Role of Microbial Biomechanics in Composting with Special Reference to Lignocellulose Biomass Digestion

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Authors’ contributions

This work was carried out in collaboration among all authors. Authors PG and JXK designed the study. Authors PG and DKA wrote the protocol. Authors PG, JXK and DKA managed the literature searches. All authors read and approved the final manuscript.

ABSTRACT

Biomass transformation of lignocellulose into compost offers ‘green’ technology for sustainable agricultural development. So far, biomass conversion into compost outweights fossil resources and other conversational techniques due to the low production cost and environmental pollution reduction. Although composting has aesthetically been resorted to in the digestibility of lignocellulose biomass, its realization has keenly been directed towards adding chemical reagents. However, inclining massively to this treatment instigated research bias as microorganisms’ biomass digestibility remains mostly inadequate. Besides, proliferated growth and activities of microorganisms native to lignocellulose biomass are usually disrupted by chemical treatment. The microbial flora (fungi, bacteria, actinomycetes, archaea, and yeast) involved in composting synthesizes complex biocatalysts (enzymes) that are crucial for solubilizing the biopolymers of lignocellulose materials at a density of \(10^{12}\) cells g\(^{-1}\). Filamentous fungi are by far excellent degraders of lignocellulose in nature. To adequately ensure sustainable lignocellulose digestibility, microbial engineers must subject research studies to surpassing conditions (feedstock formulation...
1. INTRODUCTION

Lignocellulosic residues are organic base materials that are commonly generated through agricultural intensification and industrialization. A combined network involving cellulose, hemicellulose, lignin, proteins, pectin, and ashes constitutes the polymeric material’s structural components [1]. However, percentage quantification broadly hails cellulose (40-50%), hemicellulose (25-30%), and lignin (15-25%) as tridimensional constituents [2,3]. The tethering of lignin to cellulose and hemicellulose traditionally influences the integral network complexation of biopolymers [4]. This attribution, however, promotes the recalcitrance and rigidity of lignocellulose residues that impede depolymerization [5], hence their concurrent disposal in landfills, incineration, and gasification treatments which sparks environmental pollutions that are inimical to human health.

Nonetheless, lignocellulose digestibility has often been realized with chemical reagents, which instigate research bias because of the one-way direction [6,7]. Microbial growth and population density are inhibited with chemical reagents, which affect biological activities in return [8]. Although lignocellulosic residues could have equally warranted direct soil incorporation as a requisite alternative to composting, such practice has keenly been found to promote seed dormancy, retard plant growth, and result in loss of soil organic matter [9].

Digestion of lignocellulose biomass into compost through microbially-mediated activities is more advantageous over the use of chemical reagents together with other management practices as found in biorefinery, landfills, incineration, and gasification [10]. Comparatively, composting offers in practice ‘green’ technology for sustainable agriculture, low production cost, and ensures environmental safety together with saving enough land area for other economic purposes [11]. By far, the microbial consortia roll out their reaction mechanics on lignocellulose by producing a blend of ligninolytic, cellulolytic, and hemicellulolytic enzymes that together have high synergistic effects on the degradation process [3,12]. The enzymes synthesized by the microorganisms initially act on lignocellulose structures to unveil and hydrolyze the cellulose content, leading to the release of available sugars. The available sugars are then fermented via organic acids’ production by the microorganisms to produce the fiber-rich and humus-containing product [3]. Current genetic engineering has been effective in raising microbial cell factories suitable for lignocellulose digestibility [13]. While this is a promising trend for biomass decomposition and usage, a one-stop-shop knowledge on structural composition of lignocellulosic materials and mechanisms of microbiological processes that could facilitate the degradation process remain relatively unavailable to aid decision-making. This review was thus designed to provide insights on (1) the structure and composition of lignocellulose constituents, (2) lignocellulose materials recommended for composting, (3) synergistic actions of microorganisms on lignocellulose biomass, and (4) microbial processes and responsiveness to factors affecting composting.

2. STRUCTURE AND COMPOSITION OF LIGNOCELLULOSE CONSTITUENTS

2.1 Cellulose

Cellulose is by far the most considerable biopolymer fraction (40-50%) and the plant cell wall’s critical component [2]. Ideally, cellulose has a robust hierarchical structure composed of D-glucose units interlinked with β-1,4-glycosidic bonds to form a linear and stereo-regular molecular chain [14]. Cellulosic chains are differentiated by their lengths and lateral sizes [15]. Cellulosic materials are fashioned with long microfibrils (100-40,000 nm) whose average widths range between 5-10 nm and 30-50 nm for primary and secondary cell walls, respectively [16]. Cellulose microfibrils are jointly held by van der Waals forces existing between the hydrogen bonds and the glucan chains [15]. According to [17], cellulose is paraded as crystalline and non-crystalline biomaterials. Crystalline cellulose exhibits dual allomorphs of varied recognition (cellulose I and cellulose II). The molecular chains of crystalline cellulose reckon on
hydrogen bonds situated at the flanks and in the same direction of the chains [14,17].

