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Crop residue heterogeneity: Decomposition by potential indigenous ligno-cellulolytic microbes and enzymatic profiling

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ABSTRACT

The continuous depletion of fossil resources, energy-crisis and environmental pollution has gained popularity for careful selection of suitable microbial consortium to efficiently decompose crop residue and facilitate nutrient cycling. While crop residue is commonly incorporated into soil, the impact of the heterogeneity of residue on decomposition and biological mechanisms involved in extracellular carbon (C) cycle related enzyme activities remain not fully understood. To address this problem, an incubation study was conducted on chemical heterogeneity of straw and root residue with indigenous ligno-cellulolytic microbial consortium on extracellular enzymes as their activity is crucial for making *in-situ* residue management decisions under field condition. The activity of extracellular enzymes in different substrates showed differential variation with the type of enzyme and ranged from 16.9 to 77.6 μg mL^{-1}, 135.7 to 410.8 μg mL^{-1}, 66.9 to 177.1 μg mL^{-1} and 42.1 to 160.9 μg mL^{-1} for cellulase, xylanase, laccase and lignin peroxidase, respectively. Extracellular enzyme activities were sensitive to heterogeneity of biochemical constituent's present in straw and root residues and enhanced the decomposition processes with indigenous ligno-cellulolytic microbial consortium (*Bacillus altitudinis, Streptomyces flavomacrosporus* and *Aspergillus terreus*). Correlation matrix elucidated *A. terreus* and *B. altitudinis* as potential indigenous ligno-cellulolytic microbial inoculant influencing soil enzymatic activity ($p < 0.001$). This research work demonstrates a substantial impact of chemically diverse crop residues on the decomposition of both straw and root. It also highlights the pivotal role played by key indigenous decomposers and interactions between different microorganisms in governing the decomposition of straw and root primarily through release of extracellular enzyme. Consequently, it is novel bio-emerging strategy suggested that incorporation of the crop residues under field conditions should be carried out in conjunction with the potential indigenous ligno-cellulolytic microbial consortium for efficient decomposition in the short period of time under sustainable agriculture system.

Introduction

Intensive agricultural practices along with *in-situ* burning of crop residue has resulted in substantial loss in essential nutrient pools, soil microorganisms and diminished crop production as well as emission of greenhouse gases leading to severe environmental challenges in the present climatic conditions (Saikia et al., 2019; Sharma et al., 2021). This practice has been widely adopted by marginal farmers due to labor shortage, high expenses associated with crop residue removal and composting, shortage of necessary machinery (happy seeder, rotovators and super seeder *etc*.) and unavailability of economically feasible solutions (Sharma et al., 2021). Now a days, scientists and environmentalists focus not only on utilization of resources but also on how to effectively utilize the waste materials through an environmentally friendly approach. For instance, *in-situ* residue management practices (retention and incorporation) have been broadly adapted (Sharma et al., 2019) to diminish soil nutrients loss from burning (Sharma and Singh, 2023), improve soil structure, organic matter, moisture and augment biological activity (Saikia et al., 2019). These residues are high source of ligno-cellulosic materials such as lignin, cellulose, hemicellulose, tannin

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and saponin and therefore, can alter the physical, chemical and biological properties of soil and affect the microbial proliferation and physiological activities (Singh et al., 2018). Moreover, the ligno-cellulosic crop residues have garnered increased attention and significant interest owing to their versatility, natural abundance, renewability, low cost (Kumar and Chandra, 2020) and ability to convert into green second- generation energy fuels (Hernandez-Beltran et al., 2019).

In recent years, a close relationship between C cycling, decomposition, transformation (Yang et al., 2019) and stabilization of C in soil have received widespread attention of researchers (Liang et al., 2017). Microbial-assisted residue management offers a sustainable alternative by harnessing the power of microbial communities to enhance nutrient cycling, organic matter decomposition and overall soil ecosystem functioning (Bhattacharjya et al., 2021; Dash et al., 2021). In view of fact that straw incorporation often involves the use of ligno-cellulolytic microbial consortium, to comprehend how diverse farming system impacts the decomposition of straw and underlying mechanism. Crop residue decomposition is principally impacted by both biotic such as decomposers, residue quality (Garcia-Palacios et al., 2016) and abiotic factors such as soil properties and climate conditions (Bani et al., 2018) and also related with abundance and diversity of decomposers (Handa et al., 2014). Diverse microorganisms participate in the residue decomposition process with certain fungal and bacterial genera capable of efficient decomposition (Geisen et al., 2018; Wilschut and Geisen, 2021). However, increasing evidence has emphasized the significance of key decomposers in prompting the process of decomposition (Banerjee et al., 2018; Zheng et al., 2021). Due to slower decomposition rate of crop residues resulting in the formation of complex compounds, open-field straw burning as environmental hazards has risen considerably in the previous decade (Kumar and Chandra, 2020). Thus, comprehensive research that encompasses various biological communities, chemical composition of residues, environmental situations and their intricate interactions are essential for a thorough understanding of the residue decomposition.

For successful decomposition of crop residues using microorganisms, the raw material should maintain a C: nitrogen (N) ratio of 20 to 25, lignin: N ratio of 5:1 with sufficient moisture levels ranging between 55 and 60 % of the crop residues (Shilev et al., 2007). Microorganisms play a pivotal role in facilitating nutrient transfer from agricultural residues to agricultural soils (Erickson et al., 2009). The majority and efficient degrading microbes used for recycling of agricultural waste includes the cellulolytic filamentous fungi *Trichoderma* sp. (Sagarika et al., 2022), *Phanerochaete* sp. (Chen et al., 2019; Sagarika et al., 2022), and *Aspergillus* sp. (Sukaryani et al., 2021), bacteria commonly *Bacillus* sp., *Cellulomonas* sp., (Chukwuma et al., 2021) and actinobacteria commonly *Streptomyces* sp. (Feng et al., 2021). Thus, ligno-cellulosic degraders are required to alter the structure of ligno-cellulosic waste materials by making holo-cellulose (cellulose + hemicellulose) bioavailable for bioconversion. Their remarkable enzyme activity makes them exceptionally valuable in the breaking down of complex biopolymers (Jędrzejczyk et al., 2019). Consequently, the utilization of potential indigenous ligno-cellulolytic microbes to expedite the decomposition of crop residue seems promising. This approach is not only cost-effective and environmentally friendly but also demonstrates the capacity to produce a higher amount of essential extracellular enzymes including cellulase, laccase, lignin peroxidase and xylanase.

