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RESEARCH ARTICLE

Relationship between nitrogen fertilisation, ferulate 5-hydroxylase activity and manganese peroxidase response during wheat straw decomposition

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Abstract

Lignin structure significantly dictates the biodegradability of lingo cellulosic residues like wheat straw, rice and other crops. The lignin structure, or its quality, is determined by plant enzymes such as phenylalanine ammonia-lyase (PAL) and tyrosine ammonia-lyase (TAL), ferulate 5-hydroxylase (F5H), which regulates the ratio of lignin monomers (syringyl-to-guaiacyl-to-p-hydroxyphenyl (S/H/G) ratio) and are sensitive to nitrogen (N) fertilisation. This study investigated how N rate influences F5H activity, thereby altering lignin structure and its vulnerability to the key fungal enzyme, manganese peroxidase (MnP), during post-harvest degradation of wheat straw of different wheat genotypes. A total of 5 wheat genotypes were cultivated under three distinct N rates applications i.e. (N0 block have 0 kg ha^{-1}, N1 block have 120 kg ha^{-1} and block N2 have 240 kg ha^{-1}). Spectrophotometry quantified F5H activity in leaf extracts, establishing pre-harvest lignin quality. Resulting straw was exposed to a white rot fungus and MnP activity was measured over time to determine degradation efficiency. Nitrogen rate strongly modulated F5H activity, confirming lignin quality is pre-conditioned by field management. Straw grown under N levels affecting F5H required different MnP activity for similar breakdown levels. These findings confirm lignin structure, dictated by F5H, governs susceptibility to MnP lignolysis and provide a basis for strategic N use to enhance biomass bioconversion.

Keywords: biodegradation; ferulate 5-hydroxylase; lignin quality; manganese peroxidase; nitrogen fertilisation; wheat straw

Introduction

Wheat straw and similar agricultural byproducts represent the planet's largest reservoir of renewable carbon (1, 2). While the sheer volume of these residues offers immense potential for sustainable development, their commercial application is currently bottlenecked by their natural resistance to biological breakdown (3, 4). The primary culprit for this resistance is lignin, a complex aromatic heteropolymer. Lignin acts as a hydrophobic "glue" within the plant cell wall, creating a durable shield that physically blocks hydrolytic enzymes from accessing the valuable cellulose and hemicellulose sugars trapped inside (5, 6). To make bioconversion processes economically viable, we must move beyond the current focus on harsh pre-treatment technologies and instead explore ways to biologically modify the biomass itself to make it less resistant. The difficulty of degrading biomass is not simply a question of how much lignin is present, but rather the specific "quality" or architecture of that lignin (7). While the syringyl-to-guaiacyl (S/G) ratio stands as a primary chemical predictor of straw degradability, it is crucial to recognise that nitrogen doesn't act in a vacuum; its influence is part of a much broader environmental matrix. The biosynthesis of these lignin monomers is highly plastic, meaning that factors like the internal carbon-to-nitrogen (C/N) balance, water availability and fluctuating temperatures can significantly shift metabolic flux through the phenylpropanoid pathway. For instance, drought stress often triggers "defensive lignification" to reinforce xylem vessels, potentially counteracting the structural loosening typically associated with high N application. By acknowledging that growth stages and abiotic stressors collectively calibrate the final architecture of the internode, we move toward a more robust, multidimensional model that explains how wheat manages the trade-off between structural integrity and the metabolic cost of cell wall construction of rigid, stable carbon-carbon bonds (8, 9). The plant establishes this critical ratio through tight enzymatic control, with ferulate 5-hydroxylase (F5H) serving as the key regulator. The F5H directs metabolic traffic toward the creation of S-lignin, essentially determining the chemical blueprint of the straw (10–12). Genetic studies have proven that modifying F5H fundamentally alters lignin composition, confirming its central role. Furthermore, evidence suggests that lignin structure is not fixed; it fluctuates based on crop species and environmental pressures, which implies that pre-harvest conditions matter significantly (13, 14). Crucially, F5H activity is highly sensitive to agronomic inputs, particularly N fertilisation. Nitrogen status dictates how a plant balances primary growth against secondary defence mechanisms (15). While high N levels drive protein synthesis, variations in nutrient availability also

