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Review

Role of Lignin in Wheat Plant for the Enhancement of Resistance against Lodging and Biotic and Abiotic Stresses

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Abstract: Lignification is a vital function in plants for improving tolerance against stressors. This article presents studies conducted on the relationship of wheat straw lignin with enhanced plant adaptation against lodging and stressors. Herein, we provide a thorough discussion of the chemical structure and lignin composition of straw and its alteration and uses. Lignin plays a critical role in withstanding harsh environments (biotic and abiotic). Resistance to accommodation in wheat also plays a critical role. Lignin can also produce several products, e.g., costly petroleum-based materials and other vital products, such as resins and composites, and new materials, such as biofuels and chemicals. In this study, wheat straw lignification analysis highlighted that lignin formation regulates cellulose and hemicellulose biosynthesis. In addition, the analysis showed considerable encouragement of lignin growth inside wheat straw and the formation of lignin interfaces, as for cellulose and hemicellulose. Wheat straw lignin is an important source of many essential bioactive moieties, particularly lignocelluloses, straw-based biofuels, and various chemicals. We also explored the molecular tools that influence lignin formation in wheat and the significant strides taken in broadening our understanding of nanotechnology tools. This knowledge could assist in the development of advanced wheat cultivars, increase lignin content, and strengthen feedstock efficiency, reducing the impact of other lignin-associated agronomic gains.

Keywords: wheat; lignin; lodging; biotic; abiotic; biosynthesis

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1. Importance of Wheat Crop

Cereals are one of the main staple foods for humans and animals worldwide and are mostly grown for their nutritional grains, which provide dietary calories for humans [1]. Wheat (*Triticum aestivum*) is a species of cereal belonging to the Poaceae family (order Poales). Around 40% of people on the planet regularly eat wheat as a source of energy. Wheat production extends far back in history; it was among the first domesticable crops and has been the primary grain of European, West Asian, and North African civilizations for 8000 years. Covering more than 218 million ha, wheat is the most commonly grown crop in the world, and its global exchange is greater than that of all other crops combined. Wheat plays a key function in human nutrition, supplying 20% of calories, daily protein and other nutrients. It is the primary food crop in the developing world after rice, ensuring food security, as an estimated 80 million farmers depend on wheat for their livelihoods [2]. Bread wheat (*Triticum aestivum* L., 2n = 42, hexapod, AABBDD genomes), which can be classified as hard wheat or soft wheat based on the stiffness of the crop, accounts for more than 80% of the wheat produced globally. Bread wheat is primarily used as flour for the preparation of a large variety of raised and plane breads, and for the manufacture of other baking products (completely grained or purified) [3]. In the majority of nations, wheat is

the largest appropriate starch source, and it is the main plant protein base in the human diet worldwide, with a relatively high protein content (13%), when compared to other major cereals. Wheat, when consumed as a whole grain, provides necessary nutrients and dietary grit, including minerals, vitamins, and lipids, as well as extra protein which is available in small amounts from animals or leguminous plants [3–6]. However, wheat is also a common means of feeding animals, especially in years where yields are unpleasantly impaired by precipitation and where large quantities of grain are unfit for feeding. The most important wheat-producing countries are Australia, India, China, Canada, France, Germany, Russia, the United States, Pakistan, and Ukraine, accounting for 760 million tons of production in 2017 [4]. Wheat is also used in the manufacture of biscuits, bread, food, candy, etc.

2. Role of Lignin in Wheat Plant

Lignin provides mechanical strength and resistance against both biotic and abiotic pressures, but for certain agricultural applications, it influences the use of biomass, such as wheat hay [7]. The lignin quantity in wheat straw varies from 15 to 20 percent [8]. In wheat tissues, such genes are clearly translated, suggesting the function of these genes in the wheat stem [9]. Nevertheless, waterlogging has confirmed the emergence of other genes, suggesting its main role in generating further phenylpropanoid derivative complexes with stress reaction components. In particular, the variation between the varieties of internode lignin detected, and the variation in the lignin content caused by waterlogging, are closely related to the cytokinin level [9,10]. Lodging resistance, abiotic and biotic pressures and the importance of wheat biomass feed are closely related to the consistency of its lignin. The research findings of recent studies offer a useful understanding of the molecular techniques that guide lignin production in wheat, and of critical steps towards the advancement of molecular tools that enable the development of wheat genotypes with a higher lignin content and better feedstock efficiency that are devoid of other lignin-related agronomic gains [3,11–14].

3. Structural and Chemical Composition of Lignin

Lignin is a 3-dimensional type of polymer of phenol elements with heavy-duty intermolecular bonding by strongly divided molecules. The main sources of lignins are coniferyl, *p*-coumaryl and sinapyl alcohols (Figure 1).

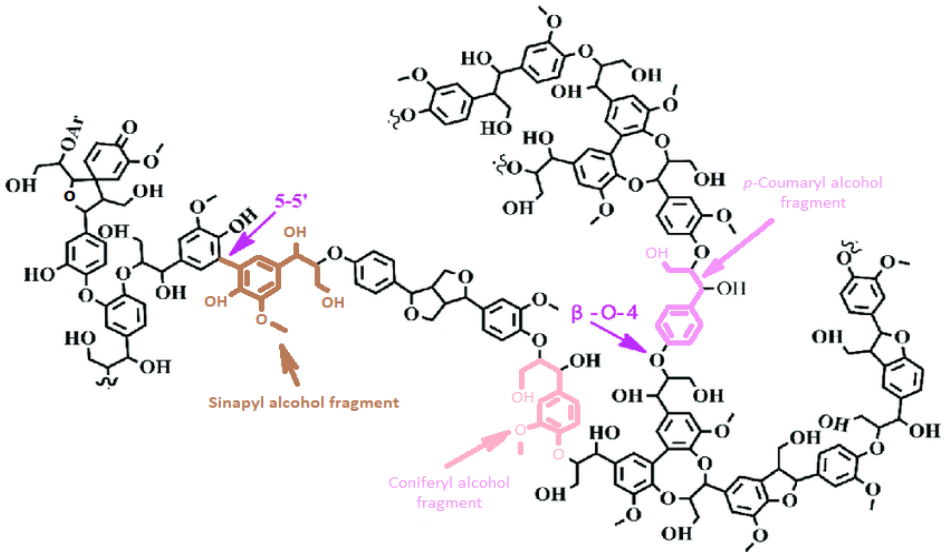

Figure 1. Structural model of wheat straw lignin. Adapted from "Lignin in Straw and its Applications as an Adhesive" by S. H. Ghaffar, 2014, International Journal of Adhesion & Adhesives 48 (2014) 92–101 [15].

