Journal of Integrative Agriculture 2026, 25(2): 659–670

Available online at ScienceDirect

Journal of Integrative Agriculture



RESEARCH ARTICLE

Optimized nitrogen and potassium fertilizers application increases stem lodging resistance and grain yield of oil flax by enhancing lignin biosynthesis

Xiqiang Li[1, 2], Yuhong Gao[2, 3, 4], Zhengjun Cui[5], Tingfeng Zhang[6], Shiyuan Chen[1, 2], Shilei Xiang[1, 2], Lingling Jia[1, 2], Bin Yan[2, 3, 4], Yifan Wang[2, 3, 4], Lizhuo Guo[2, 3, 4], Bing Wu[1, 2, 3#]

[1] *College of Life Science and Technology, Gansu Agricultural University, Lanzhou 730070, China*
[2] *State Key Laboratory of Aridland Crop Science, Lanzhou 730070, China*
[3] *Seed Industry Research Institute of Gansu Provincial University, Lanzhou 730070, China*
[4] *College of Agronomy, Gansu Agricultural University, Lanzhou 730070, China*
[5] *College of Agronomy, Tarim University, Alar 843300, China*
[6] *College of Life Science and Engineering, Hexi University, Zhangye 734000, China*

Highlights

- Utilization of nitrogen and potassium fertilizers can elevate stem bending strength and lodging resistance index and grain yield showed an increasing-then-decreasing trend with rising nitrogen and potassium fertilizer levels.
- Lignin content, stem bending strength, and lodging resistance index exhibited highly signifcant positive correlations with each other.
- Expression of *4CL1* and *F5H3* genes and the activities of four enzymes (tyrosine ammonia-lyase (TAL), phenylalanine ammonia-lyase (PAL), cinnamyl alcohol dehydrogenase (CAD), and peroxidase (POD)) were signifcantly and positively associated with lignin content.

Abstract

Lodging is a major constraint limiting oil flax production efficiency in northern China. Crop lodging susceptibility is closely related to stem lignin content, and the regulatory mechanisms by which nitrogen and potassium fertilization interactively influence lignin biosynthesis in oil flax stems require further investigation. Therefore, this study aimed to enhance lodging resistance and increase grain yield in oil flax. We examined the interactive effects of different nitrogen (75, 150, and 225 kg N ha^{-1}) and potassium (60 and 90 kg K_2O ha^{-1}) fertilizer rates on lignin metabolism, lodging resistance, and grain yield during the 2022 and 2023 growing seasons. Results indicated that nitrogen and potassium fertilizer levels and their interactions promoted lignin accumulation, improved lodging resistance, and increased grain yield. Compared to the control (CK), the 75–150 kg N ha^{-1} combined with 60 kg K_2O ha^{-1} treatments significantly enhanced the activities of key lignin-synthesizing enzymes (tyrosine ammonia-lyase (TAL), phenylalanine ammonia-lyase (PAL), cinnamyl alcohol dehydrogenase (CAD), and peroxidase (POD)) and upregulated the expression of *4CL1* and *F5H3* genes, leading to a 29.63–43.30% increase in lignin content, improved stem bending strength and lodging resistance index, and a 23.27–32.34% increase in grain yield. Correlation analysis revealed that nitrogen and potassium fertilizers positively regulated enzyme activities and gene expression related to lignin biosynthesis, thereby facilitating lignin accumulation and enhancing stem mechanical strength and lodging resistance. Positive correlations were observed among lignin-related enzyme activities, gene expression, lodging resistance traits, and grain yield. In summary, the application of 75–150 kg N ha^{-1} in conjunction with 60 kg K_2O ha^{-1} promoted lignin biosynthesis and accumulation, enhanced lodging resistance, and increased grain yield in oil flax grown in the dryland farming region of central Gansu, China. Furthermore, this treatment provides a technical basis for cultivating stress-tolerant and high-yield oil flax in arid regions.