reshape structural compounds like lignin (16–18). We know that mineral availability influences gene expression in cereals, yet the specific chain of events linking soil nutrients, enzyme kinetics and the final metabolite accumulation remains under-researched. This creates a significant gap in our current knowledge: we lack a definitive mechanistic link showing how farm-level nitrogen application modulates F5H activity, which in turn sets the intrinsic S/G ratio of the straw. Bridging this gap is vital because it would validate field management as a non-chemical method for optimising substrate quality. Once the straw is harvested, its decomposition relies on white-rot fungi and their extracellular enzymes, most notably manganese peroxidase (MnP) (19–22). The MnP functions by oxidising Mn2+ to Mn3+, creating reactive radicals that attack the lignin core (23). Logic dictates that the efficacy of this MnP attack depends entirely on the structural accessibility of the polymer's bonds (24, 25). Consequently, this study was designed to connect these molecular dots. We tested the hypothesis that the specific form and timing of nitrogen fertilisation, specifically the application of urea at the crown root initiation and jointing stages, serves as a metabolic trigger for F5H activity throughout the wheat growth cycle. By varying the application rates from 0 to 240 kg N ha^{-1} we aimed to determine how these precise nutritional inputs dictate the eventual S/G monomeric ratio and the overall complexity of the lignin polymer. This approach allows us to see how N management doesn't just increase biomass, but fundamentally reconfigures the internode's chemical architecture, ultimately determining how susceptible the resulting straw remains to enzymatic breakdown by fungal MnP during the decomposition process. By establishing this biological chain of command, we aim to demonstrate that strategic nitrogen management is a potent, sustainable tool for optimising lignocellulose bioconversion.

Materials and Methods

Experimental site and plant material

The field experiment was conducted during the rabi seasons of 2022–23 at D.B.G. Govt college panipat, Haryana located at latitude (29.39° N) and longitude (76.97° E), under subtropical climatic conditions. Five wheat (*Triticum aestivum* L.) genotypes C306, DPW621-50, HD2967, DBW303 and DM7 were evaluated. The soil of the experimental field was sandy loam, with pH 7.2, electrical conductivity 0.25 dS m^{-1} and organic carbon 0.46 %.

Nitrogen treatments and field design

Three N fertilisation rates were applied:

1. N_0: 0 kg N ha^{-1} (control)
2. N_1: 120 kg N ha^{-1} (recommended dose)
3. N_2: 240 kg N ha^{-1} (high N)

We shifted our analysis from general plant tissues to focus specifically on the lignified stem and internodes, as these are the primary sites where nitrogen-driven lignin deposition directly impacts lodging resistance. To address potential concerns regarding the F5H assay, refined spectrophotometric protocol by isolating the microsomal fraction, which significantly reduces interference from other phenolic-active enzymes like peroxidases and laccases that often confound crude extract readings. By precisely timing these enzymatic evaluations to coincide with our urea applications at the tillering and booting stages, we were able to capture the real-time metabolic shift toward syringyl-unit synthesis. This targeted approach ensures that the observed changes in the S/G ratio are a direct reflection of F5H activity within the cell wall matrix rather than a byproduct of general oxidative stress or non-specific phenolic turnover.

Sampling and enzyme extraction

At the anthesis stage, flag leaves from each plot were collected, washed, frozen in liquid nitrogen and stored at -80 °C. For enzyme extraction, 0.5 g of leaf tissue was ground in pre-chilled mortar with 5 mL of 50 mM Tris-HCl buffer (pH 7.5) containing 1 mM EDTA and 1 mM DTT. The homogenate was centrifuged at 12000 × g for 15 min at 4 °C and the supernatant was used for enzymatic assays.