The enzymatic activity in soil is significantly influenced by the diverse biochemical constituents present in root and straw residues from crops, contributing to crop heterogeneity. The introduction of organic compounds, including proteins, carbohydrates, and lignin, by these crop components serves as substrates for soil enzymes, shaping their activity and function (Srinivas et al., 2020). Root residues release sugars and soluble organic compounds during decomposition, acting as a carbon source for microorganisms and affecting enzymatic processes involved in organic matter degradation (Garcia-Palacios et al., 2016). Additionally, root exudates may contain compounds that interact with soil enzymes, modulating their activity. Straw residues, rich in cellulose, hemicellulose, and lignin, impact enzymatic activity differently. Enzymes play a crucial role in breaking down these complex compounds, releasing sugars that influence soil enzyme dynamics (Jat et al., 2021). The variability in enzymatic responses is attributed to the diverse composition of biochemical constituents in root and straw residues, crucial for understanding the overall impact on soil enzymatic activity, nutrient cycling, and organic matter decomposition in agricultural ecosystems (Shilev et al., 2007).

In the recent decade, appropriate strategic amalgamation of potent indigenous strains of fungi, bacteria and actinomycetes as a consortium has been used to augment the digestibility of ligno-cellulosic biomass through secretion of diverse enzymes by microbes which significantly impacts the nutrients cycle and soil quality (Meena and Rao , 2021). Till date, majority of the research work have concentrated on examining the comparative performance of single microbial inoculants versus microbial consortia for crop residue decomposition under *ex-situ* conditions (Bradzcova et al., 2019; Sharma et al., 2022). However, there is notable dearth of studies addressing the dynamics of enzymatic activities in the different biochemically diverse straws and roots biomass with indigenous microbial consortia. Considering these aspects, the present research work was conducted to scrutinize the impact of biochemically different crop biomass (straw and root) on specific C related enzyme activities (cellulase, laccase, xylanase, and lignin peroxidase) through application of single as well as biocompatible consortium inoculation. Apart from this, the study delved into investigating the correlation ($p < 0.001$) and relative significance of individual enzyme in contributing towards overall enzyme activity within the heterogeneous crop biomass with variable biochemical constituents (Table 1).

Material and methods

Procurement of potential indigenous ligno-cellulolytic microbial strains

The microbial strains *viz. B. altitudinis, S. flavomacrosporus* and *A. terreus* were procured from Soil Microbiology Laboratory, Department of Soil Science, Punjab Agricultural University, Ludhiana, Punjab, India. All these potential microbial strains were maintained on specific medium slants and stored at 4 °C for further studies.

Biochemical analysis of straw and roots

The diverse leguminous, cereals and oil seed straw as well as root residues samples, were collected from experimental fields of Department of Soil Science, Punjab Agricultural University, Ludhiana, Punjab, after harvest and brought in the laboratory. Following oven drying, the straw and root residue samples were finely ground to pass through a 40-mesh sieve for the examination of various cell wall fractions. The cellulose, hemicellulose and lignin were estimated *via* standard protocol described by Van Soest et al. (1991) under crude fiber hot and cold extraction unit (Foss, FT-122 Fibertec ^{TM}). Additionally, C as well as N content were quantified using the procedure described by Choudhary et al. (2016).

Molecular identification and phylogenetic tree analysis

For taxonomic confirmation of the isolates, genomic DNA was extracted using the CTAB method (Huang et al., 2013). The targeted genes were amplified using 16 S rRNA universal primers for bacteria and actinomycetes and ITS I-IV primers for fungi (Gardes and Bruns, 1993). The nucleotide sequences were capered compared with the available sequences in NCBI GenBank (Fig. 1). A Phylogenetic tree was constructed by applying the Neighbour-Joining method using MEGA-11 program based on Kimura −2 parameters with 1000 replicates of bootstrap value (Fig. 2).

Table 1
Biochemical constituents in different crop residues.

Crop residues	Family	Straw							Root						
		C (%)	N (%)	C:N	CELL (%)	HEM (%)	LIG (%)	LIG:N	C (%)	N (%)	C:N	CELL (%)	HEM (%)	LIG (%)	LIG:N
Oryza sativa	Poaceae	65.2	0.92	70.8	34.4	30.4	10.9	11.8	60.7	0.94	64.5	5.04	7.06	1.98	2.16
Zea mays	Poaceae	74.2	1.05	73.1	29.3	20.3	9.66	9.2	74.2	0.89	83.4	6.75	12.15	4.74	5.04
Arachis hypogaea	Fabaceae	12.76	2.35	4.10	7.79	1.70	2.35	0.9	11.6	1.54	7.56	11.7	5.07	4.06	2.64
Crotalaria juncea	Fabaceae	12.62	1.68	7.52	21.99	19.16	6.79	4.0	14.5	0.47	30.7	34.6	28.55	10.1	21.49
Glycine max	Fabaceae	24.45	2.44	10.0	19.25	14.84	8.66	3.5	22.7	1.92	11.8	8.28	4.34	4.87	2.54
Gossypium hirsutum	Malvaceae	29.29	0.50	58.6	10.85	16.27	10.7	22.0	23.6	0.52	45.7	26.8	9.12	5.87	11.29
Vigna radiata	Fabaceae	12.62	1.46	8.66	8.19	10.8	2.69	1.8	11.5	0.93	12.4	10.7	9.88	4.03	4.33
Vigna mungo	Fabaceae	9.52	1.11	10.3	10.11	5.09	2.99	2.7	26.5	1.15	22.95	12.3	2.49	6.15	5.35
Cajanus cajan	Fabaceae	17.70	1.31	13.5	8.84	2.84	5.26	4.0	54.6	1.38	39.7	12.2	3.45	6.67	4.83
Sesbania bispinosa	Fabaceae	11.58	1.68	6.91	9.34	7.77	4.69	2.8	18.48	1.66	11.1	3.30	6.77	8.11	4.89
Sesamum indicum	Pedaliaceae	11.47	0.80	14.4	11.99	6.95	4.04	5.1	17.43	0.55	31.93	17.1	8.62	4.53	8.24

C- Carbon; N- Nitrogen; CELL- Cellulose; Hem- Hemicellulose; LIG- Lignin.