In contrast, non-crystalline cellulose is amorphously ordered and dominated by transparent gel suitable for accommodating pressing and stretching effects [17]. The crystalline cellulose molecules are complemented with orderly arrangements, whereas that of the non-crystalline cellulose exercises lose and disordered-arrangements [14]. Cellulosic chains are congealed with intra- and inter-molecular-hydrogen bonds, which partially influence crystallinity and structural rigidity [2]. Stable cellulosic bonds are resistant to acidic and alkaline wash, heating, and stretching [18]. Naturally, cellulose forms a radical index of the carbon cycle and a preferred organic material for bacteria and fungi existence [18]. Enzymatic access to cellulose saccharification is hindered by the crystallinity of the materials [19]. Cellulose biosynthesis is accomplished by series of metabolic activities of cellulase enzymes combine with UDP-glucose monomers [20]. Enzymatic and protein groups ardently correspond to influence cellulose biosynthesis [15]. Cellulose synthase protein catalyzes the glucan chains during the polymerization process. Higher plants, bacteria, algae, and tunicates exercise cellulose biosynthesis [21].

2.2 Hemicellulose

Hemicellulose is a polysaccharide-supporting material of the plant cell wall whose relationship with cellulose and lignin is facilitated by hydrogen and covalent bonds (Fig. 1) [22]. Despite the hygroscopic and hydrophilic polymers of lignin, hemicellulose relates better with cellulose than lignin [23]. Herein, hemicellulose is ranked next to cellulose in composition, representing 25-35% of the dry weight-base of all woody materials [24]. The extraction of hemicellulose with water offers better results than alkaline reagents [25] and bridges well with esters to influence acetyl units and hydroxycinnamic acids [26]. According to [24], hemicellulose can be grouped into pentose (xylose, arabinose, and mannose), hexose (galactose, mannose, and glucose), uronic acid (glucuronic, methylgalacturonic, and galacturonic acids) and other sugars (rhamnose and fucose). However, xylans, xyloglucans, and galactomannans constitute the principal structures of hemicellulose [22].

Xylans are mainly localized within the secondary cell wall of plants and bear b-1,4-linked D-xylose backbones as their structural composition. They account for about 20-30% of hardwood and herbaceous plants [27]. Among individual grassy and cereal plants, xylan composition can increase to about 50% [28]. Galactomannans are the largest hemicellulose component of the secondary cell walls in hardwood biomass and, conversely, the least in softwood biomass. Xyloglucans have appreciable dominance within the primary cell walls of dicotyledons and non-gramineous monocotyledons. As sugars, xyloglucans are composed of b-1,4-linked D-glucose coupled with 1,6-a-xylosyl residues in their backbone [27]. Xyloglucans also serve as tethering materials for cellulose microfibrils to improve plant cell wall rigidity. Hemicellulose differs in terms of branching patterns, carbohydrate composition, and degree of polymerization based on substrate source, characteristics, and the species involved [29]. Softwood contains mannose and galactoglucomannan as primary hemicellulose composition, while hardwood contains xylose and glucuronoxylan [24]. Complex enzyme interaction involving xylanase and mannannase promotes hemicellulose’s digestibility in its native environment [30].

2.3 Lignin

Lignin is, thus, the third (15-25%) lignocellulose and heterogeneous polymer derived from monoclonal precursors. According to [31], lignin is a natural polymer closely associated with cellulose (<50%) and hemicellulose (15-30%). The backbone of lignin is typically composed of three phenylpropanoids (guaiacyl, syringyl, and p-hydroxyphenyl) sub-structures [32]. The phenylpropanoid sub-structures are embodied with carboxyls, carboxyls, hydroxyls, and methoxyl, serving as functional groups for lignin modification and utilization [33]. Besides, lignin configuration, branching patterns, and reactivities are also defined by the phenylpropanoids [34]. Content quantification and formation by lignin differ among plant species and substrate origin [31]. Hardwood lignin is made up of both coniferyl and sinapyl alcohols, whereas coniferyl alcohol makes softwood lignin’s composition. Grassy lignin exercises guaiacyl, syringyl, and p-hydroxyphenyl as composition [34]. Fungal (white-rot, red-rot, and soft-rot) and bacterial species (Sterptomycetes, Rhodococcus, Pseudomonas, and Bacillus) influence the digestibility of lignin through the secretion of ligninolytic enzymes [35].
3. SYNERGISTIC ACTIONS OF MICROORGANISMS ON DIGESTION OF LIGNOCELLULOSE BIOMASS