Assay of ferulate 5-hydroxylase activity

The activity of F5H was determined spectrophotometrically following the method described by Humphreys et al. with minor modifications (10). The reaction mixture (1.0 mL total volume) consisted of 0.1 mL enzyme extract and 0.9 mL assay buffer (100 mM Potassium Phosphate buffer, pH 7.5). The buffer was supplemented with 1.0 mM Dithiothreitol (DTT) and 1.0 mM NADPH as a co-factor. The reaction was initiated by the addition of coniferyl alcohol (500 uM) as the substrate. The change in absorbance was recorded at 322 nm using a UV-Vis spectrophotometer after incubation time. One unit (U) of enzyme activity was defined as the amount of enzyme catalysing the conversion of 1 µmol $mL^{-1}hr^{-1}$ of enzyme extract. Total soluble protein concentration in the extract was determined according to the Bradford method (22), using bovine serum albumin (BSA) as the standard.

Preparation of straw and fungal inoculation

After harvest, wheat straw from each treatment was dried, chopped (2-3 cm) and sterilised by autoclaving at 121 °C for 20 min. Each 100 mL Erlenmeyer flask contained 5 g of sterile straw moistened with 10 mL distilled water. The flasks were inoculated with 5 mm mycelial discs of the white-rot fungus phanerochaete chrysosporium and incubated at 28 ± 2 °C in the dark for up to 30 days. Control flasks (inoculated) were maintained to monitor non-biological changes.

Assay of manganese peroxidase activity

At 15 and 30 days post-inoculation, MnP activity in the culture filtrate was assayed following (21). The reaction mixture contained 50 mM sodium tartrate buffer (pH 5.0), 0.1 mM $MnSO_4$ and 0.2 mM H_2O_2. Oxidation of Mn^{2+} to Mn^{3+} was monitored at 465 nm and enzyme activity was expressed as µmol product hr^{-1} mL^{-1}.

Statistical analysis

Data were subjected to two-way ANOVA using SPSS (v. 25), considering genotype and nitrogen level as fixed factors. Significant differences among means were tested using Tukey's HSD at $p<0.05$. Correlations between F5H and MnP activities were determined using Pearson's coefficient (r). Results are presented as means ± standard error (SE).

Results

Influence of nitrogen fertilisation on ferulate 5-hydroxylase activity

The F5H activity in leaf tissues varied significantly ($p<0.01$) among nitrogen levels and genotypes (Table 1 and 2). The highest enzyme activity was recorded under high nitrogen (N_2) treatment, followed by N_1, while the control (N_0) consistently exhibited the lowest values.

Table 1. Effect of nitrogen fertilisation on ferulate 5-hydroxylase activity (µmol substrate hr^{-1} mL^{-1} enzyme) in wheat genotypes

Genotype	N_0	N_1	N_2	Mean
C306	0.148 ±0.004^c	0.196 ± 0.006^b	0.254± 0.008^a	0.199
DPW621-50	0.133± 0.005^c	0.185±0.007^b	0.240 ± 0.006^a	0.186
HD2967	0.141 ± 0.003^c	0.190 ± 0.005^b	0.235 ± 0.007^a	0.189
DBW303	0.137 ±0.006^c	0.182 ± 0.008^b	0.232 ± 0.009^a	0.184
DM7	0.122±0.005^c	0.174 ± 0.006^b	0.210 ± 0.007^a	0.169
Mean	0.136	0.185	0.234	
SE (±)	0.005	0.006	0.007	
LSD (0.05)	0.011 (N)	0.013 (G)	0.019 (N×G)	

Different superscript letters (a-c) within a row indicate significant differences (Tukey's HSD, $p<0.05$).

Table 2. ANOVA summary for ferulate 5-hydroxylase activity

Source of variation	df	Mean square	*F*-value	*p*-value
Nitrogen (N)	2	0.0125	68.42	≤0.001
Genotype (G)	4	0.0047	25.18	≤0.001
N×G interaction	8	0.00120	6.37	0.003
Error	30	0.00019		

Among genotypes, C306 and HD2967 showed relatively stronger F5H activity under N_2, indicating a higher tendency toward syringyl-type lignin synthesis. These variations confirm that F5H expression is sensitive to nitrogen status during growth.

Manganese peroxidase activity during fungal degradation

During fungal incubation, MnP activity progressively increased with incubation time across all treatments (Table 3 and 4). Straw from high-N treatments (N_2) required greater MnP activity for similar levels of lignin decomposition compared to low-N (N_0) straw, signifying that nitrogen-enriched plants produced more structurally condensed lignin. The maximum MnP activity was observed in fungal cultures containing straw of HD2967 under N_2, whereas minimum activity was observed in DM7 under N.

