

REVIEW

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Aptitude of endophytic microbes for production of novel biocontrol agents and industrial enzymes towards agro-industrial sustainability

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Abstract

Background: Endophytes have continued to receive increased attention worldwide, probably, due to the enormous biotechnological potentials spanning through various industrial sectors. This paper outlines the biotechnological potentials of endophytes in biocontrol and industrial enzyme production, and the possible contribution towards achieving agro-industrial sustainability using published articles on endophytes in both Web of Science and Scopus (1990–2020).

Main body of the abstract: This review discusses the potential of endophytes to produce novel secondary metabolites with effective biocontrol activity against insect pests and plant pathogens. More so, the aptitude of endophytes for production of a wide range of enzymes with potential applications in agriculture, energy and health is discussed in this review. Furthermore, this review highlights the emerging potentials of endophytes in the production of exopolysaccharide and fatty acids. This paper also advocates the need for bioprospecting endophytes for novel biocontrol agents against termites, which are known for causing significant damage to forest and stored products.

Short conclusion: Exploration of endophytes for biocontrol and production of biomolecules of industrial significance could contribute significantly towards agricultural and industrial sustainability.

Keywords: Agricultural sustainability, Biocontrol agents, Biotechnology, Endophytes, Enzyme production, Polysaccharides

1 Background

One of the fundamentals of Sustainable Development Goals (SDGs) as set by the United Nations (UN) is to achieve food security and engender agricultural sustainability by 2030. A major challenge confronting food security globally is the activity of insect pests and plant diseases, with resultant negative implications on annual agricultural produce, hence threatening food security. Achieving zero hunger with increasing world's

population necessitates an increase in annual agricultural productivity globally. It is, therefore, important to take proactive steps towards improving crop yield. Unarguably, effective control of crop pests and phytopathogens is vital to improving crop yield. Even though, there are efficient chemical methods for pest control, the approaches are accompanied by possible health risks [1]. Thus, biological control of pest and pathogens is a promising alternative as the method is environmentally-friendly with limited health hazards.

Interestingly, endophytes hold great dexterity for biological control of phyto-diseases as the microbes protect their host plants from pathogens' attack through

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antagonism [2, 3]. The microbes have also displayed abilities for production of secondary metabolites with antimicrobial activity [4], which could be explored for biocontrol of different pathogens. Moreover, endophytes produce some enzymes as a defence response mechanism of the host against pathogens while other enzymes from endophytes promote plant growth [5, 6]. Thus, bioprospecting endophytes for production of novel biocontrol agents will contribute significantly towards improving agricultural productivity.

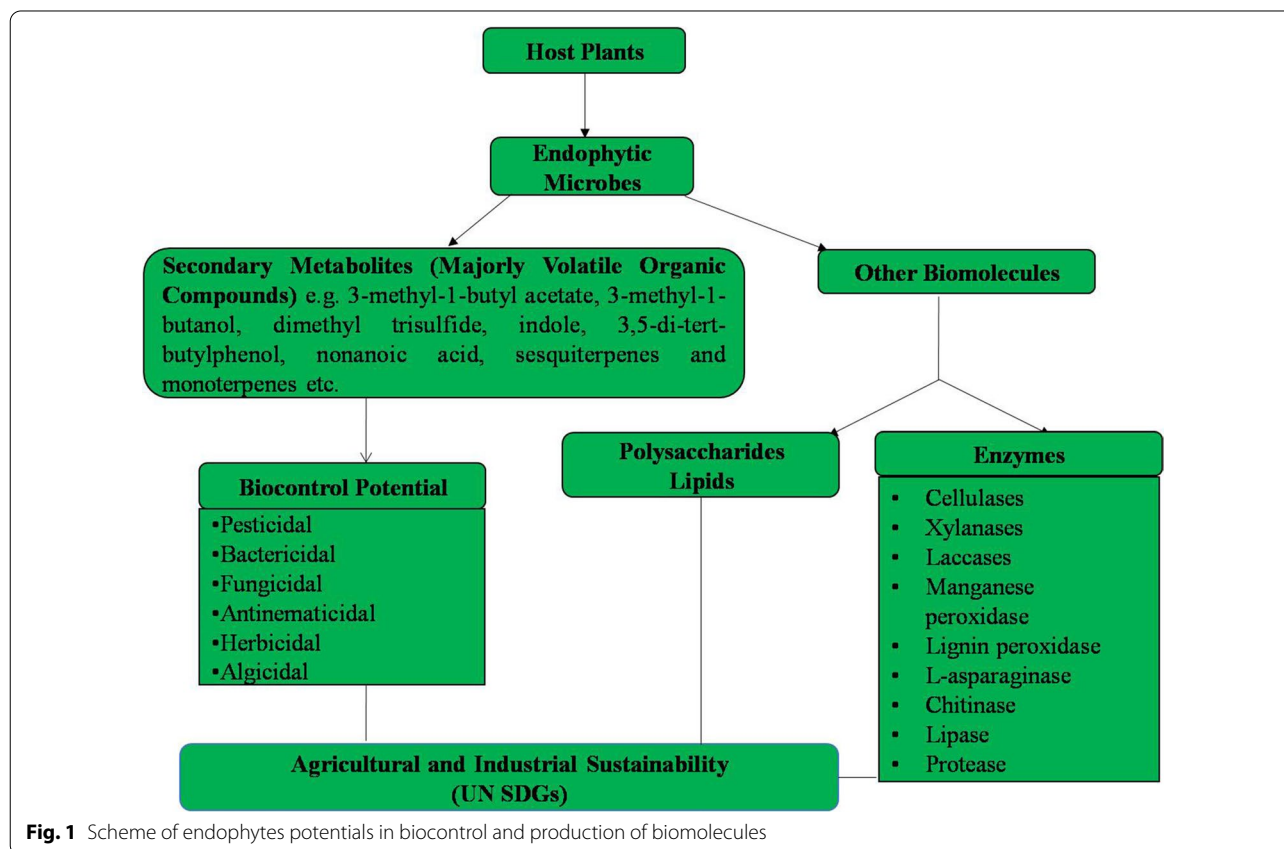
Furthermore, some studies have implicated endophytes in the production of enzymes of industrial significance including amylase, cellulase, lipase and laccase [7]. Specifically, Bezerra et al. [8] reported the potential of various endophytic fungi in a Brazilian medicinal plant, *Bauhinia forficata* for the production of some extracellular and hydrolytic enzymes such as cellulases and xylanases, with potential applications in biorefinery. The ability of endophytes to produce lignocellulolytic enzymes (Laccase, cellulases, xylanases etc.) is significant to achieving affordable and clean energy, which is the seventh of the SDGs. While ligninolytic enzymes play the role of delignification during pretreatment of feedstock for biofuel production, cellulases are responsible for cellulose hydrolysis, which enables the release of