Lignocellulose digestibility is crucial for realizing the rate of biomass transformation and nutrient availability [36]. Various microbial communities and population densities are capable of degrading and enhancing biomass humification [37]. Biologically, the transformation of lignocellulose biomass is driven by corresponding intracellular and extracellular enzymes through microbial secretions [38]. The microbial consortia, most importantly fungi, bacteria, actinomycetes, and archaea, secrete ligninolytic, cellulolytic, and hemicellulolytic enzymes, which hydrolyze the content of lignin, cellulose, and hemicellulose [39], respectively. Secretion of glycoside hydrolases aided by bacteria and actinomycetes does not sufficiently hydrolyze hemicellulose due to their reduced numbers [10]. Fungal degrading species (Trichoderma, Aspergillus, Penicillium, and Neurospora crassa) have deliberated ability owing to the digestibility of lignocellulose [10]. Synergistic actions of non-enzymatic proteins (expansins) promote the hydrolysis of cellulose and hemicellulose biomass through the executed impact of cellulases and hemicellulases [10]. In a related study, $Zea-h$ proteins extracted from freshly harvested corn stover interacted synergistically with cellulase [40]. In addition, non-enzymatic proteins purified from *Oryza sativa* escalated the action of cellulase by 2.4 times in comparison with sole enzymes [41].

Microorganisms exhibit profound tolerance to varied environmental conditions, which makes them ideal entities for biomass degradation. They influence substrate digestibility by initially attacking the material’s lignin content, which serves as a potential barrier to cellulose and hemicellulose accessibility [7]. Although the microbial degradation process is often slow, biomass decomposition and nutrient transformation safeguard the natural environment’s safety than the chemical, physical, and mechanical treatment strategies [42]. The transformational process (aerobic and anaerobic) by which microorganisms are subjected determines the resultant end-products. For instance, aerobic microorganisms end up transforming lignocellulosic materials into carbon dioxide and water, whereas anaerobic microbes ultimately produce carbon dioxide, methane, and water as end-products [43]. Biologically, bacterial and fungal strains are crucial facilitators of lignocellulose biosynthesis [44]. While all these processes and others work interchangeably to facilitate the processes and speed up biomass degradation, forecast on fungal and bacteria interaction with lignocellulose biomass are further highlighted below.