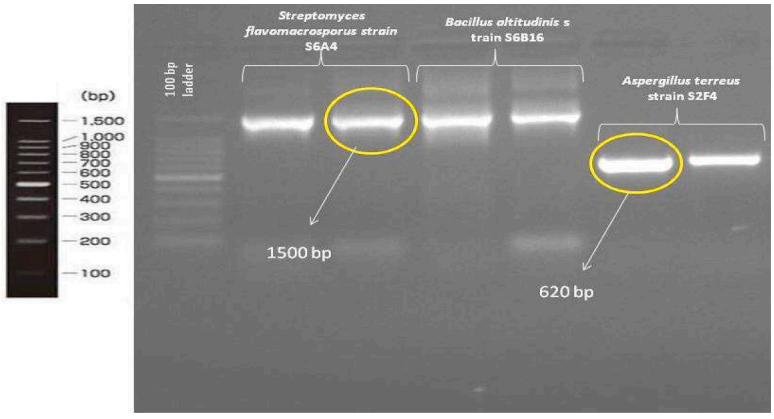

Fig. 1. PCR amplification of 16 S rRNA (bacteria and actinomycete) and 18 S rRNA (Fungus) genes; Lane-**1** show 100 bp ladder; **Lane-2 & 3** strain S6A4- *Streptomyces flavomacrosporus;* **Lane-4 & 5** strain S6B16- *Bacillus altitudinis* and **Lane- 6 & 7** strain S2F4 - *Aspergillus terreus*.

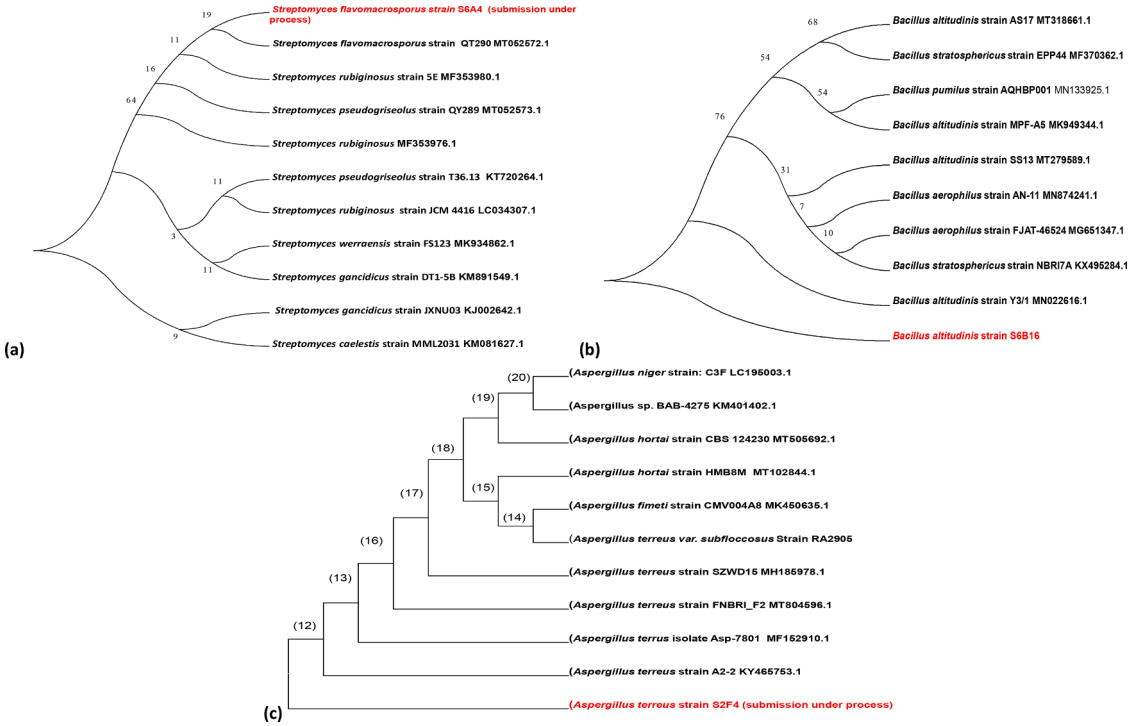

Fig. 2. Phylogenetic tree and evolutionary divergence (a) *Streptomyces flavomacrosporus strain* (b) *Bacillus altitudinis* strain and (c) *Aspergillus terreus* strain.

Inoculation of microbial cultures and enzyme assay

The selected potential indigenous compatible strains *viz.*, *B. altitudinis, S. flavomacrosporus, A. terreus*, as individual alongwith consortium were inoculated into the specific medium supplemented with 1 % straw and root residues from legume, cereals and oil seed crops as lingo-cellulolytic substrate. The mixture was then incubated for 30 days at 28±2 °C. After 30 days of incubation, the specific ligno-cellulolytic enzyme activities *i.e.* cellulase, xylanase, laccase and lignin peroxidase were estimated following standard protocols (Turner and Green, 1974; Mandel and Sternberg, 1976; Sandhu and Kalra, 1982; Tien and Kirk, 1983; Singh et al., 1988). The corresponding specific enzyme activity was determined using standard curve and expressed in μg mL^{-1}.

Statistical analysis

All the data in the present investigation are represented as mean from triplicate data. The mean of specific enzyme activity with different crop residues were compared using the two-way analysis of variance (ANOVA) followed by Tukey's honestly significant different test. Significance differences between single and indigenous consortium bio-inoculant were analyzed by Duncan's multiple range test ($p < 0.05$). All the data analyses were performed using SPSS version 16.0 software package (SPSS Inc. Chicago, USA). The R version 4.2.2. was used for statistical computing. The pearson correlation was constructed using the "ggpairs" function available in the GGally package.

Results

The biochemical composition parameters of straw and root of 11 different crop residues are recorded and present in the Table 2. The residue C and N content ranged from 9.52 to 74.2 % and 0.50 to 2.44 %, respectively and resulting in C: N ratio ranging from 5.42 to 83.4. The cellulose, hemicellulose, lignin content and lignin: N ratio varied from 3.30 to 34.4 %, 1.70 to 28.55 %, 1.98 to 10.9 % and 0.9 to 22.0 %, respectively.