The intensity of lignin in wheat stems and roots is 4.4 and 5.6, which is considerably stronger ($p < 0.001$) than in wheat leaves. Lignin differs in composition between species. For example, the composition of the aspen specimen is 5.9% hydrogen, 63.4% carbon, 0.7% ash (mineral components), and 30% oxygen (by difference), conforming to the formula $(C_{31}H_{34}O_{11})n$ [16]. As a biopolymer, lignin is unique due to the difficulty in obtaining it and the absence of a specific primary form. Lignin, in terms of molecular mass, is a lipid inter-associated with an additional 10,000 u in the form of the phenylpropanoids *p*-hydroxyphenyl (H), guaiacyl (G), and syringyl (S); such lignols are consequently integrated into lignin. Nearly all grasses have G, although most palms have S [17,18]. Limited quantities of partial or modified monolignols are present in all lignin, and other monomers are classified into non-woody plants [19]. On the alkyl lignin side chain, which is a phase in the deterioration of wood caused by many white-rot as well as some soft rot-fungi, an oxidative cleavage reaction occurs, with increases with increasing prevalence of Ad/Al [20,21]. The use of a pyrolyzer and a molecular beam mass spectrometer for the high-throughput analysis of lignin has resulted in more recent developments in the field. Using this technique, a hundred specimens can be tested in less than a day, and no wet chemistry is required. Nuclear magnetic resonance (NMR) analytical methods have been greatly strengthened for lignin research [17]. NMR provides an edge to both the study of lignin formation and the direct detection of lignin moieties, as well as the inclusion of condensed and uncondensed aryl ether and aliphatic and aromatic carbons. In addition, NMR has been developed for quantifying lignin in two-dimensional hetero-nuclear single quantum coherence (2D HSQC) [21,22].

4. Lignin Biosynthesis (Monomers, Transport, and Polymerization)

According to research, the potential lignin biosynthesis genes, which are widely expressed in wheat tissues, have average sequences of 4CL1, C3H1, CCR2, F5H2, and COMT2, and seem to be tightly related, with internode lignin material further contributing, at least slightly, to lodging tolerance. Increases in the concentrations of cytokinin, IPA, and t-zeatin are stated to coincide with variations in internode lignin content, pointing to the possible involvement of cytokinin in regulating the buildup of lignin in wheat biomass. Lignin content has a substantial correlation with the mechanical characteristics/lodging resistance, stability against biotic and abiotic stresses, and feedstock coherence of wheat straw; thus, it is crucial in the first step towards producing molecular tools that can facilitate the production of enhanced wheat varieties containing lignin, enhancing the productivity of wheat straw feedstock without affecting lignin-related agronomic characteristics [23]. A model of lignin biosynthesis in wheat plants is given in Figure 2.

Coniferyl, sinapyl, and *p*-coumaryl alcohols are three monolignols generated from phenylalanine, and are metabolized and included in the lignin complex and the three-dimensional polymer units S (syringyl), G (guaiacyl), and H. (hy-droxyphenyl) [24]. Oligolignols, which are generated during the polymerization of lignin, are monolignol racemic radical coupling products [25] (Figure 2). While the mechanism of lignin biosynthesis has still not been elaborated in wheat, the relative expression of wheat homologs of lignin biosynthetic genes has been characterized in earlier studies. The transcripts for the majority of these homologs, and in particular, the expressions of C4H, PAL6, 4CL1, CCR2, C3H1, F5H2, and F5H1, seemed be highly numerous in the stem tissue compared to the leaf blade and leaf sheath, and were considered to have a strong association with the content of lignin [7].

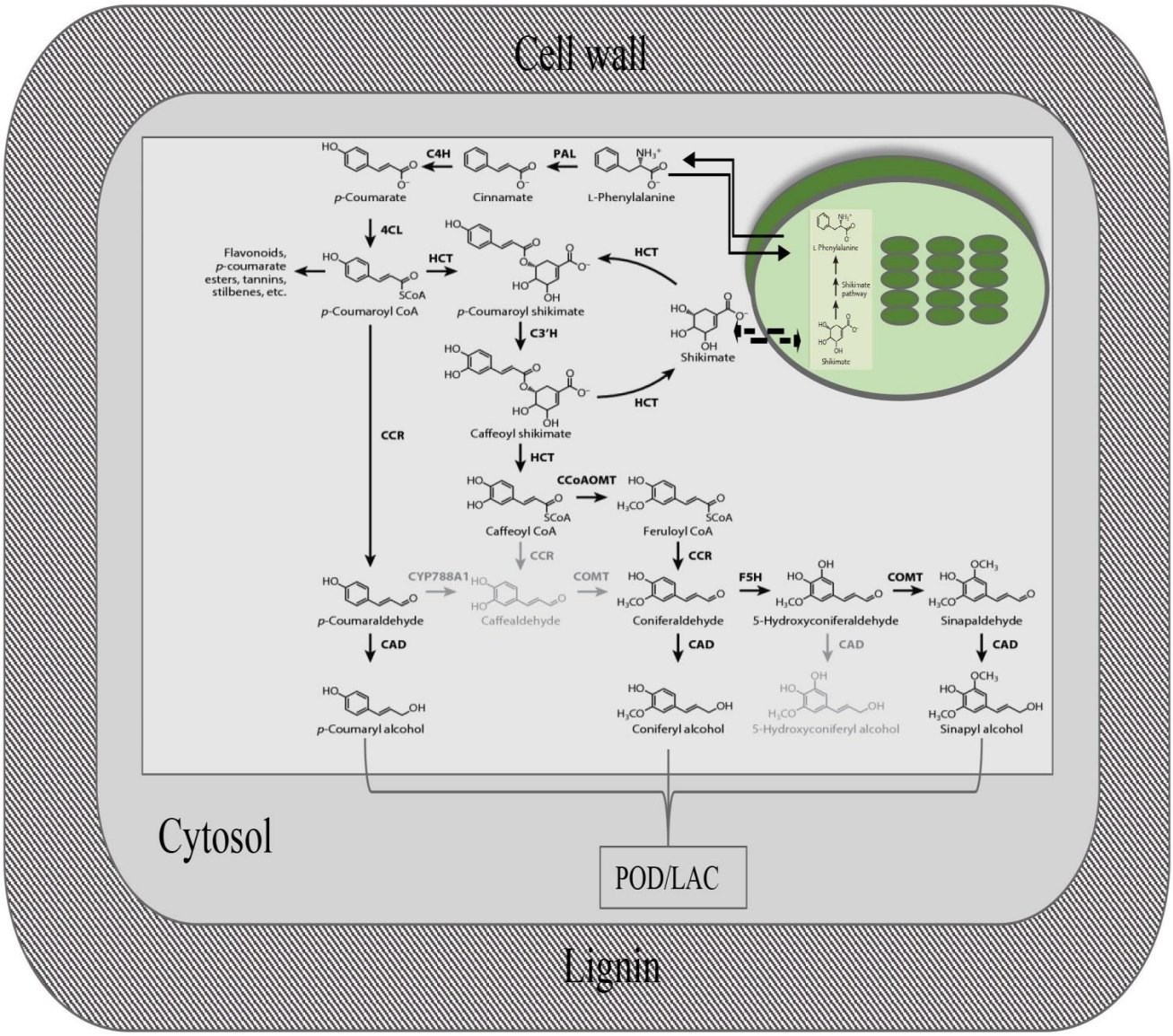

Figure 2. Pathway of lignin biosynthesis in plants. The pathway shows the main biosynthetic route toward the production of the monolignols *p*-coumaryl, coniferyl, and sinapyl alcohols. The enzymes involved are: PAL—PHENYLALANINE AMMONIA-LYASE; C4H—CINNAMATE 4-HYDROXYLASE; 4CL—4-COUMARATE:CoA LIGASE; C_3H—*p*-COUMARATE 3-HYDROXYLASE; HCT—*p*-HYDROXYCINNAMOYL-CoA:QUINATE/SHIKIMATE *p*-HYDROXYCINNAMOYLTRANSFERASE; CCoAOMT—CAFFEOYL-CoA *O*-METHYLTRANSFERASE; CCR—CINNAMOYL-CoA REDUCTASE; F5H—FERULATE 5-HYDROXYLASE; COMT—CAFFEIC ACID *O*-METHYLTRANSFERASE; and CAD—CINNAMYL ALCOHOL DEHYDROGENASE.