Keywords: oil flax, nitrogen fertilizer, potassium fertilizer, stem lodging resistance, lignin biosynthesis, yield

Received 21 March 2024; Received in revised form 17 June 2024; Accepted 15 July 2024; Available online 14 September 2024
Xiqiang Li, E-mail: 1929769260@qq.com; #Correspondence Bing Wu, E-mail: wub@gsau.edu.cn

© 2026 CAAS. Publishing services by Elsevier B.V. on behalf of KeAi Communications Co. Ltd. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/). Peer review under responsibility of Editorial Board of *Journal of Integrative Agriculture*.
doi: 10.1016/j.jia.2024.09.006

1. Introduction

Oil flax (*Linum usitatissimum* L.) is an important oilseed and economic crop cultivated in northwestern and northern China. Its seeds are rich in dietary fiber and diverse nutrients, making them widely used across various industries. Notably, they contain high levels of essential unsaturated fatty acids — particularly linolenic and linoleic acids — which are highly valued by consumers (Wu *et al.* 2023). In recent years, frequent lodging due to high planting density, storms, and other extreme weather events has not only limited grain yield but also hindered mechanized harvesting of oil flax (Gao *et al.* 2018). Lodging refers to the permanent displacement of plant stems from their upright position caused by external forces. Within certain limits, plants can self-right after disturbance; however, when mechanical thresholds are exceeded, irreversible lodging occurs (Christopher *et al.* 2019; Stubbs *et al.* 2023). Thus, stem mechanical properties play a critical role in determining lodging resistance. This phenomenon is influenced by climatic conditions, cultivation practices, and plant genetic characteristics (Liu *et al.* 2007). Studies have shown that higher stem lignin content enhances lodging resistance in crops such as wheat, oats, summer maize, and oilseed rape (Tripathi *et al.* 2004; Chen *et al.* 2018; Guo *et al.* 2021; Nan *et al.* 2022; Gong *et al.* 2023). Lignin plays vital roles in plant development and defense against biotic and abiotic stresses (Tripathi *et al.* 2004; Chen *et al.* 2018; Guo *et al.* 2021; Nan *et al.* 2022; Gong *et al.* 2023), and contributes structurally to cell walls alongside cellulose and hemicellulose. Increased lignin content improves stem bending strength and overall resistance to environmental stress and lodging (Baucher *et al.* 1998; Cosgrove 2005). Given the global variability in precipitation patterns and the importance of nutrient management in agriculture, it is crucial to investigate lignin metabolism and its response to fertilization, particularly in relation to oil flax lodging.

Prior research on crop lodging has primarily focused on morphological, physiological, biochemical, and mechanical aspects of gramineous crops (Tripathi *et al.* 2004; Xue *et al.* 2016; Zhang *et al.* 2016), providing initial insights into the mechanisms underlying lodging. However, studies on the effects of macronutrient fertilizers on oil flax stem lignin metabolism and lodging resistance are relatively recent. During crop cultivation, deficiencies in either nitrogen or potassium weaken plant stems, reduce stem length, diameter, and wall thickness, and impair root growth — all of which negatively affect lodging resistance (Zhang *et al.* 2016; Shah *et al.* 2017). Appropriate nitrogen application enhances canopy light interception, promotes lignin biosynthesis, optimizes stem mechanical properties, and improves lodging resistance (Shi *et al.* 2016; Wang *et al.* 2020; Li *et al.* 2023; Liu *et al.* 2023). Adequate potassium supply increases potassium uptake by stems, enhances tissue thickness and C/N ratio, facilitates lignin anabolism, and improves lodging resistance (Liu *et al.* 2007; Li *et al.* 2009; Xiang *et al.* 2010). Conversely, excessive fertilization leads to vigorous leaf growth, reduced basal light penetration, increased plant height, elevated center of gravity, reduced lignin accumulation, and higher lodging incidence (Wei *et al.* 2008).