Effect of enzyme activities of single and consortium lingo-cellulolytic bio-inoculants

All the selected potential indigenous microbial strains were screened qualitatively on the specific media such as CMC agar, xylan agar and lignin agar and were found to be positive for lingo-cellulolytic enzyme activities such as cellulase, xylanase, laccase and lignin peroxidase. After qualitative screenings, all the potential microbial strains were screened quantitatively for enzyme activities at 30 days of incubation in single and consortium bio-inoculant (Table 2). The cellullase, xylanase, laccase and lignin peroxidase enzyme activities varied from 13.4 to 79.2 μg mL^{-1}, 231.6 to 450.0 μg mL^{-1}, 7.9 to 18.1 μg mL^{-1} and 6.7 to 15.4 μg mL^{-1}, respectively. Maximum cellulase (79.2 μg mL^{-1}), xylanase (450.0 μg mL^{-1}), laccase (18.1 μg mL^{-1}) and lignin peroxidase (15.4 μg mL^{-1}) enzyme activities were recorded for consortium bio-inoculant i.e., *B. altitudinis* + *S. flavomacrosporus* + *A. terreus* followed by single inoculant of *A. terreus* at 30 days of incubation.

Molecular identification of potential indigenous lingo-cellulolytic microbial strains

Selected three compatible potential lingo-cellulolytic microbial strains were subjected to identify molecularly by using partial 16S rRNA and 18S rRNA sequencing at genera level through partial nucleotide blast using NCBI, blastin software tool. The partial sequences of lingo-cellulolytic microbial strains showed 99.5 %, 95.4 % and 92.1 % similarity with *Bacillus* sp., *Aspergillus* sp., and *Streptomyces* sp., and consensus sequences submission under process to NCBI, Maryland, USA. Based on consensus sequences of 16S rRNA and 18S rRNA genes for bacteria and fungus available in the NCBI GenBank database, microbial strains were identified as *A. terreus, S. flavomacrosporus* and *B. altitudinis*. Phylogenetic tree of selected potential indigenous lingo-cellulolytic microbial strains constructed through MEGA 11.0 software with other relevant sequences of microbial species in available in the GenBank database and submission under processing at NCBI, Maryland, USA (Figs. 1 and 2).

Enzyme activities with biochemically different crop residues

After the application of *B. altitudinis, S. flavomacrosporus, A. terreus* and consortia (*B. altitudinis* + *S. flavomacrosporus* + *A. terreus*) to different root and straw residues, the enzymatic activity ranged from 16.9 to 270.2 μg mL^{-1}, 18.2 to 255.7 μg mL^{-1}, 25.6 to 281.5 μg mL^{-1} and 29.7 to 272.8 μg mL^{-1}, respectively. These results indicated that after the application of consortia, the activities of enzymes significantly increased by 56.9 to 93.73 % as compared to *B. altitudinis, S. flavomacrosporus* and *A. terreus* ($p < 0.05$). It was also observed that among the incorporated root and straw residues, *A. terreus* showed maximum enzymatic activity followed by *B. altitudinis* and *S. flavomacrosporus* ($p < 0.05$).

The experiments also revealed that the activity of enzymes in different residues showed differential variation depending on the type of enzyme and ranged from 16.9 to 77.6 μg mL^{-1}, 135.7 to 281.5 μg mL^{-1}, 66.9 to 158.3 μg mL^{-1} and 38.7 to 169.9 μg mL^{-1} for cellulase, xylanase, laccase and lignin peroxidase, respectively. These findings indicated that xylanase exhibited the highest enzymatic activity, followed by laccase, lignin peroxide, and cellulase enzyme. The results also demonstrated significant variation in enzymatic activity among various straw and root amended residues, ranging from 17.5 to 272.8 μg mL^{-1} and 16.9 to 281.5 μg mL^{-1}, respectively. This indicated a more pronounced increase in enzyme activity in straw residues, with enhancement ranging from 65.8 to 93.7 % as compared to root residues which showed a modest increase of 61.2 to 85.2 % only.

The influence of incorporated straw and root residues on the

Table 2
Qualitative and quantitative enzyme assay for isolated indigenous microbial diversity.

Microbial diversity	Cellulase		Xylanase		Laccase		Lignin peroxidase	
	Qualitative	Quantitative (μg/ml)	Qualitative	Quantitative (μg/ml)	Qualitative	Quantitative (μg/ml)	Qualitative	Quantitative (μg/ml)
Actinomycetes								
Streptomyces flavomacrosporus	+++	13.4	+++	242.1	+++	7.9	++	6.7
Bacteria								
Bacillus altitudinis	++	16.1	+	231.6	+++	13.0	++	11.5
Fungus								
Aspergillus terreus	+++	72.9	++	425.8	+	16.6	++	13.2
Consortium bio-inoculants								
Bacillus altitudinis + *Aspergillus terreus* + *Streptomyces flavomacrosporus*	++++	79.2	+++	450.0	++++	18.1	++++	15.4

enzymatic activity viz. cellulase, xylanase, laccase and lignin peroxidase was studied (Tables 3; Fig. 3; $p < 0.05$). Amongst the straw residues amended with microbial consortia, significantly higher cellulase, xylanase, laccase and lignin peroxidase activity were found in *Vigna radiata* (70.7 to 272.8 μg mL^{-1}) while the minimum cellulase activity was found in *Glycine max* (27.9 μg mL^{-1}) and xylanase, laccase and lignin peroxidase activities were found to be least in *Crotalaria juncea* (87.2 to 173.1 μg mL^{-1}). Similarly, among the various root residues amended with microbial consortia, the cellulase, xylanase and laccase activities were found to be highest in *Sesamum indicum* (29.7 to 272.8 μg mL^{-1}) whereas lignin peroxidase showed maximum activity in *G. max* (129.7 μg mL^{-1}) followed by *S. indicum* (119.5 μg mL^{-1}) and *Sesbania bispinosa* (116.5 μg mL^{-1}) (Fig. 3, $p < 0.05$). However, the least enzymatic activity of cellulase and lignin peroxidase was found to be in root residues of *Oryza sativa* (29.7 μg mL^{-1} and 78.2 μg mL^{-1}) and xylanase and laccase showed least activity in *C. juncea* (163.8 μg mL^{-1}) and *V. mungo* (86.1 μg mL^{-1}), respectively.

In the present study, results demonstrated significant variation in the enzymatic activity among various straw and root amended residues and ranged from 17.5 to 272.8 μg mL^{-1} and 16.9 to 281.5 μg mL^{-1}, respectively. This indicated a more pronounced increase in the enzyme activity in straw residues, with enhancement ranging from 65.8 to 93.7 % as compared to root residues which showed a modest increase of 61.2 to 85.2 % only. The experiments also revealed that activity of enzymes in different residues showed differential variation depending on type of enzyme and ranged from 16.9 to 77.6 μg mL^{-1}, 135.7 to 281.5 μg mL^{-1}, 66.9 to 158.3 μg mL^{-1} and 38.7 to 169.9 μg mL^{-1} for cellulase, xylanase, laccase and lignin peroxidase, respectively. These findings indicated that xylanase exhibited the highest enzymatic activity followed by laccase, lignin peroxide and cellulase enzyme.

