, xylanase, β-Glucosidase, cellobiohydrolase, endoglucanase	[100]
Trichoderma harzianum	Rice straw	In situ	28	23.69	-	[101]
Aspergillus niger	Rice and wheat straw (4:1)	Solid-state fermentation	10	16	CMCase, endoglucanase, cellobiase, β-1,4-xylanase	[102]
Phanerochaete chrysosporium	Maize stover	Solid-state fermentation	28	21	-	[103]
Ganoderma lobatum	Wheat straw	Solid-state fermentation	40	21.04	β-glucosidase	[104]
Cellulomonas sp.	Rice straw	Submerged fermentation	4	49.3	β-glucosidase, endoglucanase, exoglucanase, xylanase,	[105]

Microorganism	Residue Type	Method	Days	Mass Loss, %	Enzyme(s) Evaluated	Reference
					lignin peroxidase, manganese peroxidase, laccase.	
Bacillus sp.	Wheat bran	Submerged fermentation	7	60	Cellulase, endoglucanase, xylanase, laccase, mannase	[106]
Streptomyces sp.	Barley straw	Submerged fermentation	7	60.55	Exoglucanase, endoglucanase, β-glucosidase	[107]
Enterobacter sp.	Rice straw	Submerged fermentation	7	45.52	Endoglucanases, exoglucanase, xylanase	[108]
Ganoderma lobatum + *Gloeophyllum trabeum*	Wheat straw	Solid-state fermentation	20	15.52	β-glucosidase	[104]
Cellulomonas ZJW-6 + *Acinetobacter* DA-25	Rice straw	Submerged fermentation	4	57.62	β-glucosidase, endoglucanase, xylanase, lignin peroxidase, laccase, manganese peroxidase, β-glucosidase	[109]
Streptomyces sp. G1T + *Streptomyces* sp. G2T + *Streptomyces* sp. G3T	Maize stalk	solid-state fermentation	119	66.37	-	[98]
Citrobacter freundii so4 + *Sphingobacterium multivorum* w15 + *Coniochaeta* sp. 2T2.1	Wheat straw	Submerged fermentation	10	12.82	-	[110]

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