### 3.1 Fungal Actions on Lignocellulose Biomass

Fungi traditionally exhibit an irreplaceable role in lignocellulosic biomass degradation [45,46]. Most fungi are attracted to biomass with high nitrogen content, acidic medium, and mesophilic
temperatures [47]. Contrary, fungal growth is hindered by nitrogen and carbon displacement during composting [48]. Mesophilic (Geotrichum sp., and Cladosporium cladosporioides) and thermophilic (Aspergillus sp., and Thermomyces lanuginosus) fungal count per gram on lignocellulose biomass has been estimated approximately at $10^6$ and $10^3$ to $10^5$, respectively [49]. Fungi exercise ligninolytic capabilities as an arousing mechanism of biomass delignification [45]. The bioactivities of fungi are commonly expressed on lignin and hemicellulose constituents than on cellulose [50]. Fungi roll out their digestibility mechanics by initially attacking and solubilizing lignin chains to release available sugars. The sugars are then hydrolyzed through fermentation processes to produce valuable end-products [7]. Lignocellulose materials contain iron (II), a substance which enables fungi to produce more peroxidase for the digestibility of lignin [46]. The ligninolytic enzymes synthesized invade and increase the lignocellulose materials’ surface area, making them more accessible to cellulolytic and hemicellulolytic enzymes [12]. Fungal genera such as Trichoderma, Penicillium, Aspergillus, Fusarium, and Humicola secrete enzymes (laccases, manganese peroxidase, pyranose-2 oxidase, glyoxaline, and aryl-alcohol oxidase) which are crucial in the digestibility process [6]. A complex class of fungi involving brown-rot, white-rot, and soft-rot also contributes to lignocellulose biomass’s digestibility [51]. For white-rots (Phanerochaete chrysosporium, and Ganoderma colossus), they possess a ligninolytic system, making them the most efficient lytic degraders. White-rot attacks both hardwood and softwood and professes selective and nonselective delignification characteristics. White-rot fungal genera involving Phlebia radiate and Phanerochaete chrysosporium expresses selective digestibility of lignin whereas Trametes versicolor ensures nonselective delignification [52]. Instead of white-rots releasing all their metabolic energy at once for substrate decomposition, they reserve part of it to influenceextracellular enzyme (laccase, lignin peroxidase, and manganese peroxidase) synthesis. This reservation promotes further digestibility of the biomass [53]. The establishment of Pleurotus ostreatus, Phanerochaete chrysosporium, Cyathus stercoreus, Ceriporiopsis subvermispora, and Coriolus versicolor as also genera of white-rot fungi ensures lignin digestibility and humification at a higher rate [54]. Under favorable conditions, influential white-rots can ensure 50-70% mineralization of $^{14}$C-lignin [47]. Hardwood lignocellulose is prone to white-rot degradation than that of softwood [55]. Brown-rot fungi (Basidiomycetes) respond to materials that do not require maximum alteration efficiency. Per that, they are mostly adjudged as forest litter degraders [51]. The brown discoloration and cracks discovered on forest biomass are postulated indices of brown-rot attack [56]. Instead of enhancing lignin degradation, the wood-rotting Caprinus of the brown-rot has been justified by its modification effect [47]. Soft-rot fungi are generally known for cavity creation together with invading effects on plant secondary cell walls. Some soft-rot fungi, especially Paecilomyces sp., Thielavia terrestris, and Talaromyces thermophilus expresses weak lytic effect despite their tolerance to thermophilic conditions [57]. Soft-rot fungi secrete Trichoderma reesei as enzymes for disrupting the lignin content in wood angiosperm despite the slow delignification process [58]. Comparatively, soft-rot fungi exercise minimal wood digestibility than that of white-rot and brown-rot fungi [59]. Till now, filamentous fungi are by far appraised as excellent degraders of lignocellulose in nature [60].

3.2 Bacterial Actions on Lignocellulose Biomass

Bacteria are incredibly enormous and diversified microbial entities with a special solubilization effect on lignin [61]. As unicellular microorganisms, they range between 0.5 μm to 3.0 μm in size with a high volume ratio which accelerates soluble residue conveyance into the body cells [47]. Species of bacteria (Bacillus, Pseudomonas, Zymomonas, Acinetobacter, Cellulomonas, Sphingomonas paucimobilis, Comamonadaceae, and Caulobacteraceae) produce high recombinant enzymes (peroxidases, laccases, cellulosomes, amylase, proteases, glucoamylase, and glucose-isomerase) that are necessary for lignocellulose deconstruction [6,62]. Among these biocatalysts, laccase is widespread due to its broad residue specification coupled with its ability to accommodate high temperatures and pH [63]. Cellulosome is also a multi-complex enzyme that is synthesized by anaerobic cellulolytic bacteria. They exert a more significant hydrolytic influence on biopolymer degradation [6]. Bacteria population density increases as the decomposition process reach its later phase, especially in areas where carbon mineralization is high [6,64]. Bacteria mediate the digestibility of cellulose and lignin constituents through the demonstrated tolerance of low (25-39°C) and
high (40-65°C) temperatures, slightly acidic-to-alkaline pH (between 5.5 to 9.0), and saline conditions (30% w/v total salt). Bacteria exhibit these tolerances on account of the lignocellulolytic enzymes they synthesize [65]. Although most lignocellulose residues are generally low in nitrogen, bacteria often meet their nitrogen requirement through biological N-fixation, hence attributed as critical organisms responsible for N losses during composting [43]. The *Bacillus* species involving *subtilis*, *licheniformis*, and *circulans* synthesize thick-walled endospores that are thermotolerant, highly resistant to chemical reagents, and radiations [47].