Relationship between microbial consortium, heterogeneity of crop residue and enzymatic activity

The correlation matrix revealed the interrelationships between the microbial consortium and diverse straw and root residues with soil enzymes activity during the incubation study (Figs. 4–7). The results unveiled a significantly strong positive correlation of the microbial consortium with soil enzyme activity. Among straw residues, lignin peroxidase exhibited a strong positive correlation with laccase (R^2 = 0.842***), cellulase (R^2 = 0.791***) and xylanase (R^2 = 0.700***). Among root residues, the lignin peroxidase activity was significantly and positively correlated with laccase (R^2 = 0.930***), xylanase with laccase (R^2 = 0.792***) and cellulase with xylanase (R^2 = 0.760***). The correlation analysis revealed a significant positive correlation ($p < 0.001$) in enzyme activities, with laccase activity demonstrating the highest correlation with lignin peroxidase activity in both straw and root residues. This was followed by a notable correlation between cellulase and lignin peroxidase activity in straw and xylanase and laccase in root residue. Conversely, the lowest coefficients were observed between cellulase and laccase in straw and cellulase and lignin peroxidase in root residues.

Furthermore, soil enzymes displayed a strong positive correlation with cellulase (R^2 = 0.998**–0.962*), xylanase (R^2 = 0.992**–0.952*), laccase (R^2 = 0.997**–0.952*) and lignin peroxidase (R^2 = 0.998**–0.959*) among different straw residues. Similarly, among different root residues, the correlations were also remarkably strong for cellulase (R^2 = 0.997**–0.961*), xylanase (R^2 =

Table 3
Effect of different straw residues on enzyme activity with indigenous potential microbial inoculation.

Substrates	*Cellulase* (μg/ml) at 30 days of incubation					*Xylanase* (μg/ml) at 30 days of incubation				
	Bacillus altitudinis	*Streptomyces flavomacrosporus*	*Aspergillus terreus*	Consortium	Mean	*Bacillus altitudinis*	*Streptomyces flavomacrosporus*	*Aspergillus terreus*	Consortium	Mean
Arachis hypogaea	38.0	42.40	65.9	68	53.6	213.9	165.7	231.5	237.2	212.1
Crotalaria juncea	16.9	21.00	36.6	40	28.6	154.8	140.5	168	173.1	159.1
Glycine max	24.3	22.60	30.2	34.5	27.9	210	161.8	221.8	225.7	204.8
Vigna radiata	50.1	41.90	68.5	70.7	57.8	270.2	255.7	281.5	272.8	270.1
Vigna mungo	22.6	23.20	35.3	37.1	29.5	189.5	186.2	201	201	194.4
Cajanus cajan	40.0	38.3	58.9	61	49.6	255.5	225.7	262.4	260.3	251
Sesbania bispinosa	25.9	23.6	30.5	32.9	28.2	214.2	196.6	230.3	232.6	218.4
Oryza sativa	24.1	19.5	39.5	42.9	31.5	211.8	164.1	205.8	212.5	198.6
Zea mays	23.87	23.3	37.1	40.1	31.1	205.8	175.8	216.5	219.9	204.5
Gossypium hirsutum	26.40	25.9	38.3	41.8	33.1	203.3	170.1	228.2	230.5	208
Sesamum indicum	41.70	36.6	47.3	48.5	43.5	225.7	225.9	257.1	272.1	245.2
Mean	30.35	28.94	44.37	47.05		214.06	188.01	227.65	230.7	
LSD (p< 0.05)	Microbial application (T) = 0.95; Residues (R) = 1.38; T×R = 3.69					Microbial application (T) = 1.20; Residues (R) = 2.17; T×R = 4.33				
Substrates	*Laccase* (μg/ml) at 30 days of incubation					*Lignin peroxidase* (μg/ml) at 30 days of incubation				
Arachis hypogaea	121.8	82	130.8	143.2	119.5	106	68.8	110.2	124.8	102.5
Crotalaria juncea	78.2	66.9	97	105.3	86.9	66.2	42.9	71.8	87.2	67
Glycine max	101.9	72.6	112.4	131.6	104.6	72.2	59.8	94	110.5	84.1
Vigna radiata	131.6	76.3	147.7	158.3	128.5	108.3	63.2	120.7	169.9	115.5
Vigna mungo	101.1	78.9	119.5	129.3	107.2	81.2	63.2	95.1	108.3	87
Cajanus cajan	119.5	83.5	129.3	153.4	121.4	94	60.5	110.5	147	103
Sesbania bispinosa	99.6	74.1	109	135	104.4	75.2	51.9	87.6	107.1	80.5
Oryza sativa	93.6	87.6	120.7	139.5	110.4	66.9	59.4	93.2	101.9	80.4
Zea mays	95.1	82.3	112	121.8	102.8	78.2	42.1	82.7	91.4	73.6
Gossypium hirsutum	106.8	91.7	125.2	143.6	116.8	85	60.9	94.4	110.9	87.8
Sesamum indicum	119.5	90.6	111.7	157.1	119.7	98.1	58.3	89.5	110.5	89.1
Mean	106.25	80.59	119.57	138.01		84.66	57.36	95.43	115.41	
LSD (p< 0.05)	Microbial application (T) = 1.18; Residues (R) = 2.13; T×R = 4.26					Microbial application (T) = 1.37; Residues (R) = 2.47; T×R = 4.95				