The most effective approach to elucidate the relationship between primary fertility factors and crop lodging resistance at the molecular level involves tracking changes in enzymatic activity along the lignin biosynthesis pathway and corresponding gene expression. Phenylalanine ammonia-lyase (PAL), tyrosine ammonia-lyase (TAL), cinnamyl alcohol dehydrogenase (CAD), and peroxidase (POD) play pivotal roles in the initiation and termination phases of lignin synthesis (Chen *et al.* 2018; Kamran *et al.* 2018b). PAL is a rate-limiting enzyme in the shikimate pathway that catalyzes the deamination of phenylalanine to produce *trans*-cinnamic acid. Reduced PAL activity results in significantly lower lignin content, whereas increased activity promotes lignin accumulation (Muhammad *et al.* 2018). TAL catalyzes the conversion of tyrosine to *p*-coumaric acid, serving as a key step in lignin synthesis (Mohammadi *et al.* 2002). CAD participates in the final reduction steps of lignin metabolism, producing monolignol precursors for *p*-coumaryl (H-type), coniferyl (G-type) and sinapyl (S-type) lignin units (Alexandra *et al.* 2013). POD acts as a polymerase in this pathway, utilizing H_2O_2 to oxidize and polymerize monolignols into lignin (Mónica *et al.* 2000). Polygene effects are common in plants, with variation in gene copy number and expression levels across species (Ruegger *et al.* 1999; Humphreys *et al.* 2002). In fiber flax, the *4CL1* and *F5H1* genes have been shown to play prominent roles in lignin accumulation in phloem and xylem tissues, respectively (Gao *et al.* 2008; Wang *et al.* 2009).

Existing studies on the individual effects of nitrogen or potassium fertilization on lignin synthesis mainly focus on nitrogen and potassium use efficiency, dry matter partitioning, and yield in oil flax (Qu 2010; Xun *et al.* 2015), as well as changes in lignin-related enzyme activities associated with lodging following nitrogen application, irrigation–nitrogen interactions, and density–potassium interactions (Gao *et al.* 2014, 2015; Wu *et al.* 2023). These studies have partially revealed how irrigation, nitrogen, and potassium regulate lodging resistance and yield, and influence the balance between vegetative and reproductive growth. However, fewer studies have addressed the interactive effects of nitrogen and potassium fertilizers on promoting normal plant development and improving stem lodging resistance mechanisms. The synergistic impact of nitrogen and potassium on lignin metabolism and its relationship with lodging resistance remains unclear, especially during the mid-to-late growth stages when oil flax is most susceptible to lodging. Therefore, this research aims to provide new insights into how nitrogen–potassium fertilizer interactions promote lignin biosynthesis, optimize lodging resistance, and increase grain yield, offering an empirical basis for developing improved agronomic strategies to enhance lodging resistance in oil flax.

2. Materials and methods

2.1. Site description

The experiment was conducted at the Dingxi Academy of Agricultural Science Experimental Station in Anding District, Gansu Province, China (34°26′N, 103°52′E, 2,060 m a.s.l.) during the 2022 and 2023 growing seasons.

The experimental field had cultivated loess soil. Plant density was maintained at 6.0×10^6 plants ha^{-1}. Soil baseline fertility in 2022 was 9.32 g kg^{-1} organic matter, 0.79 g kg^{-1} total nitrogen, 0.73 g kg^{-1} total phosphorus, 47.91 mg kg^{-1} alkali-hydrolyzable nitrogen, 25.43 mg kg^{-1} available phosphorus, 102.6 mg kg^{-1} available potassium, and pH 8.12. In 2023, soil fertility was 9.59 g kg^{-1} organic matter, 0.84 g kg^{-1} total nitrogen, 0.71 g kg^{-1} total phosphorus, 45.64 mg kg^{-1} alkali-hydrolyzable nitrogen, 24.67 mg kg^{-1} available phosphorus, 98.1 mg kg^{-1} available potassium, and pH 8.31.

2.2. Experimental design

The experiment followed a randomized complete block design with three replications per treatment. Each plot measured 12 m^2 (3 m×4 m) with a row spacing of 20 cm. The tested variety was 'Dingya 26'. Seven treatments were applied: CK, 0 kg N ha^{-1}+0 kg K_2O ha^{-1}; N1K1, 75 kg N ha^{-1}+60 kg K_2O ha^{-1}; N1K2, 75 kg N ha^{-1}+90 kg K_2O ha^{-1}; N2K1, 150 kg N ha^{-1}+60 kg K_2O ha^{-1}; N2K2, 150 kg N ha^{-1}+90 kg K_2O ha^{-1}; N3K1, 225 kg N ha^{-1}+60 kg K_2O ha^{-1}; N3K2, 225 kg N ha^{-1}+90 kg K_2O ha^{-1}. Nitrogen fertilizer (urea, 46% N) was applied at a basal-to-topdressing ratio of 2:1, with topdressing at the budding stage. Potassium fertilizer (potassium sulfate, 52% K_2O) was applied entirely as basal dressing. Phosphorus fertilizer (calcium superphosphate, 16% P_2O_5) was uniformly applied at 75 kg P_2O_5 ha^{-1}. Sowing dates were April 26, 2022 and April 9, 2023. All other field management practices followed standard local protocols.