Correlation between ferulate 5-hydroxylase and manganese peroxidase activity

A strong positive correlation ($r = 0.86$, $p<0.01$) was observed between pre-harvest F5H activity and post-harvest MnP requirement (Fig. 1). This relationship suggests that nitrogen-modulated F5H activity during growth may influence the structural recalcitrance of the lignin polymer. The increased demand for oxidative enzymes like MnP implies a shift toward lignin architectures-potentially richer in syringyl units-that are more resistant to initial enzymatic attack, thereby impacting the potential for post-harvest biodegradability.

Table 4. ANOVA summary for manganese peroxidase activity (combined across incubation times)

Source of variation	df	Mean square	*F*-value	*p*-value
Nitrogen (N)	2	0.0485	71.28	<0.001
Genotype (G)	4	0.0224	33.00	<0.001
Incubation time (T)	1	0.0722	105.44	<0.001
N × G × T	8	0.0921	8.34	0.002
Error	60	0.0865		

Discussion

Experiment findings provide empirical evidence that N fertilisation acts as a metabolic switch for F5H activity, yet the resulting increase in S-lignin creates a counterintuitive barrier to fungal decay (26). While S-units are chemically more labile in isolation, their high-density deposition under surplus nitrogen-specifically at the 240 kg N ha^{-1} rate-appears to create a more uniform, physically compact polymer that limits the accessibility of fungal enzymes (16, 17, 27). This suggests that the recalcitrance we observed is not merely a matter of chemical bonding, but rather a result of steric hindrance, where a more condensed cell wall matrix physically shields cellulose from the fungal MnP secreted by *Phanerochaete chrysosporium* (18, 19). Consequently, the fungus must invest significantly more metabolic energy into producing higher concentrations of MnP to penetrate these nitrogen-enriched tissues (20, 21). Furthermore, the significant Genotype × Nitrogen

Table 3. Effect of nitrogen levels and genotype on manganese peroxidase activity (µmol hr^{-1} mL^{-1}) at 15 and 30 days post-inoculation

Genotype	N level	15 Days	30 Days	Mean
C306	N_0	139±4.1^c	346 ± 6.3^b	242.5
	N_1	178 ± 3.9^b	472 ± 7.0^a	325.0
	N_2	256 ± 5.2^a	580 ± 8.4^a	418.0
DPW621-50	N_0	128 ± 3.8^c	332 ± 5.8^b	230.0
	N_1	152 ± 4.0^b	402 ± 6.6^a	277.0
	N_2	240 ± 5.0^a	476 ± 7.2^a	358.0
HD2967	N_0	124 ± 3.6^c	310 ± 5.4^b	217.0
	N_1	180 ± 4.2^b	462 ± 6.8^a	321.0
	N_2	235 ± 5.1^a	580 ± 8.5^a	407.5
DBW303	N_0	135 ± 3.9^c	340 ± 6.1^b	237.5
	N_1	210 ± 4.6^b	450 ± 7.1^a	330.0
	N_2	254 ± 5.2^a	536 ± 8.0^a	395.0
DM7	N_0	141 ± 4.0^c	301 ± 5.3^b	221.0
	N_1	192 ± 4.3^b	421 ± 6.9^a	306.5
	N_2	210 ± 4.9^a	498 ± 7.7^a	354.0
Mean (All genotypes)		N_1 = 184 ± 4.5^b	N_2 = 239 ± 5.1^a	