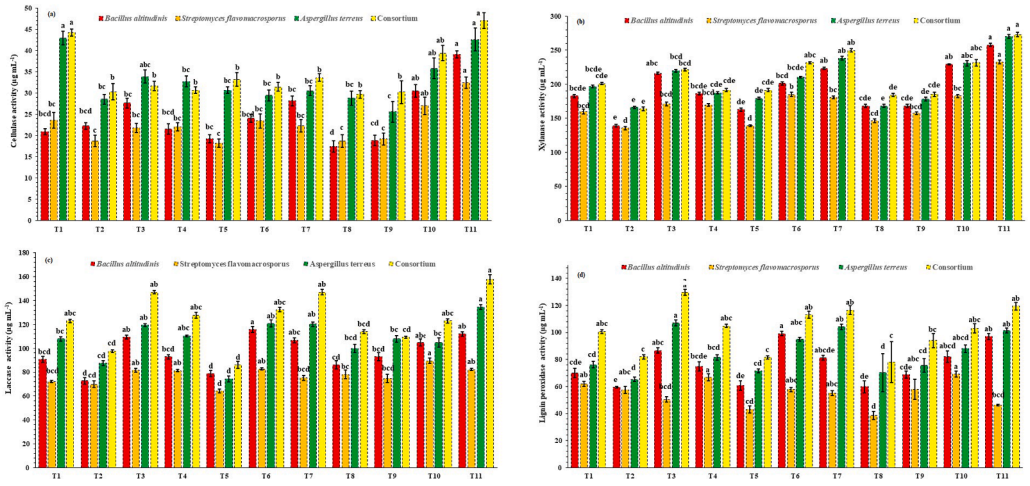

Fig. 3. Effect of root residues on (a) cellulase (b) xylanase (c) laccase (d) Lignin peroxidase (LiP) enzyme activity with potential microbial inoculants T1= *Arachis hypogaea*; T2= *Crotalaria juncea*; T3= *Glycine max*; T4= *Vigna radiata*; T5= *Vigna mungo*; T6= *Cajanus cajan*; T7= *Sesbania bispinosa*; T8= *Oryza sativa*; T9= *Zea mays*; T10= *Gossypium hirsutum*; T11=*Sesamum indicum*.

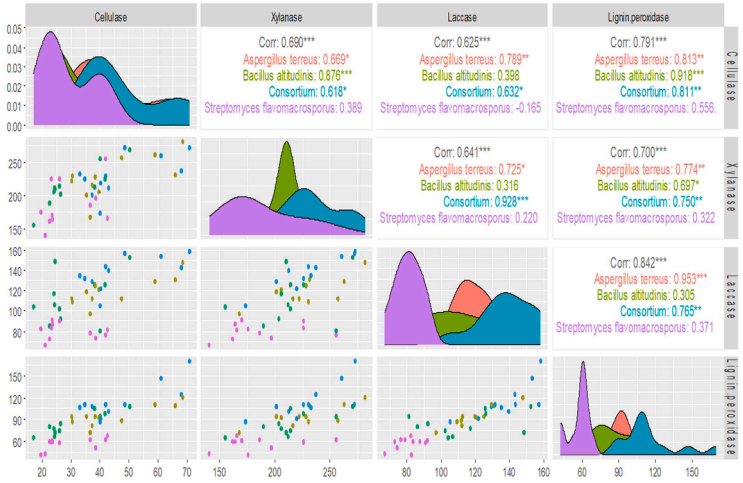

Fig. 4. Correlation between different microbial inoculants with different enzymes as affected by different straw residues. (*$p < 0.05$, **$p < 0.01$; *** $p < 0.001$).

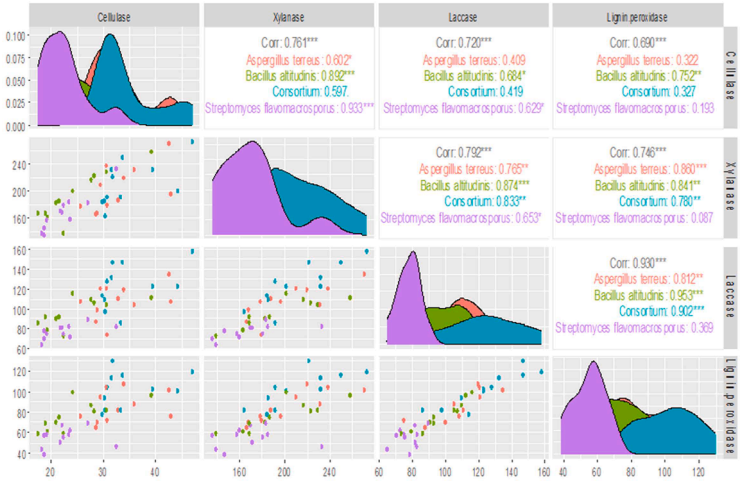

Fig. 5. Correlation between different microbial inoculants with different enzymes as affected by different root residues. (*$p < 0.05$, **$p < 0.01$; *** $p < 0.001$).

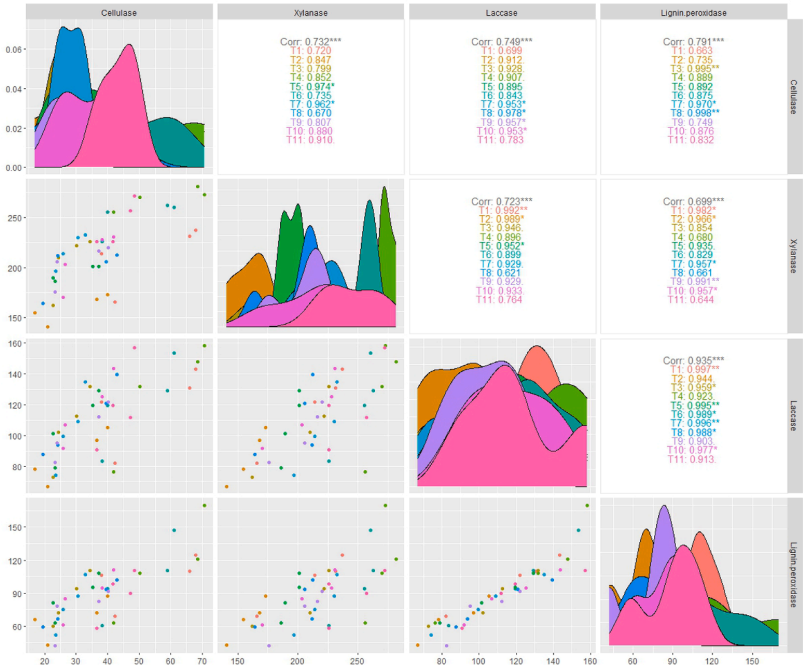

Fig. 6. Correlation among different straw residues as affected by different enzymes. (*$p < 0.05$, **$p < 0.01$; *** $p < 0.001$).