Although the framework of lignin biosynthesis in wheat is not yet understood, the relative expression of lignin biosynthetic genes in wheat homologs was discussed in previous studies. In addition, the stem exhibits better richness of CAD1 and CCR1 transcripts and a attracts greater interest regarding the related enzymes than other tissues, whereas COMT1 is split constitutively between the different tissues, including the leaf, stem, and root [26–28]. The general phenylpropanoid pathway, a monolignol-specific mechanism, and the consecutive dehydrogenation polymerization processes are used to create these monolignols from phenylalanine, resulting in the formation of units of syringyl (S), guaiacyl (G), and hydroxyphenyl (H), respectively, a complex, and a three-dimensional lignin polymer [29]. Additionally, these findings pinpointed candidate genes that facilitate the

response of lignin biosynthesis to wheat tissue waterlogging, and the authors reviewed the relationship between the concentration of lignin and selected plant hormones involved in the regulation of lignin biosynthesis [23] (Figure 2).

One of the abiotic factors that adversely influences crop production is waterlogging, which induces a decline in the diffusion of gases and thereby reduces the supply of oxygen in the rhizosphere, leading to improvements in biochemical and metabolic processes [30]. A transition from aerobic to anaerobic respiration requires a key metabolic shift, impairing the production of ATP. Compensation of the resultant energy deficit involves rapid glycolysis via increased glycolytic and fermentative enzyme activity, resulting in depletion of the stores of carbohydrates, a process known as the "Pasteur effect" [31,32]. Another study examined the association between lignin grades and certain plant hormones that have been associated with the development of lignin biosynthesis, as well as possible genes involved in controlling the response of lignin production to waterlogging in wheat tissues [23].

Lignin is among the most important secondary metabolites developed by the phenylalanine/tyrosine metabolic process in plant cells. Lignin biosynthesis is a very complex network and is divided into three processes: (i) the biosynthesis of lignin monomers, (ii) transport, and (iii) polymerization. Lignin is an aromatic biopolymer that is obtained from oxidatively bound *p*-hydroxycinnamyl alcohols (monolignols) and their affiliated compounds. Lignification, that is, lignin accumulation in the domains of apoplastic cell walls, is a hugely important biological characteristic attained by early plant species for land colonialization. In other specialized cells, such as seed coats, the endothecium (anterior lumen lining), endodermal cells, and secession cells, plants perform lignification for organ removal, as well as in response to microbial pathogens. Usually, 20–30 percent of plant dry material, that is, lignocellulosic biomass, is composed of lignins [31,33,34]. Lignin polymerization occurs through an extremely customizable combinatorial radical coupling system that allows plants to incorporate various lignin monomers in various combinations outside of the three conventional monolignols, i.e., coniferyl, sinapyl, and *p*-coumaryl alcohols, to integrate multiple lignin polymers into different types of cells. In general, some genetically modified and mutant polysaccharide-modified Arabidopsis lines demonstrate customized lignin deposition [31,35,36], while a crucial area of research is the impact of polysaccharide alterations on lignin chemical structures in plants. Once the monolignols are generated within the cytoplasm, they are transported for further polymerization into lignin via the plasma membrane to the cell wall. It has very recently been postulated that their transmission is determined by the condition of glycosylation. The ABC vessels are transported by monolignols with peroxidases and laccases, and they are polymerized [37]. Further assessment of genetic engagement in the cell wall of ABC transporters has also shown that these cassettes are extremely important for monolignol and are vital [38,39]. Liu et al. and Gall et al. [39,40] found that AtABCG29 is a monolignol transporter that is accountable for lignin biosynthesis (Figure 3).

Dirigent proteins (DPs) were first stated to be involved in the guiding of stereoselective coupling in the lignin biosynthesis of two laccase-generated monolignol radicals, and were ultimately referenced as components of the machinery for lignin polymerization. It is also noteworthy that the lack of activity of pinoresinol reductase 1, the enzyme that catalyzes the reaction in lignin synthesis following stereoselective monolignol coupling, results in a shift in the redistribution of lignin, but not in the content or structure of *A. thaliana* [25,41]. This offers more support for a model that requires lignin synthesis components to address the transmission of lignin within the cell wall.

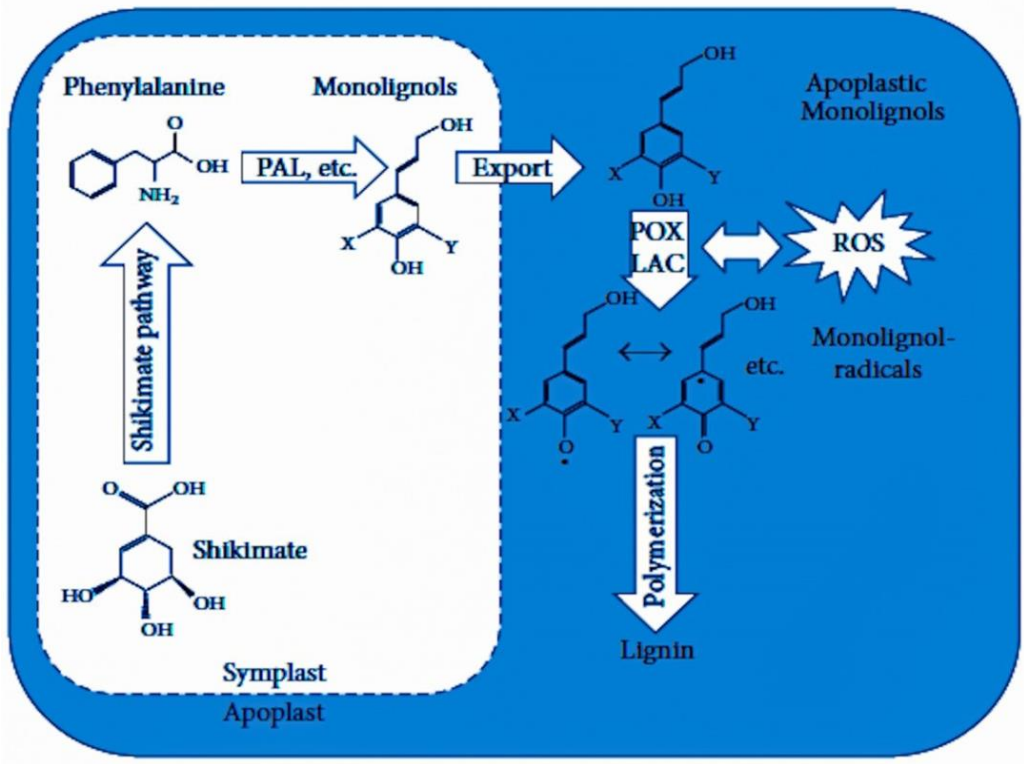

Figure 3. Model of lignin biosynthesis. Adapted from "Lignin: Characterization of a Multifaceted Crop Component" by Micheal Frei, 2013, Hindawi Publishing Corporation, *The Scientific World Journal Volume 2013* [32].