2.3. Determination parameters and methods

Samples were collected on 30 June (anthesis), 22 July (kernel), and 3 August (mature) in 2022, and on 29 June (anthesis), 14 July (kernel), and 4 August (mature) in 2023. Uniformly growing plants were randomly selected from each plot between 9:00 a.m. and 10:00 a.m.

Bending strength and lodging resistance index Three oil flax plants per plot were used to determine stem bending strength. Above-ground fresh weight was measured using an electronic balance (accuracy: 0.001 g). Stem bending strength (BS) was measured using a microcomputer-controlled electronic universal testing machine (CMT2502, SANS, Shenzhen, China; torque 2 cm, maximum test force 50 N, speed range 1–500 mm min^{-1}) at the height of the plant's center of gravity (Gao *et al.* 2015). Lodging resistance index (LRI) was calculated as: LRI=BS/(Height of center of gravity×fresh weight).

Lignin content and lignin-related enzyme activity Ten representative plants per plot were sampled at anthesis, kernel, and mature stages to measure lignin content and related enzyme activities using commercial test kits (Michy Biology, China).

After acetylation of phenolic hydroxyl groups in lignin, an absorption peak at 280 nm appears, with absorbance positively correlated with lignin content. The procedure was as follows: fresh samples were fixed at 105°C for 10–15 min, dried at 80°C to constant weight, ground, sieved, and 0.01 g powder was placed in a 2 mL Eppendorf tube with 1 mL of 80% ethanol, mixed, and incubated at 50°C for 20 min. After centrifugation at 12,000 r min^{-1} for 10 min at 25°C, the supernatant was discarded, and the precipitate was dried. The residue was processed according to kit instructions. Absorbance at 280 nm was measured using a UV spectrophotometer. Lignin content (mg g^{-1} dry weight)=$0.7422(\Delta A+0.0364)\times W^{-1}$, where ΔA=A1–A2 (A1, measurement tube absorbance; A2, blank tube absorbance); W, sample mass in grams.

Reagents from the kit were reconstituted as required. A 0.1 g sample from the center-of-gravity height was collected and stored at –80°C for subsequent analysis.

PAL catalyzes the conversion of L-phenylalanine to *trans*-cinnamic acid and ammonia, with the maximum absorbance at 290 nm. The method involved adding 1 mL extract, homogenizing on ice, centrifuging at 12,000 r min^{-1} for 10 min at 4°C, collecting the supernatant, and processing according to kit instructions. Absorbance at 290 nm was measured using a UV spectrophotometer. PAL activity (U g^{-1} fresh weight)=$26.6\times\Delta A\times W^{-1}$ (ΔA=A1–A2).

TAL decomposes tyrosine to form coumaric acid, increasing solution absorbance at 333 nm over time. The method involved adding 1 mL extract, homogenizing on ice, centrifuging at 8,000×g for 10 min at 4°C, collecting the supernatant, and following kit instructions. Absorbance at 333 nm was measured using a UV spectrophotometer. TAL activity (U g^{-1} fresh weight)=$35\times\Delta A\times W^{-1}$ (ΔA=A1–A2).

CAD catalyzes the formation of cinnamaldehyde from cinnamyl alcohol, with peak absorbance at 340 nm. The method involved adding 1 mL extract, homogenizing on ice, centrifuging at 12,000 r min^{-1} for 10 min at 4°C, collecting the supernatant, and following kit instructions. Absorbance at 340 nm was measured. CAD activity (nmol g^{-1} min^{-1} fresh weight)=$114.94\times(\Delta A+0.0051)\times W^{-1}$ (ΔA=Initial absorbance–Absorbance after 5 min).