4. LIGNOCELLULOSIC RESIDUES FOR COMPOSTING

Lignocellulose biomass quantification across the globe shows that over $200\times10^9$ tons of the raw material are produced annually [66]. Most materials serving as bulking agents, regulators, and organic substrates during composting are substantially obtained from lignocellulose [47]. The raw material warrants enormous and promising utilization that involves composting and biorefinery into fossil resources. Considering the various management methods (landfills, incineration, open dumps, gasification, and biorefinery engineering) that exist, composting remains the ultimate choice. Lignocellulose residues (shown in Table 1) emanate crucially from crop production fields (corn straw, and rice straw), forest (soft wood, and hard wood), domestic (fruit, vegetables, and food waste), municipal (waste paper), and industrial (sugarcane bagasse, and coffee straw) wastes [43]. According to [116], corn, wheat, rice, and sugarcane forms the top four crops produced in the world. The production of these crops has been phenomenal due to the rate of consumption by the human population and as feed to animals. The biomass source indicates the amount of cellulose, hemicellulose, and lignin in given lignocellulose (Table 1) proportionately.

| Residue type | Common name       | Composition of lignocellulose residues | Reference |
|--------------|-------------------|---------------------------------------|-----------|
| Cereal crop  | Barley straw      | Cellulose 36.0-43.0, Hemicellulose 24.0-33.0, Lignin 6.3-13.1 | [66]      |
|              | Barley hull       | Cellulose 34.0, Hemicellulose 36.0, Lignin 16.0 | [67]      |
|              | Corn cob          | Cellulose 33.7-41.0, Hemicellulose 31.9-36.0, Lignin 6.1 | [68]      |
|              | Corn stover       | Cellulose 37.6, Hemicellulose 21.5, Lignin 19.1 | [69]      |
|              | Corn stalk        | Cellulose 34.5, Hemicellulose 27.6, Lignin 21.8 | [70]      |
|              | Oat straw         | Cellulose 34.8, Hemicellulose 26.7, Lignin 8.7 | [71]      |
|              | Rice husk         | Cellulose 40.3, Hemicellulose 12.5, Lignin 25.4 | [72]      |
|              | Rice straw        | Cellulose 29.2-38.1, Hemicellulose 23.0-31.1, Lignin 17.0-26.4 | [66]      |
|              | Sorghum straw     | Cellulose 32.0-35.0, Hemicellulose 24.0-27.0, Lignin 15.0-21.0 | [66]      |
|              | Wheat straw       | Cellulose 44.4, Hemicellulose 19.2, Lignin 5.8 | [73]      |
| Fiber crop   | Hemp stalk        | Cellulose 52.0, Hemicellulose 25.0, Lignin 17.0 | [66]      |
|              | Cotton stalk      | Cellulose 67.0, Hemicellulose 16.0, Lignin 13.0 | [74]      |
|              | Cotton gin        | Cellulose 20.0, Hemicellulose 9.1, Lignin 17.6 | [66]      |
|              | Sponge gourd      | Cellulose 66.6, Hemicellulose 17.4, Lignin 15.5 | [75]      |
| Fruit crop   | Banana peels      | Cellulose 13.2, Hemicellulose 14.8, Lignin 14 | [75]      |
|              | Cashew apple      | Cellulose 20.6, Hemicellulose 10.2, Lignin 35.3 | [76]      |
|              | bagasse           | Cellulose 23.3, Hemicellulose 20.4, Lignin 53.5 | [77]      |
| Grass/wood   | Bamboo leaves     | Cellulose 34.1, Hemicellulose 25.6, Lignin 35.0 | [78]      |
|              | Indian grass      | Cellulose 49.8, Hemicellulose 43.1, Lignin 6.7 | [66]      |
|              | Orchard grass     | Cellulose 52.3, Hemicellulose 42.9, Lignin 6.6 | [66]      |
|              | Rye grass         | Cellulose 6.5, Hemicellulose 27.9, Lignin 42.38 | [79]      |
| Woody crop   | Pine wood pellet  | Cellulose 39.5, Hemicellulose 22.1, Lignin 37.1 | [72]      |
|              | Oak wood          | Cellulose 43.2, Hemicellulose 21.9, Lignin 35.4 | [66]      |
|              | Rubber wood       | Cellulose 39.6, Hemicellulose 28.4, Lignin 27.6 | [80]      |
|              | Eucalyptus        | Cellulose 54.0, Hemicellulose 18.0, Lignin 21.0 | [67]      |