5. Lignin Decomposition in the Soil Profile

Wheat plants are observed during planting, and again during the next planting season, for their recognition of nitrogen. Wheat straw enables microbial nitrogen control by encouraging microbes, via high plant carbon soil changes (HCA), to acquire nitrogen from the soil, controlled by sawdust. The absorption of microbial nitrogen is not motivated by pure lignin. *Triticum aestivum* L., which is cultivated in September/October but only reacts vigorously until the next timespan, together with a relatively low nitrogen uptake of up to 30 kg N ha^{-1} over this period, is already cultivated in July in German crop variations, and is mostly mapped with wheat [42].

The soil mineral nitrogen constituent, on the other hand, rarely reaches 100 kg of N ha^{-1} after the oilseed rape crop harvest [43]. Approximately 50% of the mineral nitrogen extracted from the decay of N-rich crops, such as oilseed rape seed, often occurring in sandy soil, may vanish from the soil [44]. Nitrogen-poor crop remnants such as wheat straw may be impacted by the strong immobilization of nitrogen, resulting in a loss of plant-obtainable nitrogen. The usable nitrogen in the soil is immobilized by large C:N ratios utilizing decayable, C-rich organic remains, such as wheat straw (39; 5), which can reduce crop yield throughout the next season. However, if nitrogen immobilization stops plant growth, and plant and microbial nitrogen absorption occurs in the same soil area, the possibility of bacteria being more nutrient-friendly than plants increases [45].

Organic substrates with large C:N ratios, such as wheat straw (C:N 50–100), are needed to trigger microbial nitrogen immobilization, prompting microbes to take nitrogen from the soil to keep their C:N ratio at least ten times smaller [46,47].

Woody sawdust develops more obtuse compounds than wheat grass, which are mostly in the shape of lignin. Specialists such as white-rot fungi are needed to break up the lignified structures of wood [48]. Even then, this approach is too sluggish to facilitate significant microbial growth and, consequently, the rapid immobilization of microbial nitrogen. Additionally, biotic nitrogen immobilization and adsorption (the capacity to

draw liquid and gas molecules from solid particles/surfaces) in soil are described as less bulbous forms of abiotic nitrogen immobilization [49], e.g., nitrite reaction with or by HCA-derivative lignin or its products [50].

6. Correlation between Lignin Biosynthesis and Plant Stress Response

A plant's defense mechanism against biotic and abiotic stresses is the cell wall. Reactive oxygen species and lignin formation are effects of the stress reaction. Salt, drought, sun, cold, diseases, heavy metals, and other stresses are important to the response of lignin. The authors of [51–53] administered exogenous paclobutrazol to winter wheat cultivars that are tolerant/vulnerable to lodging and discovered that paclobutrazol dramatically decreased the volume of the wheat internode, promoted lateral growth, and increased the accumulation of lignin, the operation of the lignin biosynthesis enzyme, and thickness of the internode, thus increasing the resistance to wheat lodging. Lignin has the ability to permeate the entire cell wall in the tissues of some species of vascular plant, increasing its rigidity and hydrophobicity [54]. According to a different study, crop density has a considerable impact on the morphological properties of the stem and lignin biosynthesis, thereby enhancing the stem's mechanical power and lowering the impact of lodging [55]. Hu et al. [55] indicated that the amount of lignin and lignin biosynthesis enzymes (PAL, 4CL, CAD, and POD) play a vital role in lodging resistance, as per the research on lignin metabolism.

6.1. Lignin Biosynthesis's Role in Response to Biotic Stresses (Insect Pests and Diseases)

The accumulation of lignin plays a crucial function in resistance to insect pests in plants [2,56]. When plants are infested with disease, the cell wall responds and accumulates vast amounts of lignin, of which the H unit concentration is considerably greater [13,57]. Such lignin accumulations serve as a barrier to the propagation of pathogens and decrease the activity of fungal enzymes and toxins in plant cell walls. The compounds related to lignin inhibit the activity and dissemination of pathogens [58–60]. In tolerant cultivars, Agarwal et al. [61] found that lignin content was greater than in the vulnerable ones. The results of Mafa et al. showed that during periods of infection, Tugela-Dn5 had significantly higher apoplastic peroxidase and -1,3-glucanase activity than the control [62]. Peroxidase activity is linked to the cell wall's cross-linking of lignin, which may prevent RWASA2 from feeding. At 72 and 120 h after infestation (hpi), Tugela-Dn5 underwent a dramatic increase in its total phenolic and holo-cellulose contents. The FTIR results, which demonstrated that the holocellulose and lignin areas of the resistant and susceptible wheat were changed by infestation at 72 hpi, supported these conclusions [62]. The overexpression of the 4CL gene OsAAE3 in rice lowered the accumulation of lignin and improved the rice's susceptibility to rice blast disease due to the decreased activity of POD and pathogen-related 1a (PRI) [33]. In another study, the stem rust fungus *Puccinia graminis* f.sp. *tritici* was evaluated to assess its impact on tolerant and susceptible wheat genotypes. Nitrobenzene oxidation revealed that the increase can be entirely explained by an increase in syringyl lignin units only, as shown by fluorescence emission spectroscopy [63]. The experiments also showed that the presence of a fungus pathogen that is responsible for chickpea dry root rot, *Macrophomina phaseolina*, caused local lignin deposition and LAC gene expression [64].

When a pathogen attacks, an increase in lignification is frequently seen to occur as a defense mechanism. Since lignin is an undegradable mechanical barrier for most microorganisms, this reaction is thought to represent one of a variety of strategies designed to prevent parasite invasion, thereby lowering the susceptibility of the host [52]. Chinese cabbage infection with *Erwinia carotovora* subsp. carotovora led to H_2O_2 buildup and peroxidase activity. Lignin in plants that had been inoculated also significantly increased at 12, 24, and 72 h after inoculation. An EST database analysis of Chinese cabbage revealed 12 genes, which were chosen for expression research because they may encode lignin biosynthesis-related enzymes. The expression of each of these genes was elevated in mocked and infected plants, but it remained for longer in the infected samples than in

mocked and untreated plants, indicating that they may be involved in a defense mechanism mediated by lignin [13].

Increased lignin deposition results from Sphaeropsis sapinea infection of Pinus nigra [65]. In wheat's hypersensitive response to Puccinia graminis, lignification is a defense mechanism [66]. Such a reaction in wheat results in the accumulation of lignin with syringyl units [67]. Another study showed that the lignin content of wheat leaves infected with the mosaic virus remained unchanged [68]. The study showed that in wheat, Agrobacterium stimulates the formation of ferulic acid. Because ferulic acid is a precursor to the production of lignin, it is possible that these plants have a defense mechanism that keeps bacteria from infecting them [69]. The higher resilience of E. nitensas compared to *E. globulus* is likely due to the deposition of lignin in the necrophylatic periderm during the early stages of infection with Mycosphaerella. This response may stop the transfer of toxins and fungal enzymes to the host, blocking the displacement of water and nutrients from the host cell to the fungus [70]. The amount of lignin changes as a result of fungal attack, according to a number of writers, although not all of these studies have sufficiently proved how important lignin is during these processes. There are also fewer studies that examine the modifications in plant metabolism and gene expression that cause this distinct lignin buildup.