fermentable sugars during biofuel production. The complementary roles of these enzymes would indeed promote sustainable energy through optimum utilization of renewable biomass as feedstock for biofuel production. Besides, discovery of endophytes with exceptional ability for improved enzyme production would favour industrial sustainability since poor enzyme yield is a major problem militating against industrial application of enzymes. Undoubtedly, exploration of endophytes for biocontrol and production of industrial enzymes could contribute positively towards agricultural and industrial sustainability (Fig. 1). This review, therefore, brings to the fore scientific evidences that attest to the prospect of endophytes in biocontrol and production of industrial biomolecules with the possible implication on SDGs.

2 Main text

2.1 Endophyte articles identification strategy

The study identified endophyte-related research articles hosted in WoS and Scopus within the timespan 1990–2020 (07/07/2020). The articles were identified using the term ‘endophyt*’ for inclusion of different indexes including ‘endophyte’, ‘endophytes’, and ‘endophytic’ restricted to the title-field. The retrieved article sets were finally limited to primary research articles, downloaded in CSV



format and de-duplicated in ScientoPy package [9]. The topics of interest related the objectives of the review were mined from the processed article datasets based on the average growth rate or relevant author-keywords using Eq. 1 [9]:

$$\text{Topic (average growth rate)} = \left(\sum_{i=2017_b}^{2020_c} AS_i - AS_{i-1} \right) / (2020_c - 2017_b) + 1 \quad (1)$$

2017_b=start year; 2020_c=end year; AS_b=number of endophyte-related articles connected to sustainable biocontrol, enzyme and biomolecule production in 2017; AS_c=number of endophyte-related articles related to sustainable biocontrol, enzyme and biomolecule production in 2020.

The topics considered include biocontrol potential (biological control, pest control, parasitoidal, biopesticidal, microbial control) and enzymes (glucoamylase, laccase, xylanase, 1-aminocyclopropane-1-carboxylate deaminase, alpha-amylase, alpha-glucosidase, ascorbate peroxidase, beta-glucosidase, chitinase, inulinase, L-asparaginase, asparaginase, glucuronidase, hemicellulose, keratinase, lipase, cellobiohydrolase, glutaminase, amylase, endoglucanase, protease, oxalate oxidase, polyphenol oxidase, glucanase), fatty acid and polysaccharide (fatty acid, polysaccharide, exopolysaccharide). The discussion was limited to recent studies under various subtopics.

2.2 Bioprospecting endophytes for agricultural sustainability and food security

There is plethora of chemical pesticides, bactericides and fungicides in the market, however, some of them have shown negative effects on soil and plant health [1]. Even though, chemical control of insect pests and plant diseases is efficient, it is characterized with environmental hazards [1]. There is therefore, the need to explore novel sources of pesticides and plant disease control agents with little or no negative impact on consumers. A major progress in this direction is the exploitation of endophytes for biological control of plant pathogens. Several studies have documented the efficacy of endophytic microbes to produce secondary metabolites with insecticidal and biological control activities. A survey of published articles on endophytes as identified by Eq. 1 in the study databases showed that 760 articles (Additional file 1: Table S1) have reported the biocontrol activity of endophytes, out of which 36 percent was published within the last two years. There are 40 additional articles that reported the biological control properties of endophytic microbes: pest control (19 articles), parasitoid (11

articles), biopesticide (6 articles) and microbial control (4 articles) (Additional file 1: Table S1). The aforementioned keywords form an integral part of the biocontrol potential of endophytes. There are overwhelming evidences of the enormous potential of endophytes in biocontrol of pests and plant pathogens.

In this section, we accentuate some of the most recent reports on the biological control activity of endophytes (Table 1) and the implication on agricultural productivity. Ramakuwela et al. [10] established the biocontrol activity of *Beauveria bassiana* against two pecan pests: *Melanocallis caryaefoliae* and *Monellia caryella*. In their study, Ramakuwela et al. [10] showed that populations of the pecan aphids significantly reduced on pecan leaves colonized with *B. bassiana*. This, therefore, confirms the aptitude of *B. bassiana* for application in pecan pest management as its usage will reduce the pest-damaging effects on foliage and shucks of pecan, thereby increasing the rate of photosynthesis with consequent effect on crop yield. Also, a number of chloramphenicol derivatives isolated from *Acremonium vitellinum*, a marine-alga endophyte showed considerable insecticidal activity against the cotton bollworm, *Helicoverpa armigera* [11]. Recent studies have also reported the potential use of extracts from endophytic microbes and their bioactive compounds as antifeedants for biological control of pests such as *Plutella xylostella* larvae and *Myzus persicae* [12, 13].