The tridimensional constituents represent the percentage (%) dry weight of the lignocellulose biomass.
Most importantly, the largest chunk of lignocellulose generated through crop production is accessed from sugarcane (>1.9 billion metric tons), maize (1.1 billion metric tons), wheat (771.7 million metric tons), and rice (769.6 million metric tons) [42, 66]. Other crops involving cotton (17-20 million metric tons), banana (13-15 million metric tons), sunflower (7.5-9.0 million metric tons), and coffee (1.6-1.9 million metric tons) also contributes massively to the lignocellulosic waste generated globally [117]. Fiber wastes (bagasse) are generated from sugarcane after extraction of the juice. Cultivation of maize generates corn stover composed of stalks, leaves, husks, tassels, and cobs. Stems, leaves, and straws are generated as by-products of wheat and rice after pre-and post-harvest operations [42]. The United States, China, and Brazil remain top producers and end-users of the resources [116]. Lignocellulose residues are carbon-rich materials and account for 30-50% of plant materials’ dry weight base [10]. Besides, they also serve as nutritional materials for the cultivation of fungi, bacteria, and other microorganisms involved in substrate decomposition [11]. Although the directives of EU regard these materials as waste [116], the context of sustainable development project the materials as resources worth transformable into valuable products like compost.

5. MICROBIAL PROCESSES AND RESPONSIVENESS TO FACTORS AFFECTING COMPOSTING

Composting is a biochemical process by which different and complex microbial communities mediate biomass decomposition. During the biochemical process, microorganisms utilize carbon, nitrogen, oxygen, and water to complement the production of Thermo energy (heat), carbon dioxide, water vapor, and humus-like end-product [48, 81]. Microorganisms serve as driving forces in regulating organic matter decomposition time and ensuring value addition of the end-product thereof [81, 82]. Biomass hydrolysis into stable and mature compost is carried out by enzymes synthesized by microorganisms [83]. Because of the fermentation process, most composting processes are implemented by aerobic microbes other than the anaerobic counterparts [84]. Herein, the activities of anaerobic microbes (including Clostridium) are reduced and, in some cases, inactivated under oxygen-rich environments [81]. Nutrient mineralization of compost occurs as a result of microbially-mediated activities [81]. Native microorganisms of compost also exert biocontrol efficiency and suppressive influence on soil-borne pathogens as a means of ensuring product hygienisation [85]. Fungi, mostly Ascomycetes and Basidiomycetes dominates the entire composting process while bacteria (Actinobacteria and Proteobacteria bacteroidets) become dominant during the active phase of composting [86].

Microbial activities and engagements in composting are influenced by factors categorized as feedstock formulation and management processes [87]. For the feedstock formulation, microorganisms are generally affected by nutrient content and particle size. Generally, the higher the nutrient content, the faster the rate of decomposition. On the other hand, there is an inverse relationship between particle size and the rate of decomposition. Other factors, including temperature, pH, oxygen supply, and moisture content, relate to the decomposition’s management processes [87]. A decrease or excess in any of the factors significantly affects the microbial consortia’s operationalization, which affects the composting process in return. Apart from the characteristics of the feedstock, its composition regarding nutrient content, particle size, and management practices, microorganisms play an essential role in the composting process. A high population of decomposing organisms (approximately $10^{12}$ cells g$^{-1}$) has been observed to result in higher degradation efficiency of the organic substrates [88]. Microbial communities and population densities vary within a composting stretch. The study of [37] disclosed that anaerobic thermophiles dominated the central and the bottom regions of the composting stretch whilst mesophilic bacteria were prevalent in the surface regions.

5.1 Carbon and Nitrogen Balance

Carbon and nitrogen balance provide microorganisms with preferential nutritional balance for growth and functioning. Microorganisms utilize carbon as an energy source and nitrogen as an element for cell growth and capacitation [89]. Microorganisms use partly the energy gained for metabolic processes, whereas the rest is liberated as heat. Nitrogen promotes proteins, nucleic acids, enzymes, and co-enzymes formation [48, 89]. The extent of biodegradation is dependent on the carbon to nitrogen (C/N) ratio of the formulated materials. Organic substrates are swiftly and slowly degraded under low and high C/N ratios,
respectively [87]. Overstocking of composting pile with substrates tends to hinder microorganisms from meeting their nutrient requirements. Several postulations on C/N ratios have been opined to influence microbes despite their dependence on the organic substrate [87,90,91]. Research conducted by [90] indicated a C/N ratio of 20-50 to be suitable for composting. A further assertion by [91] showed a C/N ratio between 25-35 as a useful index for enhancing compost quality. The toxic effect in composting are significantly minimized with initial carbon to nitrogen ratio of 25 [92]. Besides, 30 parts of carbon to a nitrogen unit was demonstrated by [86] to be associated with good microbial efficiencies. Carbon digestibility by microorganisms showed an impressive result among piles formulated at a C/N ratio of 10-20 [89]. The ratio adjustment of carbon and nitrogen has been juxtaposed to alter most biological strains’ structures except bacteria [93]. Pile digestibility is slowly harnessed under limited nitrogen content, whereas ammonia (NH$_3$) and nitrous oxide (N$_2$O) gases get lost under excess nitrogen accumulation. Initial C/N ratio at high levels promotes and stabilizes organic matter oxidation [47]. With a reduced C/N ratio, the assemblage of organic matter is partly oxidized, favoring the production of immature compost and loss of compost N content [94].