POD is a key enzyme in the plant enzymatic defense system under stress and exhibits an absorption peak at 470 nm. The method involved adding 1 mL extract, homogenizing on ice, centrifuging at 12,000 r min^{-1} for 10 min at 4°C, collecting the supernatant, and following kit instructions. Absorbance at 470 nm was measured using a visible spectrophotometer. POD activity (U g^{-1} fresh weight)=$20\times\Delta A\times W^{-1}$ (ΔA=Absorbance at 10 s–Absorbance at 1 min 10 s).

Fluorescence quantitative PCR expression analysis of *4CL1* and *F5H3* genes in lignin metabolism Fresh stem samples were collected for gene expression analysis. A 3 cm segment at the height of the center of gravity was immediately frozen in liquid nitrogen. Total RNA extraction, reverse transcription, and qPCR setup were performed using reagents from Tiangen Biotech (Beijing) Co., Ltd. *Actin* served as the reference gene, and relative expression was analyzed using the $2^{-\Delta\Delta C_T}$ method (Livak *et al.* 2001). Gene sequences were obtained from NCBI, and primers were synthesized by SBS Genetech Co., Ltd. Primer sequences are listed in Table 1.

Yield When 75% of the oil flax capsules turned yellow and basal leaves had abscised from the stems, 10 plants were randomly selected per plot. Branch number, number of effective capsules, thousand-kernel weight, and grain number

were measured. Grain yield was calculated as the actual harvested yield following plot separation.

2.4. Statistical analysis

For each measurement, three replicates were used, and the effects of various treatments on the measured variables were analyzed using one-way analysis of variance (ANOVA). The *F*-test was applied, and the least significant difference (LSD) ($P<0.05$) was used for multiple comparisons. Data were analyzed using SPSS statistical software v.24.0 (SPSS Inst., Cary, NC), and graphs were generated using Origin 2021 (Systat Software Inc.), IBM SPSS Amos 24 (SPSS Inst., Cary, NC), and Canoco 5 (microcomputer power).

3. Results

3.1. Grain yield and yield components

As shown in Table 2, both nitrogen and potassium fertilizer levels, as well as their interaction, significantly influenced grain yield and its components in oil flax. Under the K1 treatment, grain yield was significantly higher than under K2, increasing by 7.81 and 2.17% over two years, respectively. For all potassium fertilizer levels, grain yield was significantly greater than in the CK. At the same potassium level, different nitrogen treatments affected grain yield. Under K1, the N2 treatment yielded significantly more than N1 and N3, with increases of 11.70–11.86% and 3.48–5.41% across two years, respectively. Under K2, N2 increased yield by 5.34 and 8.48% compared to N1 and N3, respectively (two-year average). In terms of nitrogen–potassium interactions, the N2K1 treatment significantly increased grain yield by 8.58–21.16% in 2022; however, no significant differences among interaction treatments were observed in 2023. Over the two years, fertilization treatments increased grain yield significantly by 20.05–45.45% and 12.28–21.77% compared to CK.

Thousand-kernel weight, branch number, number of effective capsules, and grain number peaked at 150 kg N ha^{-1}, with average increases of 1.99–3.47%, 6.07–10.24%, 2.66–6.08%, and 4.44–6.74%, respectively, over the two years compared to other nitrogen levels. All nitrogen fertilizer treatments resulted in significantly higher yield components than CK. Under K1, thousand-kernel weight, branch number, effective capsule count, and grain number were higher than

Table 1 Oil flax primer information and the amplified fragments

Gene name	Accession no.	Primer sequences (5′→3′)	Fragment size (bp)
4CL1	EF214737	F: CCGTTGGGGAAGGAACTCGAAGAC	315
		R: CCACCCTTGCTGGTCTATCGTTCTT	
F5H3	EF214747	F: CGCTGGCCGGGCGTTGAACG	321
		R: ATGTCGGAGATAGGATCGTC	
Actin	AY857865	F: CGACTGCTGAAGGGAAATTGT	458
		R: CTGCTGGAAGGTGCTGAGGGAA	

Table 2 Changes in grain yield and yield components of oil flax under different nitrogen (N) and potassium (P) fertilizer treatments