Moreover, endophytic microbes have shown effective antagonistic activity against phytopathogens. Chen et al. [19] reported the biocontrol activity of *Lactobacillus plantarum* CM-3, an endophytic lactic acid bacterium against *Botrytis cinerea*, which causes “grey mold”, a sternly destructive strawberry disease. A *Streptomyces* species showed a promising biocontrol potential against “anthracnose”, also a strawberry disease but caused by *Glomerella cingulata* as the endophytic bacteria was reported to suppress the development of “strawberry anthracnose” lesions [20]. Meanwhile, Latz et al. [21] identified *Penicillium olsonii* ML37 and *Acremonium alternatum* ML38 as promising biocontrol agents against wheat *Septoria tritici* blotch (STB). It is noteworthy that the identified endophytic fungi were effective for the control of the disease in the two wheat cultivars investigated: cv. Sevin and cv. Mariboss. *Bacillus velezensis* 8–4, an endophytic bacterium isolated from potato was reported to have exhibited robust inhibitory effect on *Streptomyces galilaeus*, a causative agent of potato scab, a severe soil-borne disease of potato [22]. Likewise, the endophytic bacterium was effective against four other potato pathogens of fungal origin including *Phoma foveata*, *Rhizoctonia solani*, *Fusarium avenaceum* and *Colletotrichum coccodes* [22]. It is remarkable

Table 1 Biocontrol potential of endophytes against insect pest and phytopathogens

Endophytes	Pathogen/pest	Plant/disease	References
<i>Bacillus subtilis</i> and <i>B. pumilus</i>	<i>Plasmopara viticola</i>	Grapevine (Grapevine downy mildew)	Zhang et al. [14]
<i>Pseudomonas stutzeri</i> E25 and <i>Stenotrophomonas maltophilia</i> CR71	<i>Botrytis cinerea</i>	Tomato	Rojas-Solis et al. [15]
<i>Hypoxyylon anthochroum</i>	<i>Fusarium oxysporum</i>	Cherry Tomatoes	Macias-Rubalcava et al. [16]
<i>Acremonium vitellinum</i>	<i>Helicoverpa armigera</i>	Cotton (Cotton bollworm)	Chen et al. [11]
<i>Bacillus amyloliquefaciens</i>	<i>Fusarium chlamydosporum</i>	<i>Jacaranda acutifolia</i> (stem rot)	Zhu and Pan [17]
<i>Bacillus halotolerans</i>	<i>Fusarium oxysporum</i> f. sp. <i>albedinis</i>	Date palm (Bayoud disease)	Ben Slama et al. [18]
<i>Bacillus subtilis</i> SCB-1	<i>Saccharicola</i> ; <i>Cochliobolus</i> ; <i>Alternaria</i> ; and <i>Fusarium</i>	Sugarcane/mung bean seed	Hazarika et al. [1]
<i>Lactobacillus plantarum</i> CM-3	<i>Botrytis cinerea</i>	Strawberry fruit (Grey mold)	Chen et al. [19]
<i>Streptomyces thermocarboxydus</i> -related species	<i>Glomerella cingulata</i>	Strawberry (Anthracnose)	Marian et al. [20]
<i>Beauveria bassiana</i>	<i>Melanocallis caryaefoliae</i> and <i>Monellia caryella</i>	Pecan	Ramakuwela et al. [10]
<i>Penicillium olsonii</i> ML37 and <i>Acremonium alternatum</i> ML38	<i>Zymoseptoria tritici</i>	Wheat (<i>Septoria tritici</i> blotch-STB)	Latz et al. [21]
<i>Bacillus velezensis</i> 8–4	<i>Streptomyces galilaeus</i> ; <i>Phomafoveat</i> ; <i>Rhizoctonia solani</i> ; <i>Fusarium avenaceum</i> and <i>Colletotrichum coccodes</i>	Potato (Potato scab)	Cui et al. [22]
Endophytic fungi (<i>Fusarium</i> , <i>Chaetomium</i> , <i>Colletotrichum</i> and <i>Acrocalymma</i>)	<i>Rhizoctonia solani</i>	Cucumber (<i>Rhizoctonia</i> root rot)	Huang et al. [23]
<i>Burkholderia cepacia</i> complex	<i>Calonectria pseudonaviculata</i>	Boxwood (Boxwood blight disease)	Kong and Hong [24]
<i>Wickerhamomyces anomalus</i>	<i>Curvularia lunata</i> <i>Fusarium moniliforme</i> ; <i>R. solani</i>	Rice (Dirty panicle disease) Corn (Stalk rot disease) Rice (Sheath blight disease)	Khunnamwong et al. [25]
<i>Kodamae ohmeri</i>	<i>Fusarium moniliforme</i>	Rice (Bakanae disease)	Khunnamwong et al. [25]
<i>Trichoderma asperellum</i> T1	<i>Corynesporacassiicola</i> and <i>Curvularia aerea</i>	Lettuces (Leaf spot)	Wonglom et al. [26]
<i>Streptomyces albidoflavus</i> Osilf-2	<i>Magnaporthe oryzae</i>	Rice (Rice blast disease)	Gao et al. [27]
<i>Beauveria bassiana</i>	<i>Botrytis cinerea</i>	Tomato and Chilli pepper	Barra-Bucarei et al. [28]
<i>Bacillus safensis</i> B21	<i>Magnaporthe oryzae</i>	Rice (Rice blast disease)	Rong et al. [29]
<i>Aspergillus awamori</i>	<i>Verticillium dahliae</i> and <i>Phytophthora drechsleri</i>	Almond trees	Rezvani et al. [30]
<i>Cyperus iria</i> and <i>Diaporthemiriciae</i>	<i>Plutellaxylostella</i>	Cabbage	Ratnaweera et al. [12]
<i>Trichoderma</i> sp. EFI 671	<i>Myzus persicae</i>	-	Kaushik et al. [13]
<i>Pseudomonas poae</i> CO	<i>Fusarium graminearum</i>	Wheat (<i>Fusarium</i> head blight disease)	Ibrahim et al. [31]

that the *Bacillus* strain exhibited higher control efficiency against potato scab over other types of treatments with resultant improvement on potato yield. Similarly, Huang et al. [23] documented the control efficacy of two hundred and eighty-eight endophytic fungal strains against cucumber *Rhizoctonia* root rot with about 33 percent showing above 80 percent control efficiency against the disease while approximately 74 percent of the endophytic fungi exhibited over 50 percent control efficiency against *Rhizoctonia solani*. Also, an endophytic bacterium isolated from boxwood leaves and identified as a member of *Burkholderia cepacia* complex displayed an impressive biocontrol activity against *Calonectria pseudonaviculata*,

implicated in boxwood blight disease [24]. The endophytic bacterial strain significantly reduced spore formation by the pathogen, thus, alleviated the occurrence of blight by about 90 percent [24]. Koohakan et al. [32] showed that an unidentified endophytic bacterium reduced the occurrence and severity of *Fusarium* wilt disease of tomato. Besides, coating of tomato seed with the endophytic bacteria improved growth performance of tomato plant and production quality [32]. Furthermore, *Bacillus subtilis* SCB-1, an endophytic bacterium from sugarcane, displayed a remarkable biocontrol activity as it exhibited powerful antagonistic activity against a wide range of sugarcane pathogens belonging to the

following genera: *Saccharicola*, *Cochliobolus*, *Alternaria* and *Fusarium* [1]. In addition, treatment of mung bean seeds with *Bacillus subtilis* SCB-1 extract resisted infection by *Fusarium*. The authors associated the significant biocontrol activity of *Bacillus subtilis* SCB-1 against phytopathogens with lipopeptide surfactin, an antifungal compound detected in the bacterial extract [1].