Upon infection with *Xanthomonas campestris*, the expression of two CCR-coding genes (*AtCCR1* and *AtCCR2*) in *A. thaliana* differs. While *AtCCR2* has lower levels of expression, *AtCCR1* is selectively expressed throughout the formation of healthy tissues. The fact that this relationship is reversed in response to *X. campestris* infection suggests that these genes may be involved in the pathogen's hypersensitive response [71]. Following *Ophiostomis new-ulmi* inoculation, metabolic studies on changes in the xylem tissues of *Ulmus minor* and *Ulmus minor* × *Ulmus pumila* demonstrated that the hybrid has a quicker defense response, which is characterized by an increase in the amount of lignin, reducing the likelihood of pathogen invasion [72]. In response to *Botrytis cinerea*, *Fusarium oxysporum*, and *Phoma exigua mycelium* extracts, the differential accumulation of lignin and lignans in cell suspension cultures of *Linum usitatissimum* was studied from physiological and molecular perspectives. The experiment showed that the expression of the genes encoding PAL, CCR, and CAD was increased, as was PAL activity [73]. Additionally, following *Blumeria graminis* inoculation, diploid wheat (*Triticum monococcum*) exhibited increased COMT expression [74].

6.2. Lignin Biosynthesis' Role in Response to Abiotic Stresses (Drought, Salinity, and Low and High Temperatures)

Osmotic stress is typically brought on by simultaneous severe drought and significant salt stress, which triggers water loss and sometimes the death of plant cells, directly impacting plant growth and development and leading to significant losses in crop yields [75,76]. The invasion and transpiration of plant cell wall water can be decreased by lignin, which helps to sustain cell osmotic equilibrium and defensive membrane integrity [77]. Moreover, several studies have revealed that dry circumstances enhance lignin production. In the Eucalyptus urograndis stem's basal zone and the Eucalyptus globulus stem's apical zone, lignin content was significantly raised in cases of drought stimulation [11]. Under the conditions of drought stress, CCR1/2 was a major gene in the lignin monomer biosynthesis pathway; in the maize root elongation area, CCR1/2 was significantly upregulated [78]. Additionally, Kovaicik et al. [79] reported that drought stress significantly increased the lignin and CCR protein content in the growth of the stem of Leucaena seedlings, and hypothesized that CCR-catalyzed lignin biosynthesis may be essential for Leucaena's ability to withstand drought stress. Previous findings have also shown that lignin deposition is likely to play a role in salt tolerance in plants. The increased expression of Ipomoea batatas due to the lignin aggregation of IbLEA14 genes improved transgenic callus salt and resistance to osmotic stress [5]. The activities of syringaldazine peroxidase (SPX), guaiacol peroxidase (GPX), and coniferyl alcohol peroxidase (CPX) were all enhanced by drought and high temperatures. The location of lignin by histochemistry in specific grain cells suggested that

DAO was involved in the supply of H_2O_2 in the CPX-mediated lignification process [80]. H_2O_2, which also plays an essential regulatory role in lignin biosynthesis [53,81], is a stress-induced reactive oxygen (ROS) organism. According to Guo et al. [82], MYBs play an important role in both secondary cell wall biosynthesis and tolerance to abiotic stress, and the inhibition of Betula platyphylla BplMYB46 strengthened salt and osmotic stress resistance and increased lignin aggregation in transgenic birch; this indicates that there could be a correlation between the reaction to abiotic stress and the pathways of lignin biosynthesis. The lignified cell wall thus confers resistance to drought and a high osmotic state to plants as a waterproof lignin-rich shield [83]. Biomacromolecules, such as protein and nucleic acid, are impaired by higher temperatures, and membrane lipid peroxidation is increased and plant physiological metabolism is interrupted [84]. The temperature of a plant growth system is impacted by climate change. However, on the other hand, low temperatures also cause the degradation of cell membranes, decrease photosynthesis and respiration in plants, and severely inhibit their ability to grow and develop [85]. The expression of the C_3H gene was significantly higher in cold-acclimated Rhododendron leaves than in control leaves, and C_3H was able to affect the cell wall's torsional stiffness and water permeability by altering the S/G ratio and interfering in the Rhododendron's cold resistance. The lignin content in plant tissues was significantly increased during cold acclimation [86]. A study revealed that LTC dysregulated the expression of the HSF gene EjHSF3, which is involved in fruit lignification through an interaction with the lignin biosynthetic regulator EjAP2-1 [87]. Furthermore, heat and low-temperature conditioning (LTC) in loquat fruit might reduce low-temperature-induced lignification.

The amount of lignin was significantly smaller in the *Medicago truncatula* CAD1 mutant than in its natural form, and at room temperature (22 °C), there was no discernible difference in growth between the two. At 30 °C, furthermore, the MtCAD1 mutant's growth was greatly hindered, and the development phenotype of the compensated lines was identical to that of the wild form. The probable cause is that reduced lignin accumulation contributes to vascular damage, thereby reducing transpiration and causing overheating of the plant body [88]. A model of factors that affect lignification processes is provided in Figure 4.

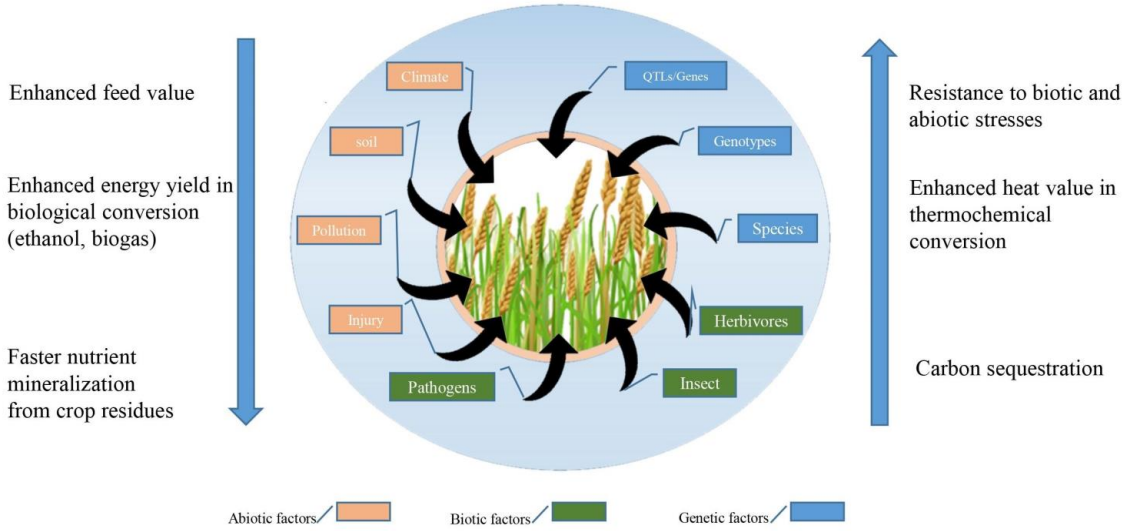

Figure 4. Model of the biotic and abiotic factors that influence the lignification process.