Treatment	2022[1)]					2023[1)]				
	GY (kg ha^{-1})	TKW (g)	BN (no./plant)	EC (no./plant)	GN (grain no./capsule)	GY (kg ha^{-1})	TKW (g)	BN (no./plant)	EC (no./plant)	GN (grain no./capsule)
N fertilization (kg ha^{-1})										
0	1,038.89 c	5.75 b	9.93 d	9.07 b	7.27 b	1,288.89 b	6.33 a	11.11 b	11.44 b	7.33 b
75	1,312.50 b	6.03 ab	12.63 b	11.53 a	8.57 a	1,511.11 a	6.55 a	14.56 a	16.33 a	8.56 ab
150	1,451.39 a	6.11 a	13.90 a	11.93 a	8.83 a	1,547.22 a	6.72 a	14.94 a	16.67 a	9.06 a
225	1,300.00 b	5.90 ab	11.83 c	11.40 a	8.43 a	1,468.06 a	6.50 a	14.33 a	15.56 ab	8.33 ab
K fertilization (kg ha^{-1})										
0	1,038.89 c	5.75 b	9.93 c	9.07 c	7.27 b	1,288.89 b	6.33 b	11.11 b	11.44 b	7.33 b
60	1,405.56 a	6.08 a	13.33 a	12.38 a	8.76 a	1,525.00 a	6.71 a	15.52 a	17.22 a	9.07 a
90	1,303.70 b	5.94 ab	12.24 b	10.87 b	8.47 a	1,492.59 a	6.47 ab	13.70 ab	15.15 ab	8.22 ab
N×K interaction										
CK	1,038.89 e	5.75 a	9.93 f	9.07 c	7.27 b	1,288.89 b	6.33 b	11.11 b	11.44 b	7.33 b
N1K1	1,352.78 c	6.05 a	13.13 bc	12.40 a	8.60 a	1,516.67 a	6.63 ab	15.44 a	17.55 a	9.00 ab
N1K2	1,272.22 d	6.00 a	12.13 d	10.67 b	8.53 a	1,505.56 a	6.47 ab	13.66 ab	15.11 a	8.11 ab
N2K1	1,511.11 a	6.20 a	14.47 a	12.40 a	9.07 a	1,569.44 a	6.90 a	16.00 a	17.66 a	9.67 a
N2K2	1,391.67 b	6.02 a	13.33 b	11.47 ab	8.60 a	1,525.00 a	6.53 ab	13.89 ab	15.67 a	8.44 ab
N3K1	1,352.78 c	5.98 a	12.40 cd	12.33 a	8.60 a	1,488.89 a	6.60 ab	15.11 ab	16.44 a	8.56 ab
N3K2	1,247.22 d	5.82 a	11.27 e	10.47 b	8.27 a	1,447.22 a	6.40 ab	13.56 ab	14.67 a	8.11 ab
Source of variance										
N	***	***	***	***	***	***	**	***	***	***
K	***	***	***	***	***	**	*	***	**	*
N×K	**	*	**	**	NS	*	**	**	*	NS

[1)] GY, grain yield; TKW, thousand-kernel weight; BN, branch number; EC, effective capsule; GN, grain number.
Different letters show signifcant differences according to the least-signifcant difference (LSD) test at $P<0.05$ level. *, ** and *** indicate that the significant level of difference among treatments reached $P<0.05$, $P<0.01$ and $P<0.001$, respectively; NS, not significant.

under K2. Compared to CK, the K1 treatment increased thousand-kernel weight, branch number, effective capsules, and grain number by 5.88, 37.12, 44.32, and 22.12%, respectively (two-year average). Compared to CK, branch numbers increased significantly by 45.72 and 44.01%, and effective capsules increased by 36.71 and 54.37% under the N2K1 treatment in the two years. ANOVA results indicated that nitrogen and potassium fertilizer effects on grain yield, thousand-kernel weight, branch number, effective capsule count, and grain number were statistically significant. Their interaction exerted significant positive regulatory effects on grain yield, thousand-kernel weight, branch number, and effective capsule count in both growing seasons.