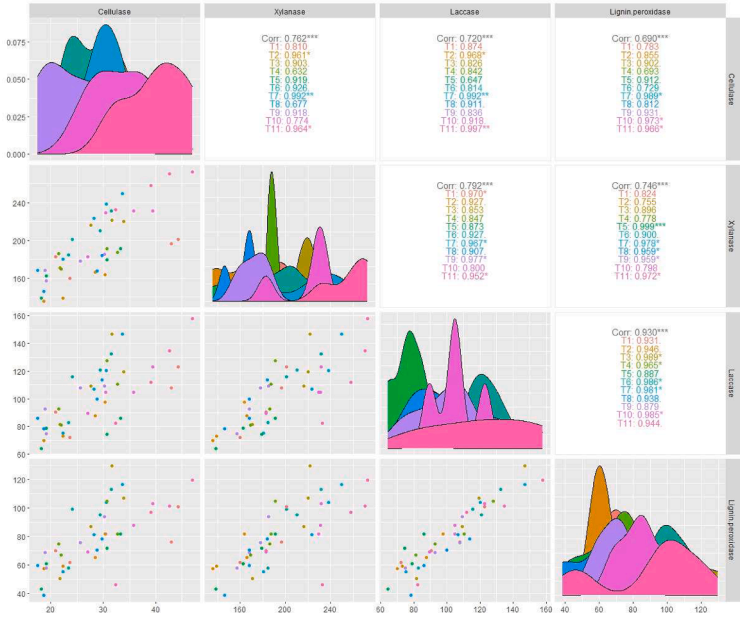

Fig. 7. Correlation among different root residues as affected by different enzymes. (*$p < 0.05$, **$p < 0.01$; *** $p < 0.001$).

0.999**−0.961*), laccase (R^2 = 0.997**−0.952*) and peroxidase (R^2 = 0.999**−0.959*). Moreover, when considering the average across all enzyme activities, *A. terreus* exhibited the highest coefficient (R^2 = 0.787***) among the microbial cultures, showing significant positive correlations among all the enzymes in straw residues. In contrast, for root residues, *B. altitudinis* demonstrated the highest coefficient (R^2 = 0.832***) and contributed significantly to positive correlations between enzyme activities. Similarly, among different residue substrates, *S. bispinosa* had highest average coefficient value in straw residues (R^2 = 0.961*) as well as in root residues (R^2 = 0.983*).

Discussion

The activity of soil microorganisms, their biomass and enzyme activities are interconnected through the organic matter composition of the soil, which encompasses microbial biomass carbon (MBC) (Zuber and Villamil, 2016). The microbiological characteristics, particularly soil enzyme activity, are utilized to evaluate effect of different treatments on decomposition rates and soil quality (Sharma et al., 2022; Katyal et al., 2022). Soil enzymes constitute one of the most significant components of soil composition and have an important role in driving soil biogeochemical nutrient cycling (Pankaj et al., 2023; Sharma and Singh, 2023). Several investigations have indicated that use of microbial consortia has many advantages as compared to single inoculants, which

facilitates the functioning of target strain through synergistic cooperation resulting in effective outcomes (Bradzcova et al., 2019; Minchev et al., 2021; Zhang and Zhang, 2022; Liu et al., 2023). However, microbial inoculation may cause a deliberate biotic disturbance that could lead to unpredictable and unreliable outcomes (Liu et al., 2022).

In the present study, the application of ligno-cellulolytic microbial consortia augmented the activity of cellulase, xylanase, laccase and lignin peroxidase as compared to single inoculants. Several data support the concept that, due to higher decomposition resistance, residue inclusion enhance enzymatic activity and MBC through quick decomposition as compared to single inoculant with indigenous consortium (Devevre and Horwath, 2000; Sharma et al., 2022). Similarly, the rate of residue decomposition also enhanced significantly with application of microbial consortium due to increased microbial activity and MBC, according to several publications (Jamily et al., 2019; Moreira et al., 2020). Chaudhary et al. (2016) also observed a noteworthy decrease in cellulose and lignin content in rice straw when it was inoculated with mixed culture of *Rhizopus oryzae, A. oryzae* and *A. fumigatus* as opposed to their specific application. Ribeiro et al. (2017) conducted an analysis of four compost piles, which were inoculated with *B. cereus, B.megaterium, B. cereus* + *B. megaterium* and a control with no inoculation. Their findings indicated that bacterial inoculum had significant impact on composting process due to alterations in the decomposition of cellulose and hemicellulose, which varied the temperature and nitrogen levels throughout the composting process. Singh et al. (2020) reported enhanced activities of dehydrogenase and alkaline phosphatase in soil using consortia mixture of *R.irregularis, P. jessenii* and *P. synxantha* as compared to individual inoculant in *Triticum aestivum*.

Microbial diversity and enzymes play a significant role in C dynamics, biochemical processes and has been a good indicator of soil respiration changes, soil nutrient cycling, microbial activity, and soil health (Jian et al., 2016; Liang et al., 2019). In the present study, the enzymatic activity after residue incorporation was found to be maximum for xylanase followed by laccase, lignin peroxide and cellulase enzyme probably due to readily available biomass-C input supplies from crop residues for higher enzymes activity (Hok et al., 2018; Hannula and Morrien, 2022). Cellulase are a group of enzymes that catalyzes the breakdown of cellulose, which performs a crucial role in the decomposition of crop residues in soil. Jat et al. (2021) also demonstrated that higher cellulase activity under zero tillage with residue retention practices provided favorable conditions to microbes and microbial transformation processes for higher soil enzyme activities. Latha et al. (2022) also reported that a higher level of cellulase activity was observed in soil treated with crop residue inoculated with microbial consortium and chemical fertilizer as compared to control due to higher C source into soils in the form of plant residue or synthesized by microorganisms in soils. The lowest activity in the control was due to non-addition of C source for accumulation of cellulose in soil. These results were in corroboration with the findings of Nagaraju et al. (2009) and Sakia et al. (2019).

Xylanase enzymes are primarily liable for decomposition of hemicelluloses into short chain glycosides. Chen et al. (2012) reported non-significant variation in the activity of xylanase in soils amended with biogas residuals but the activity enhanced significantly after addition of maize straw residue probably due to low C availability in biogas residues than maize straw which resulted in the formation of ligno-cellulose complexes and resisted the attack of enzyme. Similarly, Feng et al. (2018) also observed higher xylanase activity in bulk soil of the afforested ecosystems compared to open area and cropland due to elevated levels of MBC and labile C concentrations in the afforested soils than those found in open area and cropland.