6.3. Gene Expression under Waterlogging, and Molecular Mechanisms for the Control of Lignin Biosynthesis

This research first investigated the distribution of lignin biosynthetic genes in different wheat tissues in order to develop a better understanding of the molecular mechanisms for the control of lignin biosynthesis in wheat tissues; then, it examined the expression patterns of genetic variants in the internode tissue across two separate wheat cultivars,

demonstrating various levels of adaptation sensitivity. Lignin buildup in plants is thought to be controlled by the PAL and CAD enzymes [41,89,90]. It demonstrates that the activation of PAL by essential substrates, such as L-phenylalanine and L-tyrosine, produces a significant 20% increase in lignin in experimental plants compared to control plants. Moreover, the quantity of lignin synthesis-related gene transcripts (PAL6, C4H1, 4CL1, and C3H1) increased as a result of the presence of these substances in nutritional medium [91]. Studies have also analyzed the effect of waterlogging on the quantity of vital lignocellulosic components and the expression of genes involved in lignin biosynthesis. Additionally, researchers have investigated whether the amounts of plant hormones in charge of regulating lignin biosynthesis in other species correlates with the amount of lignin present. The outcomes of the gene expression analysis showed elevated transcript abundance in the C4H1, PAL6, HCT1, 4CL1, C3H1, CCR2, CCoAOMT1, F5H2, CCR5, CAD2, and COMT2 genes in wheat tissues; so, these genes are more likely to play an important role in the regulation of wheat lignin biosynthesis. These findings support the lignin biosynthetic gene expression patterns reported earlier in both wheat and *Arabidopsis* [7,92]. In comparison to younger internode parts, older internodes appeared to have higher expression of some of the candidate genes inside their stems. The roles of the established lignin biosynthetic genes and the level of lignin were repeatedly proven to help increase the internode age [93]. Two members of the CCR gene family displayed tissue specialization, with CCR5 being primarily expressed in the flag leaf and CCR2 being expressed in the internode, whereas one member of each gene family had was expressed the most across the various wheat tissues. As more wheat gene sequences have been updated in the GenBank database, and since the publication of the Bi et al. report [7], the TaGI release of 12 genes composed of 221,925 TCs has been made available, and the catalog of possible biosynthetic wheat lignin genes has been updated and revamped for further database processing. Bi et al. showed that the specific ESTs allocated by Bi et al. to specific gene family members [7] appear to come from the same unigene, representing different members of the same family member of the gene. The ESTs defined in Bi et al. as 4CL1 and 4CL2 [7] are said to refer to the same unigene (Ta. 45,532), illustrating the same ESTs as those described in CCoAOMT1; the 4CL genes, such as 4CL1, and CCoAOMT4 are from the same unigene (Ta. 18,653). The ESTs referred to as CCoAOMT3 and CCoAOMT5 are derived from the same unigene (Ta. 48,354), indicating the same CCoAOMT gene and the same ESTs as those referred to in CCoAOMT3. The ESTs identified as PAL5, 6, 7, and 8 [7] are, therefore, reclassified as PAL3, 4, 5, and 6. In addition, it is noted that the EST allocated by the same authors as CAD2 is a CCR gene homolog; so, it is renamed as CCR5 hereinafter. The search also led to the discovery of new candidate biosynthetic lignin genes attributable to the CCR (designated as CCR6), COMT (designated as COMT3), and C_3H (designated as C3H3) gene families. The transcriptional repression of PAL6, CCR2, and F5H2 among the genes reported as highly expressed in wheat biomass was specifically evident in the internodes of waterlogged wheat plants, suggesting the transcriptional repression of PAL6, CCR2, and F5H2. Waterlogging triggered a decrease in the role of PAL derived from the internode, an enzyme that facilitates the first dedicated step in the general phenylpropanoid pathway and, thus, regulates lignin synthesis [89], which is consistent with the lignin profile and PAL6 gene expression. As a result of waterlogging, however, PAL1, 2, 3, and 5 are upregulated in the internode, while PAL6 is upregulated in the leaf. This upregulation of PAL6 in the leaf is associated with a rise in PAL enzyme production in the internode and leaf tissues. Various PAL genes respond differently to abiotic stresses [89], as well as the manufacture of additional phenylpropanoid-derived compounds (such as tannins and anthocyanin) by specific PAL genes [94,95], which have been demonstrated to serve in various stress reactions [96,97]; therefore, it is feasible that upregulated PAL genes in waterlogged plant tissues play a significant role in improving product reactions, since PAL1, 2, 3, and 5, the waterlogged internode genes, are upregulated [85].

Waterlogging, which dramatically reduces lignin content, also causes numerous PAL downstream genes to be upregulated twice, including the internodes HCT1, C4H1, and

CCoAOMT1 and the internodes 4CL1, C4H1, HCT1, F5H2, CCoAOMT1, CAD1, CAD3, and COMT2 in the leaf, and enhances the induction of CAD1 and CAD3 in the leaf (Figure 5). Furthermore, waterlogged wheat plant internodes are linked to increased CAD activity. These results may indicate the significance of IAA signaling rather than the IAA level in regulating the formation of lignin in the wheat stem. Internode lignin content is closely associated with the levels of two bioactive cytokinins (IPA and t-zeatin), which is consistent with their function in optimizing lignin synthesis [98,99], suggesting that the level of lignin in wheat biomass can be raised by altering the value of cytokinin. The molecular processes underlying the role of hormonal interactions in the control of lignin production in wheat tissues need to be better understood, given that plant hormones communicate synergistically or antagonistically in the operation of a broad range of plant growth processes [100]. This represents an important advancement in the creation of molecular tools that will make it easier to produce specialist wheat cultivars with lignin content. This, in turn, will maximize the performance of wheat straw raw material without disrupting the study of the lignin-associated lignin biosynthetic pathway in the two wheat cultivars, displaying a clear association of lodging resistance with internode lignin content and the presence of the internode lignin, such as one of the genes extensively expressed in tissues of wheat; this is because the role of these genes is to modulate the aggregation of lignin in the wheat stem. The lignin content of internodes is reduced by the waterlogging of wheat plants, and this effect is accompanied by the transcriptional suppression of three highly expressed genes in wheat internodes, namely, phenylalanine ammonia lyase6 (PAL6), CCR2, and F5H2, as well as the reduced activity of PAL [31].