5.2 Moisture Content

Moisture content (MC) promotes oxygen uptake and regulates pile temperatures for microbial habitation [95]. Microbial adaptability, survivability, and operations occur differently under various moisture regimes and levels [96]. The cross-sectional movement of microorganisms that influences biomass decomposition is executed via the ultra-thin films of water. Composting piles with 40-70% water by weight satisfactorily improves biological activities [81]. Flooded piles hinder the flow rate of oxygen and act as a cessation mechanism for biological activities with increased substrate odor. Leaching of nutrients is very common among excessively wet composting piles. The interstices air spaces of overly wet piles are generally blocked, displacing the oxygen needed to complement biomass digestibility by microorganisms. Dormancy and death of biological entities often set in when piles are insufficiently moistened. Moisture content below critical level deprives microorganisms of water and influences anaerobic fermentation [96]. The rapid development of conventional biochemical processes is rarely achieved under very low MC [62]. A very low MC promotes pile dehydration and hypothermic conditions inhabitable by decomposing microbes [97].

5.3 Temperature

As an exothermic process, composting is staged to vary in phases due to microbial responsiveness to various temperature regimes. Composting is driven through three main temperature evolution phases adaptable by microorganisms: (1) mesophilic phase, (2) thermophilic phase, and (3) curing phase [81,87]. Mesophiles are largely observed at the initial composting phase, where temperatures are low to moderate of 25-40 °C [89]. Mesophilic bacteria (Bacillus, Pseudomonas, Azobacter, Streptococcus, and Proteus) and mesophilic fungal species (Aspergillus, Emericella, and Penicillium) have dominant engagement in this phase [62]. Mesofauna such as worms, mites, and millipedes also adapt highly to mesophilic temperatures [88]. The mesophilic bacteria and fungi have a profound digestibility influence on simple and readily degradable compounds such as sugars, amino acids, and lipids [98]. The pH (slightly acidic) of the composting pile decreases due to the formation of organic acids from the compounds. Through accelerated digestibility actions of microorganisms, composting piles increase in heat development, thereby transforming the process into a thermophilic phase with 40-65 °C [87]. The principal part of biomass digestibility is crucially harnessed in this phase, making the process the most active phase in composting. The thermophilic phase can last within few to several days. Microorganisms increase the composting mass’s temperature by solubilizing the biomass’s protein content, thereby influencing the release of ammonium (NH$_3$) and increasing the pH of the substrates [89]. Following the carbon materials' digestibility, the tridimensional (cellulose, hemicellulose, and lignin) constituents are partly humified by thermophiles [99]. The proliferation of bacterial species encompassing Actinobacteria, and Bacillus, predominantly dominates the thermophilic phase [82]. The population of nitrifying bacteria declines upon exposure to hypothermic temperatures (>70 °C) [100]. The research findings of [101] has indicated temperatures above 65 °C to halt the activities of fungi, actinomycetes, and certain bacteria species. Maintaining thermophilic activities is best realized between 52-60°C [81]. Hydrolysis of complex organic constituents such
as cellulose, hemicellulose, lignin, fats, and proteins are promoted by this phase [87]. Compost pathogenicity and weed seeds are controlled by the activities of thermophiles [102]. However, the reoccurrence of the mesophilic (10-40°C) phase is often termed the curing stage. This phase represents the decomposition process’s final stage, where mesophiles colonize and transform residual sugars into stable and mature compost [103]. The curing phase is the period set out to cool the end-product and can last for several months. Following the digestibility process, the humus-like end-product is characterized as incomplete when there is high and low amount of fulvic and humic acids, respectively. Actinomycetes commonly mediate the curing phase.