Endophytes with biocontrol activities have transcended fungi and bacteria as Khunnamwong et al. [25] reported the antagonistic potential of yeasts against some phytopathogens. Specifically, different strains of *Wickerhamomyces anomalus* exhibited impressive antagonistic property against *Curvularia lunata*, *Fusarium moniliforme* and *Rhizoctonia solani*, which are causative agents of rice dirty panicle disease, corn stalk rot disease and rice sheath blight disease, respectively. However, *Kodamae ohmeri* repressed the development of only *F. moniliforme*, which is implicated in the pathogenesis of rice bakanae disease. The antagonistic behavior of the yeasts was attributed to the production of secondary metabolites such as “3-methyl-1-butyl acetate and 3-methyl-1-butanol”; “ β -1,3-glucanase and chitinase”, with the capacity to degrade fungal cell wall; and “siderophores”. Solubilization of PO_4^{3-} and ZnO was also identified as a possible antagonistic mechanism employed by the yeast strains against the different plant pathogens [25]. This is corroborated by Wonglom et al. [26], who implicated volatile organic compounds (VOCs) secreted by *Trichoderma asperellum* in the biocontrol of *Corynespora cassiicola* and *Curvularia aeria*, which are responsible for the pathogenesis of lettuce leaf spot disease. Moreover, VOCs elicited increased chitinase and β -1,3-glucanase activity, which probably arose from increased degradation of the fungal pathogen's cell wall by the enzymes. Besides, VOCs from *Trichoderma asperellum* stimulated lettuce growth and improved chlorophyll content, which is significant to photosynthesis. Similarly, Rojas-Solis et al. [15] attributed the impressive antagonistic and antifungal activity exhibited by two novel endophytic bacterial strains: *Pseudomonas stutzeri* E25 and *Stenotrophomonas maltophilia* CR71 against *B. cinerea* to production of VOCs, specifically, dimethyl disulphide (DMDS). DMDS elicited its biocontrol activity through mycelial inhibition mechanism. It is noteworthy that the endophytic bacterial strains also promoted the growth of tomato plants and as well improved the chlorophyll content [15]. Four different strains of endophytic *Hypoxylon anthochroum* emitted VOCs (majorly sesquiterpenes and monoterpenes) with inhibitory activity against *F. oxysporum* growth on cherry tomatoes [16]. It is evident from these studies that VOCs from endophytes are promising biocontrol agents against phytopathogens with plant growth stimulatory potentials. Therefore, researchers

should continue to explore the biodiversity of endophytic microbes for novel VOCs and other secondary metabolites with excellent antagonistic property against pathogens affecting crop yield.

Additionally, Gao et al. [27] reported the antagonistic activity of *Streptomyces albidoflavus* OsiLf-2 (an endophytic bacterium isolated from rice) against *Magnaporthe oryzae*, which is implicated in rice blast pathogenesis. The endophyte displayed its biocontrol activity by impeding the pathogen's mycelial growth. Likewise, metabolites in the endophyte culture supernatant were reported to have obstructed mycelial development and sporulation as well as “appressorial formation” in the pathogen [27]. *Streptomyces albidoflavus* OsiLf-2 also exhibited significant antifungal activity, which may be linked to its ability to produce “antimicrobial compounds”, “cell wall lytic enzymes”, “siderophore” and “phytohormones”. Besides, treatment of rice with the endophytic bacterial stimulated diverse defence responses including enzyme activation, buildup of hydrogen peroxide and increased expression of salicylic acid. It is evident that this endophytic bacterial strain is an auspicious candidate for managing rice blast disease.

A recent development in the application of endophytes as biocontrol agents is the introduction of nanotechnology for production of ecofriendly biocontrol agents as a substitute for conventional chemical fungicides. Ibrahim et al. [31] biosynthesized silver nanoparticles using an endophytic bacterium (*Pseudomonas poae* CO) from garlic. The biosynthesized nanoparticles showed antagonistic activity against *Fusarium graminearum*, which causes wheat Fusarium head blight by inhibiting the “mycelium growth, spore germination and mycotoxin production” by the pathogen [31]. The study indicated that biosynthesized nanoparticles from endophytic microbes may play a significant role in the management of phyto diseases. However, there is need for researchers to leverage the biocontrol potential of endophytes for development of nanoparticles with biological control activity against a wide range of plant pathogens.

The ability of endophytes to produce a wide range of secondary metabolites, (majorly VOCs) characterized by remarkable pesticidal, bactericidal, fungicidal, antinematicidal, herbicidal and algicidal properties, suggests the potential of endophytes to contribute significantly to achieving sustainable agriculture because integrated pest management (IPM) is one of the key sustainable farming practices. More so, biological control of pests is an integral part of IPM. Exploitation of endophytes for production of biocontrol agents will further minimize the use of chemical pesticides in line with the IPM [33]. Economically, effective pest management through the use of biocontrol agents from endophytes would definitely

improve agricultural productivity, thereby ensuring farmers' profitability. Overall, biological control using endophytes-derived compounds would further protect the environment and enhance public health, which are hallmarks of sustainable agriculture.