Laccase belongs to a family of copper oxidases and is present in various higher plants, bacteria, fungi and actinomycetes. It readily undergoes detoxification and degradation of phenolic and non-phenolic compounds present in ligno-cellulosic substances and is therefore, extensively used in various biotechnological, bioremediation and biodegradation process (Hernandez-Beltran et al., 2019; Kumar and Chandra, 2020). Chen et al. (2018) investigated the dynamics of enzymatic activity after 13-year long-term and one-year short-term crop straw incorporation into upland and upland-paddy soils. The experiments revealed that laccase activity was lower in upland-paddy than in upland soils owing to the higher accumulation rates of lignin. Similar results have also been reported by Zapata et al. (2017) and Feng et al. (2019). On the contrary, Zhang et al. (2020) investigated that the effect of fertilizer and wheat residue incorporation on laccase activity and observed a reduction in the potential activity of laccase in the treatment plots as compared to control plots probably due to N fertilization which led to a reduction in phenol oxidase activity in soil. Lignin peroxidase are heme-containing enzymes secreted mainly by higher fungi and some bacteria. These belongs to family of oxidoreductase which degrade lignin and its derivatives in the presence of hydrogen peroxide. Lignin degradation is efficiently carried out by specific ligninolytic fungus *via* production of ligninolytic and lignin-cellulolytic enzymes majorly laccase, manganese peroxide, lignin peroxide (Zhang et al., 2022). Zhang et al. (2020) investigated the effect of fertilization and wheat straw residue incorporation (combined and alone) for continuous 10 years on the lignin peroxidase activity. It was observed that enzyme activity was 24 % higher in the fertilizer + wheat straw residue incorporated treatment as compared to inorganic fertilizer alone as the straw incorporation provides C-containing substrates and nutrients, which stimulates the growth of microbial populations. Many other authors revealed that the benefits of using microbial consortium in the decomposition of different ligno-cellulosic substrates such as wheat straw (Cannella et al., 2012), sugarcane baggase (Rodriguez-Zuniga et al., 2015), maize stover, lodge pole pine, polar (Hu et al., 2015).

The quantity and quality of straw and roots depends on type, growth stages of plants and production of volatile organic compounds released by roots which also influence the diversity and activity of microbes, biochemical processes and enzyme activities (Sharma et al., 2019; Saikia et al., 2019). Generally, lignin within the crop residues is regarded as the primary source of stable soil organic carbon (SOC). However, its dense structure poses a challenge by limiting the accessibility of enzymes to the cellulose and hemicellulose components. Thus, the degradation of lignin is essential for the efficient release of cellulose and hemicellulose, promoting their decomposition and incorporation into the soil organic pool. It has been documented those fungi, bacteria and actinomycetes have the capability to degrade complex lignin structure into simpler compounds that can be further metabolized into soil organic matter. Moreover, the interactive effects of lignin content and nitrogen (N) content can also have an impact on the N mineralization and nutrient release and subsequently, impact the enzyme activity. The complex interplay between lignin and nitrogen levels can significantly affect overall nutrient cycling process in ecosystems. Thus, lignin: N ratio has been recommended as more informative indicator of chemical recalcitrance than lignin content alone. It has been used to differentiate if the plant residues are easily biodegradable (low lignin: N ratio) or difficult to biodegrade (high lignin/N ratio) (Moore et al., 1999). In the present study, the lignin: N ratio in different root residues was 0.18 to 5.32-fold higher as compared to straw residues showing rapid decomposition of substrate utilization of nutrients through microbial metabolic activities as well as secretion of large quantities of enzymes. Similar findings have also been documented by Srinivas et al. (2020) demonstrating a 2 to 3-fold higher lignin: N ratio for roots of various crops and cultivars as compared to shoot owing to the higher lignin content and less availability of C and N. Furthermore, Bonanomi et al. (2021) also reported a reduced rate of decomposition for root litter than leaves litter decomposition. This delayed decay of fine roots was due to specific chemical characteristics, primarily a lower N concentration combined with higher lignin content as compared to corresponding leaf litter. In another research conducted by Amin et al. (2014) elevated levels of cellulase, xylanase and laccase activity were documented in soil amended with leaved as compared to soil amended with root residues. This variation

was attributed to the slower decomposition of root residues, which can be attributed to their higher phenolic acid content and the presence of recalcitrant polysaccharides with lignified cell walls. These factors collectively reduced the degradability of root residues and consequently lowered specific activity of enzymes. Similar findings have also been documented in studies conducted by Cleveland et al. (2014), Sun et al. (2016) and Zhou et al. (2018). These studies have consistently demonstrated that litter chemistry, specifically factors such as the C: N ratio and lignin: N ratio plays a significant role in contributing to the variation in the decomposition rates.

Conclusion

The experiments demonstrated that synergistic effect of individual inoculant i.e. *B. altitudinis, S. flavomacrosporus, A. terreus* as a consortium with *V. radiata* straw residues augmented the enzymatic activity of cellulase, xylanase, laccase and lignin peroxidase. Enzymes activity ranged from 16.9 to 77.6 μg mL^{-1} for cellulase, 135.7 to 281.5 μg mL^{-1} for xylanase, 66.9 to 158.3 μg mL^{-1} for laccase and 38.7 to 169.9 μg mL^{-1} for lignin peroxidase. Xylanase exhibited the highest activity after residue incorporation, followed by laccase, lignin peroxide, and cellulase. Correlation analysis showed that laccase activity significant positive correlation with lignin peroxidase in straw and roots residue. Additionally, the crop residue chemistry *viz.* lignin: N ratio primarily influenced the rate of residue decomposition Therefore, it can be inferred that *ex-situ* decomposition of crop residue by ligno-cellulolytic microbial consortia represents a promising feasible and eco-friendly substitute to crop residue burning practices. However, a comprehensive knowledge about the various biotic and abiotic factors which may alters the behavior of consortium is essential. Furthermore, there is a need for technology refinement to enhance the utilization of more efficient ligno-cellulolytic microbes, thereby reducing the duration of the decomposition process and making it more appealing to farmers. Additionally, field trials are essential to validate and establish the promising potential of *in-situ* crop residue decomposition as a successful alternative to combat the issue of crop residue burning.

CRediT authorship contribution statement

Sandeep Sharma: Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Kailash Chand Kumawat:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing, Supervision. **Paawan Kaur:** Resources, Writing – review & editing, Writing – original draft, Data curation. **Sukhjinder Kaur:** Conceptualization, Methodology, Data curation. **Nihar Gupta:** Writing – review & editing, Writing – original draft, Data curation.

Declaration of competing interest

None.

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