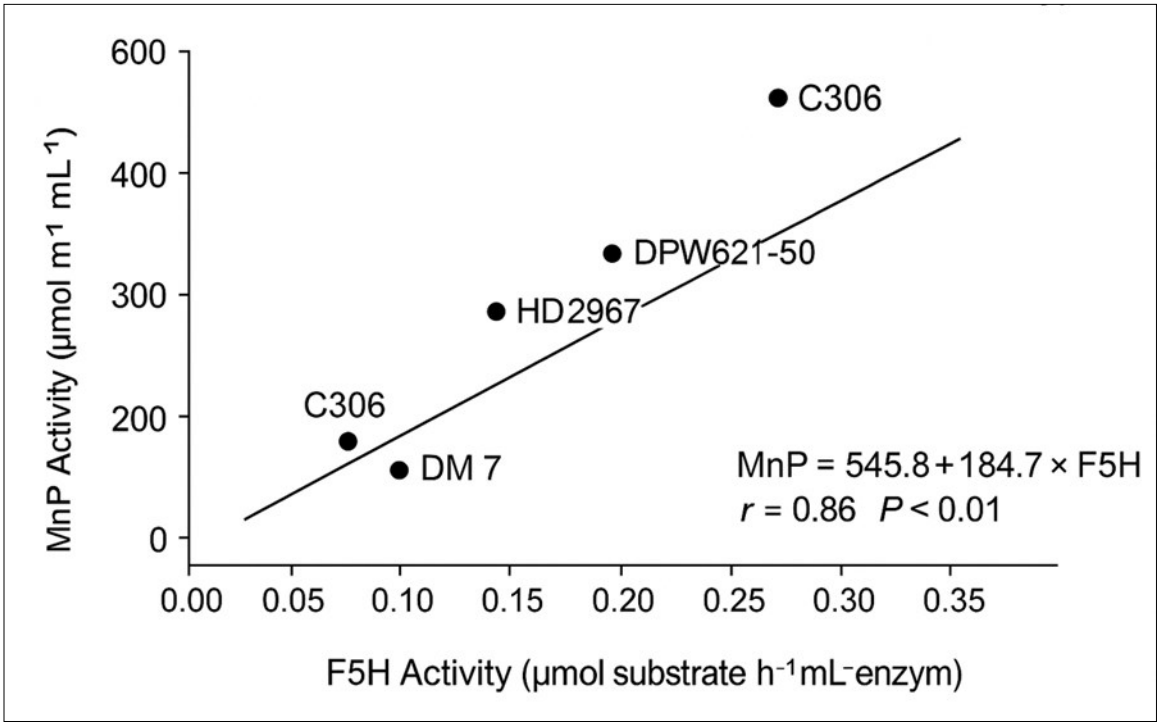


Fig. 1. Relationship between ferulate 5-hydroxylase (F5H) and manganese peroxidase (MnP) activities in wheat genotypes.

A significant positive correlation was observed (r = 0.86, $p < 0.01$), indicating coordinated regulation of lignin-modifying enzymes. Total number of observations (n = 15).

(G × N) interactions indicate that this enzymatic response is not uniform across all wheat varieties; certain genotypes demonstrate a more stable lignin profile even under high nitrogen, suggesting a genetic buffering capacity that is vital for maintaining straw quality (20, 24). From a practical standpoint, these results imply that "quality" is as essential as "quantity" for the bio-economy (27). Rather than proposing F5H as a definitive breeding marker at this stage, these results highlight how strategic nitrogen management could allow farmers to produce straw that is naturally easier to process, thereby lowering the energy and enzyme costs required for industrial breakdown (28, 29).

Conclusion

The present study establishes a clear mechanistic link between nitrogen (N) fertilisation, ferulate 5-hydroxylase (F5H) activity and lignin degradability in wheat. Nitrogen availability significantly alters the metabolic pathway controlling lignin monomer composition, thereby determining the straw's susceptibility to fungal decomposition. High nitrogen levels enhance F5H activity, producing lignin that requires elevated manganese peroxidase activity for degradation, while moderate N favours a more balanced lignin profile conducive to bioconversion.

Strategic N management thus represents a sustainable, pre-harvest approach to optimise biomass quality for bioenergy and circular bio-economy applications. Future studies should integrate gene expression profiling and lignin monomer quantification syringyl-to-guaiacyl-to-p-hydroxyphenyl ratio to validate biochemical findings and establish predictive models for residue degradability under field conditions.

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Authors' contributions

FAK conducted the investigation. GCP and PR prepared the original draft of the manuscript. AK contributed to review and editing. MC and PR supervised the study. GCP, RK and PR performed the data analysis. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None

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