2.3 Aptitude of endophytes for enzyme production

Given the high utility of enzymes in different industrial sectors, there is increased market demand for purified enzymes. Hence, the need for exploration of novel sources of various classes of industrial enzymes, with robust production yield and improved enzyme titre. Endophytic microbes have shown excellent aptitude for production of a wide range of enzymes with industrial and biotechnological significance. A survey of published articles on endophytes over the last three decades as available in WoS and Scopus databases revealed that the following enzymes have been produced by endophytes: cellulase, chitinase, α -glucosidase, protease, L-asparaginase, amylase, laccase, lipase, xylanase, β -glucosidase, glutaminase, endoglucanase, keratinase etc. A summary of enzyme production by some endophytic microbes is presented in Table 2.

One of the most desirable industrial enzymes globally is cellulases, which comprise of exoglucanases, endoglucanases and β -glucosidase. The increased interest in cellulases is, perhaps, attributed to the robust industrial application potentials in biorefinery as well as paper and pulp industry. Cellulases are involved in cellulose hydrolysis by cleaving the β -1,4 linkages in the complex structure thereby releasing the sugars for fermentation during biofuel production. Another enzyme of significance in biorefinery is xylanase because it has the ability to break the varied β -1,4-glycoside linkage in xylan to release xylose, hence, its involvement in hemicellulose degradation. Undoubtedly, cellulases, xylanases and other accessory enzymes from microbes can be used as "emerging green tool" [66] for biofuel production from lignocellulose biomass.

To achieve goal 7 of the UN SDGs: ensuring access to affordable and clean energy, there is an unarguable need for sustainable production of cellulases and xylanases. Hence, bioprospecting of endophytes as bioresources for enhanced and sustainable cellulase and xylanase production is imperative. The good news is that there are recent research efforts toward exploring diverse endophytic microbes for production of lignocellulolytic enzymes (Table 2). One of such research endeavours is the work of Robl et al. [39], where optimum xylanase production (458 U/mL) by an endophytic fungus: *Aspergillus niger* DR02 was reported in a "constant fed-batch" fermentation. Interestingly, proteomics of the endophytic fungus revealed the activity of other enzymes including

cellobiohydrolase, beta-glucosidase and beta-xylosidase, which also play important role in biofuel production. Cellobiohydrolase involves in the degradation of cellulose by breaking the 1,4- β -D-glycosidic bonds, leading to the cleavage of cellobiose unit from the cellulose chain ends while beta-glucosidase works in synergy with endo- β -1,4-glucanases and cellobiohydrolases to convert cellobiose to glucose [67] for biofuel production. Also, beta-xylosidase is an integral part of the enzyme battery (cellulases and hemicellulases) involved in the degradation of lignocellulose biomass [68]. Similarly, *A. terreus*, an endophyte from *Corchorus olitorius* exhibited excellent xylanase production with improved production of the enzyme achieved using the host plant and pea peel as substrate [41]. It is worthy of note that hydrolysis of wheat bran by crude xylanase from *A. terreus* generated significant fermentable sugars and improved saccharification, suggesting that xylanase could play a significant role in the utilization of wheat bran as feedstock for biofuel production. Besides, it has potential for application in various other industrial processes including clarification of juice, bread production, biobleaching and deinking of waste paper [66].

Apart from *Aspergillus*, endophytes belonging to other fungal genera such as *Fusarium*, *Trichoderma*, *Botryosphaeria*, *Saccharicola* and *Diaporthe* have shown vigorous potential for cellulolytic enzymes production. Out of fourteen endophytic fungi screened by Marques et al. [45] for their ability to produce cellulolytic enzymes, *Botryosphaeria* sp. AM01 and *Saccharicola* sp. EJC 04 displayed auspicious potential for production of cellulases and xylanases, with prospect in sugarcane bagasse saccharification. Furthermore, two different endophytic fungal strains of *Fusarium* genus (*Fusarium sambucinum* and *Fusarium* sp.) have been reported to show impressive capability for production of lignin peroxidase, manganese-dependent peroxidase and laccase [53], which are significant in delignification of feedstock for biofuel production [69]. In the same study, *Trichoderma camerunense* expressed appreciable cellulase and xylanase activity [53]. The production of lignocellulolytic enzymes by endophytes is a desirable trait for sustainable biorefinery as the enzyme system is a promising alternative to chemical pretreatment of feedstock for biofuel production. However, Goukanapalle et al. [61] reported the expression of the following cellulases: filter paperase, carboxymethyl cellulase and β -glucosidase by *Pestalotiopsis microspora* TKBRR. It is remarkable that cellulase production is not limited to endophytic fungi alone as some endophytic bacteria isolated from *Capsicum chinese* plant have shown the potential for production of endoglucanase and filter paper cellulase [60]. Likewise, some