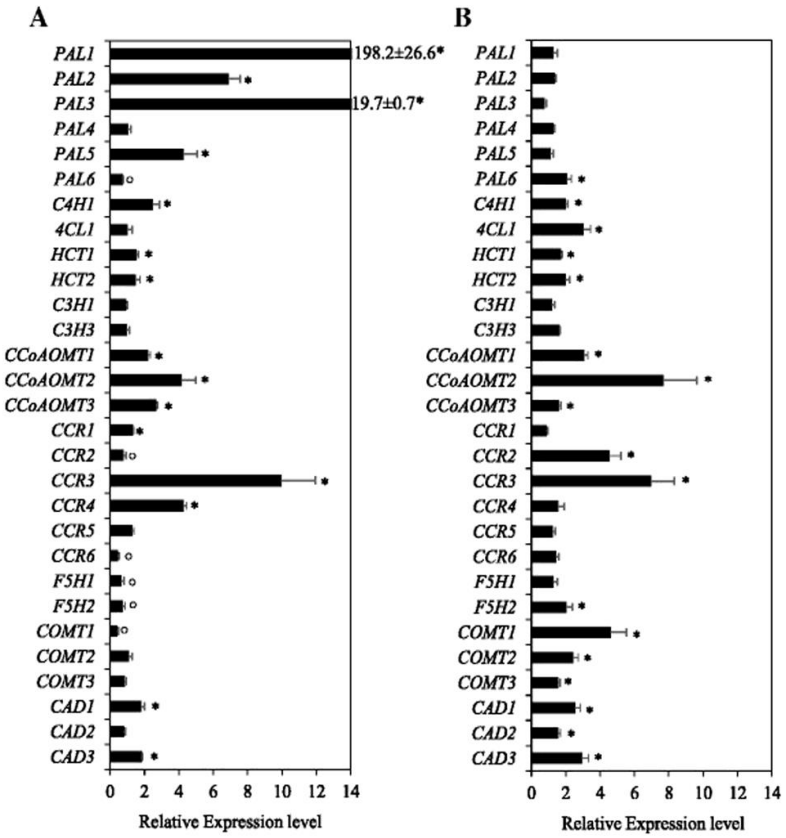

Figure 5. Expression of lignin biosynthesis genes in the internode (**A**) and flag leaf (**B**) in response to waterlogging. The * and ○ symbols indicate statistically significant upregulation and downregulation of the taget genes in response to waterlogging, respectively, as compared to that of the control at $p < 0.05$. Adapted from "Lignin Biosynthesis in Wheat (*Triticum aestivum* L.): Its Response to Waterlogging and Association with Hormonal Levels" by Nguyen et al. *BMC Plant Biology* (2016) 16:28 [23] (under Creative Commons CC BY license).

7. Plant Heavy Metal Stress Tolerance: The Role of Lignin

As the very first entry barrier for ions and in the response of the plant to heavy metal stress [75,101], the absorption and transport of heavy metals are heavily influenced by the cell wall. Heavy metal stress will stimulate the phenolic secondary metabolic synthesis pathway and enhance the thickness of the cell wall by increasing the secondary cell wall's lignin content. Because the lignin polymer has a large number of functional groups (hydroxyl, carboxyl, methoxyl, etc.), it can connect a variety of different heavy metal ions (Cu^{2+}, Cd^{2+}, Pb^{2+}, etc.) [44] and minimize the absorption of heavy metals into the cytoplasm [102,103].

One of the major factors restricting plant growth in acid soils is the toxicity of aluminum (Al). A typical symptom of Al toxicity is the suppression of plant development [104]. The tea plant is perceived to be extremely immune to Al, and high levels of Al can induce its growth [95]. Mao et al. [105] revealed that the function of cell wall POD and phenylalanine ammonia-lyase (PAL) in the lignin production process in tea plants was substantially lowered at high levels of Al. The amount of lignin, which may help us understand the flourishing nature of high-Al-concentration tea, was also reduced. Another study found that in the pathway of lignin biosynthesis, Al could elicit the expression of enzyme genes, while Al stress expanded the expression of 4CL, CAD, C_3H, and PAL genes [106]. Stress can also increase lignin concentration in other plants that contain heavy metals such as copper (Cu), cadmium (Cd), zinc (Zn), and manganese (Mn) [10,53,79,93,107,108]. Excessive Cu content in the culture medium in ginseng root suspension cells increased PAL, CAD, caffeic acid POD, phenolic compound aggregation, and lignin activity [109]. Bhuiyan et al. [74] observed that the growth of soybean roots was influenced by Cd treatment; the amount of lignin increased, along with a larger output of POD and LAC, and the expression of the POD gene involved in lignin biosynthesis was elevated. Lignin biosynthesis is also closely related to plant heavy metal uptake, transmission, and resistance. The accumulation of lignin in the root endoderm's cell wall can hinder the transport of heavy metal parts into or out of the xylem or outward from the vascular bundle [33,108,110,111]. The level of expression of elevated Zn-induced lignin biosynthesis genes was higher in Zn/Cd hyperaccumulator Thlaspi caerulescens roots than in Arabidopsis roots; tissue sections demonstrated that lignin absorption in the endodermis cell wall of Thlaspi caerulescens roots was significantly higher than that in *Arabidopsis* [112]. Their results indicate that lignin biosynthesis is extremely important for Zn/Cd hyperaccumulation in Thlaspi caerulescens and may be related to ion absorption and transport. Earlier studies have also shown that lignin deposition reduces the harmful effects of Mn, which plays an active role in the hyperaccumulator *Phytolacca americana* [106]. The lignification of xylem in the roots could even mitigate the transportation of Cd into the shoots in [86]. The results demonstrated that Cu stress could boost the buildup of lignin in the roots of rice by enhancing lignin polymerization. It has been found that Cu stress-induced hydrogen peroxide (H_2O_2) regulates lignin monomer polymerization and lignin accumulation, which has a direct effect on the transport of Cu in rice seedlings from the root to the shoot [113]. Bhuiyan et al. [74] identified the gene involved in the biosynthesis of methyl units, which plays an important role in biotic and abiotic stress tolerance in wheat.

8. Role of Lignin against Lodging Resistance in Wheat

Lodging resistance has been shown to result in increased grain yields and crop improvement. This is possible due to wheat's solid stems. Its resistance to lodging, together with the structure of its cell walls, is related to the success of the plant's stem, biomass, height, and features. Lignin accumulation in the cell wall boosts the overall performance of plant stalks. Lodging resistance resulting from this deposition has improved. Lodging resistance, one of the most important features impacting crop growth and grain yield, can prevent the tilting or bursting of plant stems [114]. Research indicates that the majority of the resistance of crops to housing is related to the composition and properties of the plant, including its height, biomass, stem diameter, and stem cell wall [22,115,116]. Lignin depo-

sition in the cell wall highly enhances the system efficiency of plant stalks. It has significant effects on seed accommodation tolerance [116]. Nutrient elements have a significant effect on plant lignin production and lodging resistance. Silicon can boost the complexity of the stalk, the buildup of lignin, and the expression of rice CAD genes, thus also improving resistance to lodging [117]. By reducing lignin biosynthesis in buckwheat, rapeseed, and japonica rice, high nitrogen fertilizer significantly affects the mechanical power of the stalk and lodging resistance [118–120]. Kong et al. [120] discovered that the effects of excessive NH_4^+ on the toughness of wheat culms could be greatly reduced through the addition of K^+. Then, it was suggested that the reduction in lodging resistance brought on by nitrogen fertilizer was likely related to the inhibition of K^+ absorption, which boosted lignin aggregation in the vascular bundles [121].

Peng et al. [63] applied exogenous paclobutrazol to a winter wheat cultivar that was both lodging-resistant and -susceptible, and discovered that paclobutrazol dramatically decreased the internode length of wheat, encouraged lateral growth, and increased lignin deposition and the activities of lignin biosynthesis enzymes, as well as the thickness of the internode, enhancing wheat lodging resistance. Scientists discovered, in another study, that plant density helped contribute to the enhancement of the characteristics of the plant stem and the lignin biosynthesis, and enriched the mechanical power of the stem. Moreover, in the biosynthesis and tolerance of plant lignin, nutrients play an integral role. The decrease in intensity is mainly due to the mere use of resistance to lodging, and the tolerance of biotic and abiotic stress and the consistency of the wheat biomass feedstock are highly linked to its lignin content. The genes and the greater actions of corresponding enzymes in a lodging-resistant cultivar stem were associated with the heading level, and these factors were shown to be closely correlated with stem mechanical strength and lignin content [122]. Muhammad et al. [122] reported a highly significant relationship between stem breaking force and wheat straw fresh weight, as well as between the second internode and both the flag leaf width and SiO_2 content. The lignin monomer ratios and the allocation of the two vascular bundles should be given more importance in breeding programs. A high level of lodging resistance can be achieved through different combinations of resistance to lodging compound traits [23].