3.2. Lignin synthesis accumulation

Expression of lignin biosynthetic *4CL1* and *F5H3* genes The relative expression levels of *4CL1* and *F5H3* exhibited a trend of initial increase followed by decline across developmental stages, peaking at the kernel stage (Fig. 1). During the anthesis to mature stages, *4CL1* expression under the K1 treatment was significantly higher than under K2, with increases of 12.58, 28.14, and 26.19% (two-year average). Both K1 and K2 were significantly above the CK. At anthesis, under K1, the N2 treatment increased *4CL1* expression by 10.02–30.76% and 5.18–10.11% compared to N1 and N3 in 2022 and 2023, respectively. Under K2, N2 showed a significant increase of 19.75 and 6.55% over N3 in the two growing seasons. Under nitrogen and potassium fertilizer interaction, all fertilization treatments significantly enhanced *4CL1* expression by 16.18–66.01% and 20.29–41.11% relative to CK across both years. At the kernel stage, under K1, N2 achieved the highest expression, increasing by 1.78- and 0.50-fold over CK in 2022 and 2023, respectively. Under K2, no significant differences were observed between N1 and N3, though both were lower than N2. At maturity, *4CL1* expression under N2K1 was significantly higher than other treatments, showing increases of 30.70–71.33% over other fertilization regimes in 2022. Compared to CK, N1K1 and N2K1 treatments increased expression by 47.24 and 49.88% in 2023, respectively. From anthesis to maturity, *F5H3* expression under K1 was significantly higher than under K2, with a two-year average increase of 10.22, 7.92, and 14.06%. Under K1, N2 significantly increased *F5H3* expression by 13.78–17.16% compared to other nitrogen treatments in 2022, although no significant differences among N1, N2, and N3 were detected at anthesis in 2023. Under N1 and N2, *F5H3* expression increased significantly by 39.23% and 41.89% (two-year average), respectively, relative to CK at the