Table 2 Aptitude of endophytes for enzyme production

Endophytic microbe	Host	Enzyme produced	Biotechnological potential	References
<i>Phomopsis liquidambari</i>	NA	Laccase	Plant growth promotion	Wang et al. [34]
<i>Fusarium</i> sp. AEF17	Coastal sand dune plants	Laccase	Dye decolorization	Muthezhilan et al. [35]
<i>Pseudomonas fluorescens</i> J18-3	<i>Panax ginseng</i>	1-aminocyclopropane-1-carboxylate deaminase	Promotion of plant growth/stress tolerance	Tian et al. [5]
<i>Cercosporakikuchii</i>	NA	Lipase	Detergent additives; Flavour development in dairy products; removal of triglycerides during pulp and paper production; waste/effluent treatment	Costa-Silva et al. [36], Choudhury, [37]
<i>Bacillus pumilus</i> PC1	<i>Pistacia chinensis</i> Bunge	Lipase	As above	Chun-Zhu and Dong-Hong [38]
<i>Aspergillus niger</i> DR02	NA	Xylanase; Cellobiohydrolase; β -glucosidase; and β -xylosidase	Lignocellulose degradation	Robl et al. [39]
<i>Hormonemasp</i> ; <i>Pringsheimiastmiliadis</i> ; <i>Ulocladium</i> sp; <i>Neofusicoccum luteum</i> ; and <i>N. austral</i>	Eucalyptus trees	Laccase	Lignocellulose degradation	Fillat et al. [40]
<i>Aspergillus terreus</i> KP900973	<i>Corchorus olitorius</i>	Xylanase	Wheat bran hydrolysis; Juice clarification; alternative emulsifier and additives in bread production	Ahmed et al. [41]
<i>Aspergillus</i> sp. ALAA-2000	Marine soft sponge <i>Aplysina fistularis</i>	L-Glutaminases	Tumor inhibition	El-Gendy et al. [42]
<i>Trichoderma harzianum</i> TH5-1-2	<i>Pistacia vera</i>	Chitinase	Biocontrol/plant growth promotion	Dolatabad et al. [6]
<i>Micrococcus aloeverae</i> AE-6 and <i>Micrococcus yunnanensis</i>	Aloe vera (<i>Aloe barbadensis</i>)	Alkaline protease	Detergent ingredient	Prakash et al. [43]
<i>Bipolaris</i> sp.; <i>Phlebia</i> sp.; <i>Marasmius-cladophyllus</i> ; <i>Phyllosticta capitata</i> ; and <i>Schizophyllum commune</i>	<i>Piper hispidum</i> Sw	Amylase	Starch hydrolysis	Orlandelli et al. [44]
<i>Botryosphaeria</i> sp. AM01 and <i>Saccharicola</i> sp. EJC 04	NA	Cellulases and Xylanases	Sugarcane bagasse saccharification	Marques et al. [45]
<i>Curvularia australiensis</i> and <i>Alternaria citrimaculans</i>	Aeglemarmelos	Amylase; protease; lipase; cellulase; laccase and xylanase	–	Mani et al. [46]
<i>Bacillus halotolerans</i> CT2	Tunisian potatoes	Alkaline protease	Detergent ingredient	Dorra et al. [47]
<i>Phomopsis</i> sp.		Laccase	Degradation/detoxification of anthraquinone dyes	Navada et al. [48]
<i>Humicola fuscoatra</i> LBKURCC68 and <i>Fusarium oxysporum</i> LBKURCC69	<i>Dahlia variabilis</i>	Inulinase	Biofuel production from inulin-containing biomass	Mohan et al. [49], Silvera et al. [50]
<i>Diaporthe</i> sp. KM362392	Grapevine (<i>Vitis labrusca</i> L)	Endoglucanase	Cellulose hydrolysis	Felber et al. [51]
<i>Streptomyces</i> species	NA	Hemicellulases	Lignocellulosic biomass degradation	Robl et al. [52]
<i>Fusarium sambucinum</i> ; <i>Fusarium</i> sp and <i>Trichoderma camerunense</i>	NA	Lignin peroxidase; manganese peroxidase; laccase; cellulase and xylanase	Lignocellulolytic potential	Martinho et al. [53]
<i>Penicillium bilaiae</i>	Date palm trees	Acidic protease	Production of protein hydrolysate and digestive aids	Ben Meffeh et al. [54]

Table 2 (continued)

Endophytic microbe	Host	Enzyme produced	Biotechnological potential	References
<i>Fusarium solani</i> ; <i>F. oxysporum</i> ; <i>Penicillium</i> sp.; <i>Aspergillus</i> sp.; and <i>Alternaria</i> sp.	<i>Curcuma longa</i> ; <i>Murrayakoenigii</i> ; <i>Catharanthus roseus</i> ; and <i>Withanias-omnifera</i>	Glutaminase-free L-asparaginase	Chemotherapeutic agent to treat lymphoproliferative and lymphoma diseases such as acute lymphoblastic leukemia	Cachumba et al. [56], Bhosale and As-Suhbani [56]
<i>Penicillium chrysogenum</i>	<i>Rauvolfia densiflora</i> (Apocynaceae)	L-asparaginase	Anticancer agent	Alrumman et al. [57], Bhavana et al. [58]
<i>Aspergillus</i> sp.	NA	Pullulanase	Starch hydrolysis	Naik et al. [59]
Unidentified endophytic bacteria	<i>Capsicum chinese</i> plant	Endoglucanase and Filter paper cellulase (FPCase)	Cellulolytic potential	Sharma et al. [60]
<i>Pestalotiopsis microspora</i> TKBRR	NA	Filterpaperase (FPase); Carboxymethyl cellulase (CMCase); and Beta-glucosidase (BGL)		Goukanapalle et al. [61]
<i>Bacillus subtilis</i> P4	<i>Pseudobrickellia brasiliensis</i>	Protease		Cardoso et al. [62]
<i>Lysinibacillus fusiformis</i> B27	<i>Rhizophora mucronata</i>	Glutamate-free L-asparaginase	Cancer therapy	Prihanto et al. [63]
<i>Talaromyces pinophilus</i>	<i>Curcuma amada</i>	L-asparaginase	Anticancer agent	Krishnapura and Beler [64]
<i>Phormopsis</i> sp.	NA	Laccase	Dye decolorization/degradation; textile effluent decolorization	Navada and Kulal [65]

NA: Not available

Streptomyces species isolated from plants in Brazil exhibited remarkable potential as hemicellulase producers while the extracts from the endophytic strains showed prospect for lignocellulose biomass deconstruction and biofuel production [52].

Another enzyme of industrial significance reported to have been produced by endophytes is laccase. Apart from being a lignin-degrading biocatalyst, laccase is characterized by several other application potentials including juice clarification, dye decolourization, degradation of emerging environmental pollutants and so on. The diverse applications of laccase in different industrial sectors have necessitated exploration of new sources with enhanced production capacity to meet the increasing demand. It is noteworthy that a few of the laccase-producing endophytic fungi discussed in this paper belong to *Phomopsis* genus. Wang et al. [34] detected a new laccase gene in *Phomopsis liquidambari*, which was subsequently cloned and expressed. The expressed *P. liquidambari* laccase exhibited remarkable industrial properties as it was acidotolerant and thermostable, with about 50% of the enzyme activity being retained after 20 h. Besides, the enzyme displayed prospective application in the agricultural sector as it promoted peanut growth in the study and as well reduced soil phenolic contents. Likewise, *Phomopsis* sp. exhibited improved laccase production with about twofold due to its exposure to “electron beam radiation” [48]. The enzyme was metallotolerant and displayed good thermostability, with potential application in remediation of synthetic dyes. Moreover, γ -irradiation of the aforementioned endophytic fungus boosted laccase production [65] and improved the enzyme catalytic efficiency, which was evident in the effective degradation of a recalcitrant dye, aniline blue and textile effluent [65]. More so, members of *Fusarium* genus have exhibited robust laccase-producing potential. This was demonstrated by Muthezihlan et al. [35] who identified *Fusarium* sp. AEF17 as the most promising laccase-producer in a screening that involved twenty-nine endophytic fungi from different coastal sand dune plants. Interestingly, purified laccase from *Fusarium* sp. AEF17 exhibited outstanding remediation potential as it showed significant decolourization activity on a wide range of synthetic dyes [35]. Furthermore, endophytic fungal strains belonging to *Hormonema*, *Pringsheimia*, *Ulocladium* and *Neofusicoccum* genera have also shown promising potential for laccase production [40].