### 5.4 Particle Size

Particle size evaluation has an expedient influence on microbial bioactivities, gas exchange, water-holding capacity, temperature, and pH adjustment of the composting mass [104]. Composting piles with large particle sizes result in slow digestion, whereas those with smaller particle sizes speed-up the digestion process and reduce the porosity due to insufficient aeration [104,98]. Piles with large particle sizes tend to have a small surface area for reaction, making digestibility more complex to the degrading microbes. Large pile sizes do not retain sufficient heat as a result of the high ventilated system. Anaerobic fermentation also arises from composting masses with smaller particle sizes. The incidence of anaerobic fermentation sets in as a result of the compact nature of the piles, which does not sufficiently allow air circulation [105]. Coarse particle-fractions were exploited in a research to maintain high content of nitrogen and phosphorus in composting. The exploited-use of the coarse particle fractions may be deduced in part that biomass with fine particle sizes liberates more N and P despite the abundance of the carbon fraction [106]. Microorganisms have high attraction and digestibility optimization to reduced particle size between 25-27 mm [87,104].

### 5.5 pH

In practice, pH demonstrates the acidity or alkalinity level of the composting materials due to the hydrogen ions present. Evidence of microbial growth and actions in a composting system shows that the microbes’ activities, most importantly that of the fungi, is dependent on the pH of the decomposing piles. However, the pH may vary across raw materials and the time of decomposition [107]. The composting period is initially characterized by low pH due to organic acid synthesis by bacteria [81]. Low pH was identified by [89] to stimulate the production of volatile fatty acids with low molecular weight. The production of fatty acids with low molecular weight creates imbalance conditions within the composting pile for the microbes [108]. Fungi and bacteria have pronounced digestibility at pH of 5.5-8.0 and 6.0-7.5, respectively [109]. Zhang and Sun [110] cited a pH of 7.5-8.5 as a reasonable level in promoting microbial actions. Mitigation of ammonia losses was also observed at a pH <7.5 [86,98]. Methanogenic activities are mostly sustained at pH ranging between 6.5-8.2 [111]. Nitrifying bacteria harbor compost nitrification at low pH, facilitating the volatility of ammonium nitrate [81]. A decrease in pH has been opined to decrease fungal growth adversely, while its increases are noted for the breakdown of organic acids and the oxidation of phenolic compounds [112]. In general, compost evaluation at 7.0 pH is considered efficient for agricultural utilization [112].

### 5.6 Oxygen Supply

Biological actions on biomass decomposition depend on oxygen supplied to microorganisms [88]. During decomposition, varied oxygen concentrations have differential roles they play [110,113]. Oxygen supply rate between 15-20% has been observed to enhance microbial actions on substrate decomposition [114]. Oxygen sufficiency was found by [88] to regulate compost temperature and moisture content for microbial survivability. Compost C/N ratio and overy production of CO₂ and NH₃ are well managed and controlled under proper-aerated conditions [87]. The duration of composting and ammonification is reduced by oxygen sufficiency supplied at the early stages of the decomposition process [115].

In contrast, organic matter decomposition is slowly achieved under insufficient oxygen (<0.2 L min⁻¹/kg/OM) supply [113]. With limited oxygen, hydrolytic and acid-forming microbes significantly respond to persisting conditions other than microbes that are naturally produced for substrate hydrolysis. Oxygenated microbes exercise faster growth than unoxygenated microbes [89].
6. CONCLUSION

Globally, lignocellulose biomass represents the most abundant (200×10^9 tons per annual production) renewable materials with enormous utilization potentials. The composting industry mostly has access to the raw material, making biomass utilization a potential substitute for fossil resources and inorganic fertilizers. Interest in transforming lignocellulose biomass into compost remains high as the process is associated with low production cost, environmental safety, and sustainability to agriculture. However, realizing the digestibility of the material is traditionally driven by microorganisms through enzyme-mediated activities. Microorganisms such as bacteria, fungi, actinomycetes, archaea, and yeast host ligninolytic, cellulolytic, and hemicellulolytic enzymes which helps in the solubilization of lignin, cellulose, and hemicellulose polymers. Microbial population density estimated at 10^12 cells g^{-1} influences the efficient breakdown of lignocellulose materials. Optimization of composting factors that include feedstock formulation (nutrients contents, particle size, and pH) and management processes (Temperature, oxygen supply, and moisture content) expeditiously improve biosynthesis. The digestibility of cellulose and hemicellulose is more straightforward than that of lignin. Unlike fungi which are virtually involved in the hydrolysis of lignin, hemicellulose, and cellulose constituents, bacteria actively digest lignin. The less digestible the biomass, the more diversified and synergistic enzyme actions that are needed. To ensure sustainable and efficient lignocellulose digestibility, microbial engineers must subject decomposition processes to appropriate conditions suitable for inducing ligninolytic, cellulolytic, and hemicellulolytic enzyme actions.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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