9. Interrelationship between Cellulose and Sterols Pathways

Sterol-responsive genes have been reported to enhance plant resistance against stressors (biotic and abiotic). For example, SGTL1 (sterol glycosyltransferase) in *Withania somifera* participates in the glycosylation process using withanolide, which is involved in plant tolerance against stressors [123]. Additionally, WsSGTL1 uses target specificity to alter 3-beta hydroxy, a step that regulates the catalytic activity of glycosylate through sterol and anolide [123]. The transcript expression of WsSGTL1 is affected due to stressors and the treatment of elicitors, and it displays a physiological function under harsh environments. It is also reported that squalene synthase silencing using VIGS (virus-induced-gene silencing) in *Withania somifera* impaired plant tolerance by negatively regulating the defense- and sterol-related genes and reducing withanolides [123–126].

Significantly, an association between sterols and cellulose can be established directly or indirectly during plant synthesis machinery, which remains to be explored. Previously, KOR (endo-1, 4-b-glucanase) showed an important role in cellulose biosynthesis [127]. The transcript expression of KOR was normal in the seedlings of fk mutants. In contrast, the transcript expression of CESA (cellulose synthase catalytic subunits) constituents may be affected among mutants to explore sterol biosynthesis [128]. A cotton membrane treatment using glucose (glu) showed that UDP-glu is associated with a sterol mixture. This mixture analysis showed that 95% of the contents belonged to sitosterol [128]. However, more studies are required to define target genes that can improve the biosynthesis of lignin, cellulose, hemicellulose, etc., to increase plant tolerance against stressors.

When sitosterol was exogenously applied to wheat plants' leaves for 50% of crop evapotranspiration for 45 days, the damage caused by drought stress was repaired, and

wheat production increased [114]. Moreover, sterols can improve cold tolerance, as well as the stability of the membrane in *T. aestivum* leaves, as evidenced by the fact that a drop in sterol content, caused by MCD chelator treatment, exacerbated cold stress injury to wheat roots. Improved salt tolerance in wheat was substantially correlated with the up-regulation of campesterol and cholesterol levels [114].

10. Modification of Lignin Synthesis Using Genetic Engineering Technology

The material, structure, and composition of lignin can be changed using methods of genetic alteration. In recent years, several researchers have used lignin engineering for the alteration and structural modification of lignin content in plants [25]. The most common biopolymer on Earth is lignin. The adaptability of plants to terrestrial life has played a significant role in lignification. Numerous genes have been identified that direct lignin biosynthesis-related enzymes and are presently being cloned. Different genetic modification experiments have been performed on the modification and function of these genes, with researchers creating plants that contain altered lignin [129]. Successfully changed lignin content in *Arabidopsis thaliana* quadrupled the mutant pal1, pal2, pal3, and pal4 of the pal genes, with lignin decreased by 20–25% relative to the wild forms [130]. In addition, the modified mutant showed decreased salicylic acid levels and an increase in pathogenic susceptibility [130]. According to Rana et al. [131], changing the lignin quality in rice resulted in decreased growth and lignin quality due to the inhibition of Os4CL3. In addition, according to Gui et al., due to the inhibition of 4CL gene mRNA levels, which resulted in a dwarfed plant phenotype, there was a 36–50 percent reduction in lignin content in *Pinus radiata*.

Lignin seems to be very significant, as it influences the efficiency of wood and impacts both pulp and paper processing and the digestibility of grass species. For all of these factors, the lignin biosynthesis pathway has been the subject of many studies. Some genes that carry enzymes responsible for the biosynthesis of lignin have recently been cloned and sequenced. Many other recent studies suggest that the expression of such genes can be altered through genetic manipulation, producing plants with modified lignin. Moreover, some mutants with differences in the consistency of lignin or lignin development, resulting in altered properties, have been studied. In addition to typical homologs from many other organisms (9 to 34 genes, depending on the gene family), a phylogenetic analysis of biosynthetic wheat candidate lignin genes revealed that far more than one homolog from other species is clustered with each wheat candidate gene, except that all three wheat COMT genes created separate groups [23].

In different tissues and processes of wheat, the expression levels of candidate lignin biosynthetic genes have traditionally been characterized as in [7]. The different research materials include wheat cultivars that are distinct from all of those used by Bi et al. [7], as the list of candidate genes has been revised using the new databases. These findings suggest that all the candidate genes exhibited better exposure than those in the flag leaf blade/sheath in the peduncle and/or internode tissues, while the CCR1 and CCR5 genes exhibited considerably higher expression in the flag leaf blade than in the other tissues tested in different reviews; moreover, it was found that COMT2 and CAD2 had major effects on both flag leaf sheaths. At a very minimal/undetectable level, the genes C3H2, CCoAOMT2, and CCR4 were found to be expressed in all the examined tissues in [23,61].

As reported earlier, several enzymes of the lignin biosynthetic pathway have already been analyzed in wheat, such as cinnamoyl-CoA reductase (CCR), caffeic acid 3-O-methyltransferase (COMT), and cinnamyl alcohol dehydrogenase (CAD). Transcription factors plays an important role in the regulation of the pathways of genes involved in wheat lignin biosynthesis. Thus far, only a few instances of MYB gene expression profiling have been reported for different wheat hybrids or stress conditions. Ma et al. studied subgroup 4 of the R2R3-MYB transcription factors and proposed its function as repressor regulating the phenylpropanoid pathway. They reported the cDNA encoding of a subgroup 4 R2R3-MYB factor from wheat, designated as TaMYB4, which was overexpressed in stem

and root tissues. This overexpression of TaMYB4 in transgenic tobacco led to transcriptional reduction in both the cinnamyl alcohol dehydrogenase (CAD) and cinnamoyl-CoA reductase (CCR) genes involved in lignin biosynthesis [116].

11. Conclusions

Wheat straw is a lignocellulosic biomass consisting of lignin, cellulose, and hemicellulose. Cellulose and hemicellulose have shorter chains of sugar units and differ in their structure, as cellulose is unbranched and hemicellulose has divided polymers. The lignin from wheat straw is an H:G:S lignin, with a predominance of G-lignin units and with some quantities of associated *p*-coumarates and ferulates. The main lignin interunit linkages are β–O–4′ alkyl-aryl ethers, followed by phenylcoumarans and minor amounts of resinols, spirodienones, dibenzodioxocins, and β-diaryl ethers, together with cinnamyl alcohol and cinnamaldehyde end-groups. Lignin, which makes up a significant portion of the cell wall and is essential for plant growth and pathogen defense, has a detrimental influence on how easily biomass may be processed for use in biofuels. Resistance to lodging, resistance to biotic and abiotic stresses, and the consistency of the wheat biomass feedstock are strongly linked to its lignin content. The growth and productivity of plants should not be severely impacted by silencing the target lignin genes for increased biomass processability, yet disease resistance must not be compromised. The results of this study provide some valuable insights into the molecular mechanisms responsible for the formation of lignin in wheat, and represent an essential milestone towards the creation of molecular techniques that can promote the production of wheat cultivars with optimized lignin content and feedstock quality, without disrupting other agronomic benefits associated with lignin.

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