Apart from the popular industrial enzymes discussed in the earlier paragraphs, endophytes have also shown emerging potential for production of some relatively rare and unique enzymes such as inulinase, pullulanase and L-asparaginase. Two endophytic fungi of *Humicola* and *Fusarium* genera have shown dexterity for production of

inulinase [50], an industrial food biocatalyst that hydrolyzes inulin into simple sugars, particularly fructose. Inulinase activity has promoted utilization of inulin as an alternative to starch in various food industries [49]. Moreover, inulinase has shown promising application potential in biorefinery as inulin-containing biomass has been utilized for production of biofuels [49]. Pullulanase, a debranching enzyme, was also secreted by an endophyte, *Aspergillus* sp. [59]. The ability of endophytes to produce pullulanase holds enormous potential in the starch industry because of the enzyme peculiarity in hydrolyzing the α -1,6-glucosidic linkages of pullulan. Another enzyme that has recently been produced by endophytes is L-asparaginase, which is used as a chemotherapeutic agent for the treatment of lymphoblastic leukemia [55]. Production of L-asparaginase has been reported in a wide range of endophytic fungi including *Fusarium*, *Penicillium*, *Aspergillus*, *Alternaria* and *Talaromyces* species [56, 58, 64]. The potential of endophytic bacterial strains for asparaginase production has also been reported [63]. However, endophytic bacteria seemed to be underexplored for the production of asparaginase, hence, researchers should channel more efforts towards exploring novel endophytic bacteria for asparaginase production as this would further alleviate the pains of patients with leukemia.

Furthermore, endophytes have shown prospect for production of agriculture-relevant enzymes including 1-aminocyclopropane-1-carboxylate deaminase (ACCD) and chitinase [5, 6]. Chitinase is usually produced by endophytes as a defence response mechanism of the host plants against pests and pathogens whereas ACCD promotes plant growth and stress tolerance by hydrolyzing 1-aminocyclopropane-1-carboxylate to α -ketobutyrate and ammonia, thereby reducing ethylene concentration in the host plant. Apart from the plant-health promoting significance of the enzymes produced by endophytic microbes, most of these enzymes have specific industrial applications, which are articulated in the previous paragraphs.

The use of endophytes-derived enzymes in industrial processes is capable of improving the economic performance of various industries [70]. For instance, lignocellulolytic enzymes from endophytes could stimulate the use of lignocellulose waste biomass as cheap feedstock for biofuel production. This is not only cost-effective for the industry but also environmentally-friendly and sustainable. More so, production of plant-health and -growth promoting enzymes by endophytes would enhance agricultural productivity and as such contribute to agro-industrial sustainability. Therefore, it is important for biotechnologists and researchers to continue to harness

the biodiversity of endophytes for enhanced enzyme production towards achieving industrial sustainability.

2.4 Prospect of endophytes in polysaccharide and fatty acid production

Apart from enzymes, a copious number of endophytic microbes have displayed the potential for production of other biomolecules including exopolysaccharides and lipids (Table 3). Interestingly, polysaccharides are characterized by enormous therapeutic potential as some have been reported to possess remarkable antioxidant properties [71–73] while others exhibited promising anticancer, antitumor and antiproliferative activities [11]. Table 3 gives a summary of endophytic polysaccharides: their compositions and bioactivity. *Bacillus amyloliquefaciens* isolated from *Ophiopogon japonicus* produced polysaccharides with anticancer property [74] but the

composition of the biomolecule was not determined in the study, as such, it is difficult to ascertain the bioactive component of the polysaccharide. Likewise, Zheng et al. [75] reported the production of an uncharacterized exopolysaccharide by an endophytic *Bacillus* species from *Artemisia annua* L, which exhibited antioxidant property and prevented oxidative deoxyribonucleic acid damage. Another uncharacterized polysaccharide which was produced by a *Staphylococcus* species isolated *O. japonicus* displayed antitumor activity [76]. Similarly, Chen et al. [77] reported exopolysaccharide production by an endophytic *Bacillus* strain from *Codonopsis pilosula*. The study also revealed the anticancer activity of polysaccharide with the following compositions: galactose, glucose, rhamnose, fucose, arabinose and mannose. Just recently, *Glutamicibacter halophytocola* showed the

Table 3 Polysaccharide and fatty acid production by endophytes

Endophytes	Host	Biomolecule composition	Bioactivity	References
<i>Bacillus amyloliquefaciens</i>	<i>Ophiopogon japonicus</i>	NC	Anticancer	Chen et al. [74]
<i>Aspergillus ochraceus</i>	Coral <i>Dichotella gemmacea</i>	Mannose and Galactose	ND	Guo et al. [78]
<i>Bionectria ochroleuca</i> XF-38	Chinese <i>Torreya grandis</i>	Linoleic acid, oleic acid and sciadonic acid	ND	Yang et al. [79]
<i>Bacillus cereus</i> SZ1	<i>Artemisia annua</i> L	NC	Antioxidant and DNA-damaging protecting activity	Zheng et al. [75]
<i>Pestalotiopsis</i> sp. BC55	NA	1,3-linked β -D-glucopyranosyl moiety	ND	Mahapatra and Banerjee [80]
<i>Chaetomium</i> sp.	<i>Gynostemma pentaphylla</i>	Glucose, mannose, arabinose and galactose	Antioxidant and antiproliferative	Zhang et al. [81]
<i>Diaporthesp.</i> JF766998 <i>Diaporthesp.</i> JF767007	<i>Piper hispidum</i> Sw	Galactose, glucose, mannose and glucan	Antiproliferative	Orlandelli et al. [82]
<i>Mangrovihabitansendophyticus</i> gen. Nov., sp. nov	<i>Bruguiera sexangula</i>	Polysaccharide: glucose, galactose, mannose, arabinose, xylose and ribose Lipid: diphosphatidyl glycerol, phosphatidyl ethanolamine and phosphatidyl inositol	ND	Liu et al. [83]
<i>Staphylococcus</i> sp.	<i>Ophiopogon japonicus</i>	NC	Antitumor	Xu et al. [76]
<i>Bacillus</i> sp.	<i>Codonopsis pilosula</i>	Galactose, glucose, rhamnose, fucose, arabinose and mannose	Anticancer	Chen et al. [77]
<i>Fusarium solani</i> DO7	<i>Dendrobium officinale</i>	Galactoglucan	Immune enhancement	Zeng et al. [84]
<i>Fusarium</i> sp. A14	<i>Fritillaria unibracteata</i>	Mannose, rhamnose, glucose, galactose, xylose, arabinose and pyranose	Antioxidant and antiproliferative	Pan et al. [71]
<i>Alternaria tenuissima</i> FI	<i>Angelica sinensis</i>	O-galacturonic acid, rhamnose, O-mannose, glucose and O-galactose	Antioxidant	Wang et al. [85]
<i>Glutamicibacter halophytocola</i> KLBMP 5180	NA	Rhamnose, galacturonic acid, glucose, glucuronic acid, xylose and arabinose	Antioxidant	Xiong et al. [73]
<i>Pilidiella guizhouensis</i> ZJSRU-M1	<i>Eupatorium chunense</i> L	Glucose alone	Antioxidant	Zhang et al. [72]

NA: Not available; NC: not characterized; ND: not determined

dexterity for production of polysaccharide with excellent antioxidant activity [73].

Moreover, a broader range of endophytic fungi have shown intrinsic ability for production of polysaccharides. A *Chaetomium* species isolated from *Gynostemma pentaphyllum* produced polysaccharide with the following composition: glucose, mannose, arabinose and galactose [81]. It is noteworthy that the *Chaetomium* exopolysaccharide showed antioxidant property and inhibited cell proliferation. In the same vein, two endophytic *Diaporthe* species from *Piper hispidum* were able to produce exopolysaccharide with characteristic ability to inhibit cell proliferation. Furthermore, Zeng et al. [84] reported the production of a galactoglucan by a member of *Fusarium* genus from *Dendrobium officinale*. The polysaccharide was biologically active as it enhanced immune response, hence it could be used for the development of functional food for the treatment of patients with hypo-immunity. However, a *Fusarium* species from *Fritillaria unibracteata* produced a polysaccharide with entirely different composition: “mannose, rhamnose, glucose, galactose, xylose, arabinose and pyranose” [71] but was characterized by efficient antioxidant and cell proliferation inhibitory activities [71]. Other endophytic fungi with polysaccharide production potential include *Alternaria tenuissima* and *Pilidiella guizhouensis* [72, 85]. Meanwhile, *Mangrovhabitansendophyticus*, in addition to exopolysaccharide, produced lipid with the following composition: diphosphatidyl glycerol, phosphatidyl ethanolamine, and phosphatidyl inositol [83]. More so, linoleic, oleic and sciadonic acids were produced by an endophytic fungus isolated from *Torreya grandis*, *Bionectria ochroleuca* [79]. Linoleic and oleic acids are polyunsaturated fatty acids with enormous health benefits [86]. Specifically, linoleic acid is one of the major fatty acids essential in human diets as it cannot be synthesized in the body. Endophytes may be a promising source of linoleic acid and other polyunsaturated fatty acids.

3 Conclusions

Endophytes, indeed, possess robust aptitude in biocontrol of phytopathogens and enzyme production, which are significant to agro-industrial sustainability. Nevertheless, there is still dearth of research on the application of endophytes in the biocontrol of termites, which are known for causing substantial damage to agriculture, specifically forest products, with consequent huge economic loss. More so, chemical methods of controlling termites are characterized by low efficiency and high cost. As well, they are not eco-friendly. Future studies should, therefore, explore endophytes for production of novel biocontrol agents against termites.

Furthermore, literature survey showed that endophytes have been poorly explored for production of versatile peroxidase (VP) and dye decolourizing peroxidase (DyP), which are integral part of the ligninolytic enzyme system, with promising potentials in biofuel production and bioremediation. Research effort in this direction is therefore imperative.

Despite the effectiveness of endophytes in biological control of plant pathogens, care must be taken in the direct usage of endophytes so as not to introduce pathogenic microbes in the environment. Researchers can however, exploit the biocontrol potential of endophytes for development of nanoparticles with biocontrol activity against a wide range of phytopathogens. Future studies should focus more on isolating bioactive compounds from endophytes for development of effective biocontrol agents as part of integrated pest management. Therefore, there is a need for metagenomics study of endophytes so as to explore the diversity of endophytic microbes towards discovering novel secondary metabolites of industrial and agricultural significance. It is also important to decipher the biosynthetic pathway of biocontrol agents and enzyme production in endophytes as this can be exploited for large scale production through genetic engineering.

Abbreviations

ACCD: 1-Aminocyclopropane-1-carboxylate deaminase; DyP: Dye decolourizing peroxidase; STB: *Septoria tritici* blotch; SDGs: Sustainable development goals; UN: United nations; VP: Versatile peroxidase; VOCs: Volatile organic compounds; WoS: Web of science.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s43088-021-00146-3>.

Additional file 1. Details of published articles on endophytes.

Acknowledgements

Not applicable.

Authors' contributions

AO and KE conceptualized the idea for the article; TC designed the methodology; AO, KE and TC drafted and critically revised the work. All authors approved the final version of the manuscript.

Funding

Not applicable.

Availability of data and materials

Not applicable.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

Authors declare that they have no competing interests.

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Received: 30 October 2020 Accepted: 5 September 2021

Published online: 07 October 2021

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