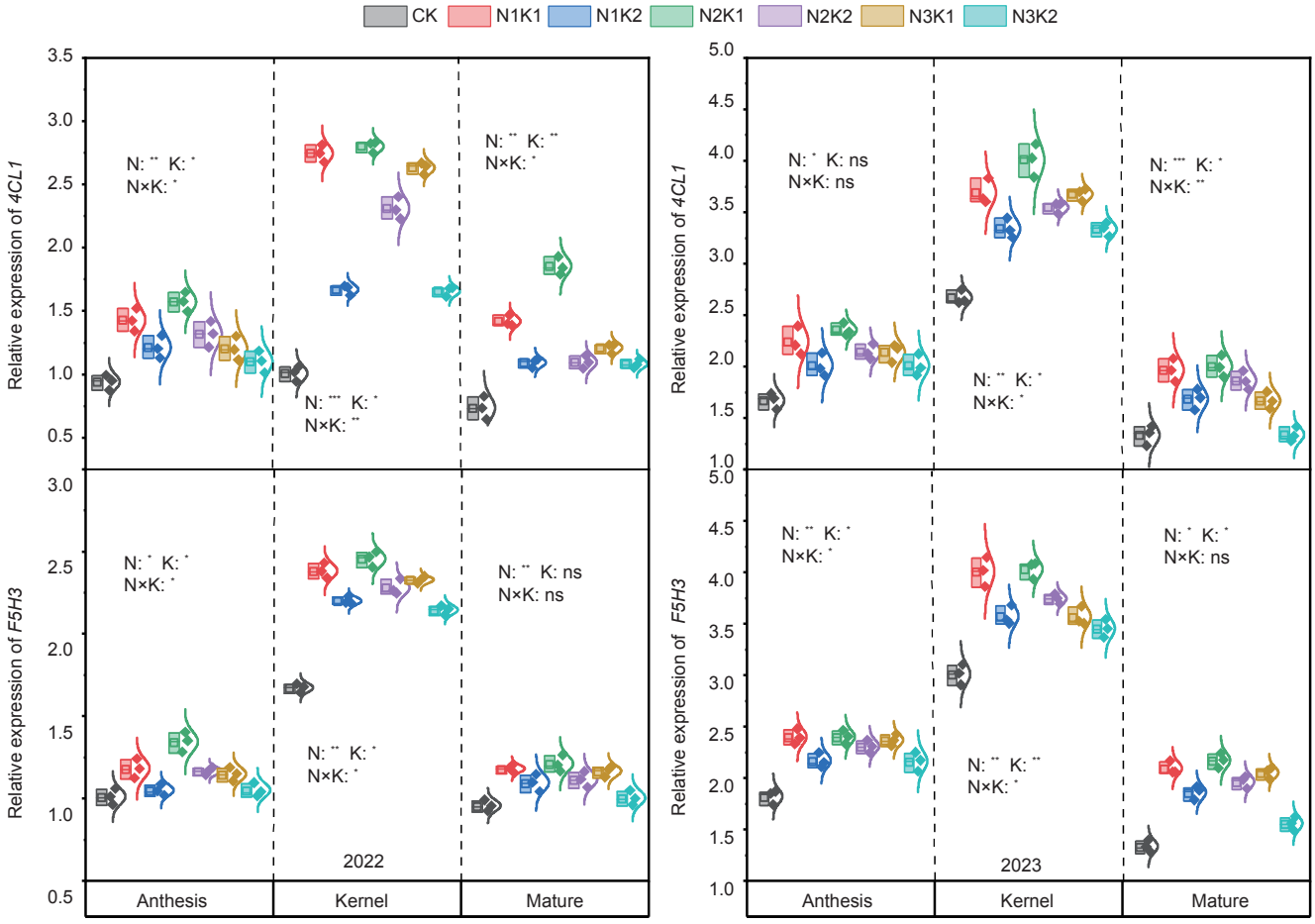


Fig. 1 Changes in the relative expression of genes involved in lignin synthesis in the stems of oil flax under different nitrogen (N) and potassium (K) fertilizer treatments. CK, control; N1–N3, 75, 150, and 225 kg N ha^{-1}, respectively; K1 and K2, 60 and 90 kg K_2O ha^{-1}, respectively. *, **, and ***, significant at $P<0.05$, $P<0.01$, and $P<0.001$, respectively; ns, not significant.

kernel stage. At maturity, *F5H3* expression was significantly lower under N3 than under N1 and N2 in 2023. Under K2, *F5H3* expression was significantly higher under N2 than under other nitrogen treatments, increasing by 8.83–9.00%, 4.31–7.45%, and 3.75–18.64% (two-year average) during the anthesis to mature stages. These results indicate that *4CL1* and *F5H3* expression peaked at the kernel stage compared to anthesis and maturity, and the application of 75–150 kg N ha^{-1} with 60 kg K_2O ha^{-1} significantly enhanced the relative expression of both genes.

Relative activity of lignin biosynthetic enzymes As shown in Fig. 2, the response of lignin-related enzyme activities to nitrogen and potassium fertilizers varied across growth stages, with consistent trends observed in both years. At the K1 level, PAL, TAL, POD, and CAD enzyme activities increased by 8.04, 9.55, 14.37, and 9.43% in 2022, respectively, and by 13.25, 12.32, 6.20, and 5.49% in 2023, respectively (averaged across three growth stages). In 2022, TAL and POD enzyme activities at the N2 level peaked; compared to other nitrogen levels, these activities were significantly higher by 8.40–20.66% and 19.82–49.81%, respectively. PAL and CAD enzyme activities were greater at N1 and N2 than at N3, showing significant increases of 8.78 and 12.61% for PAL, and 8.02 and 17.86% for CAD in the 2022 and 2023 growing seasons, respectively. Across all three nitrogen levels, the four enzyme activities were significantly higher than in the CK. In 2023, PAL activity at N1 and N3 was significantly lower than at N2, decreasing by 3.85 and 5.12%, respectively. At N1 and N2, TAL activity was significantly elevated by 22.23 and 34.91%, respectively, compared to CK, while POD activity increased significantly by 14.31 and 20.59%. No significant differences were observed in CAD activity among nitrogen levels, although all were significantly higher than CK. Compared to CK, each nitrogen level significantly increased enzyme activity by 8.12–14.27% (three-stage average) in 2023.

Under nitrogen and potassium fertilizer interaction, PAL activity was significantly enhanced by 32.06 and 38.87% (three-stage average) in the N1K1 and N2K1 treatments, respectively, relative to CK. TAL, POD, and CAD activities were markedly higher in the N2K1 treatment than in others, increasing by 11.01–32.95%, 13.73–80.06%, and 13.65–31.37% in 2022, respectively. Although PAL activity did not differ significantly between N1K1 and N2K1 in 2023, both treatments showed significantly higher values than the other treatments. Under N2K1, TAL, POD, and CAD activities

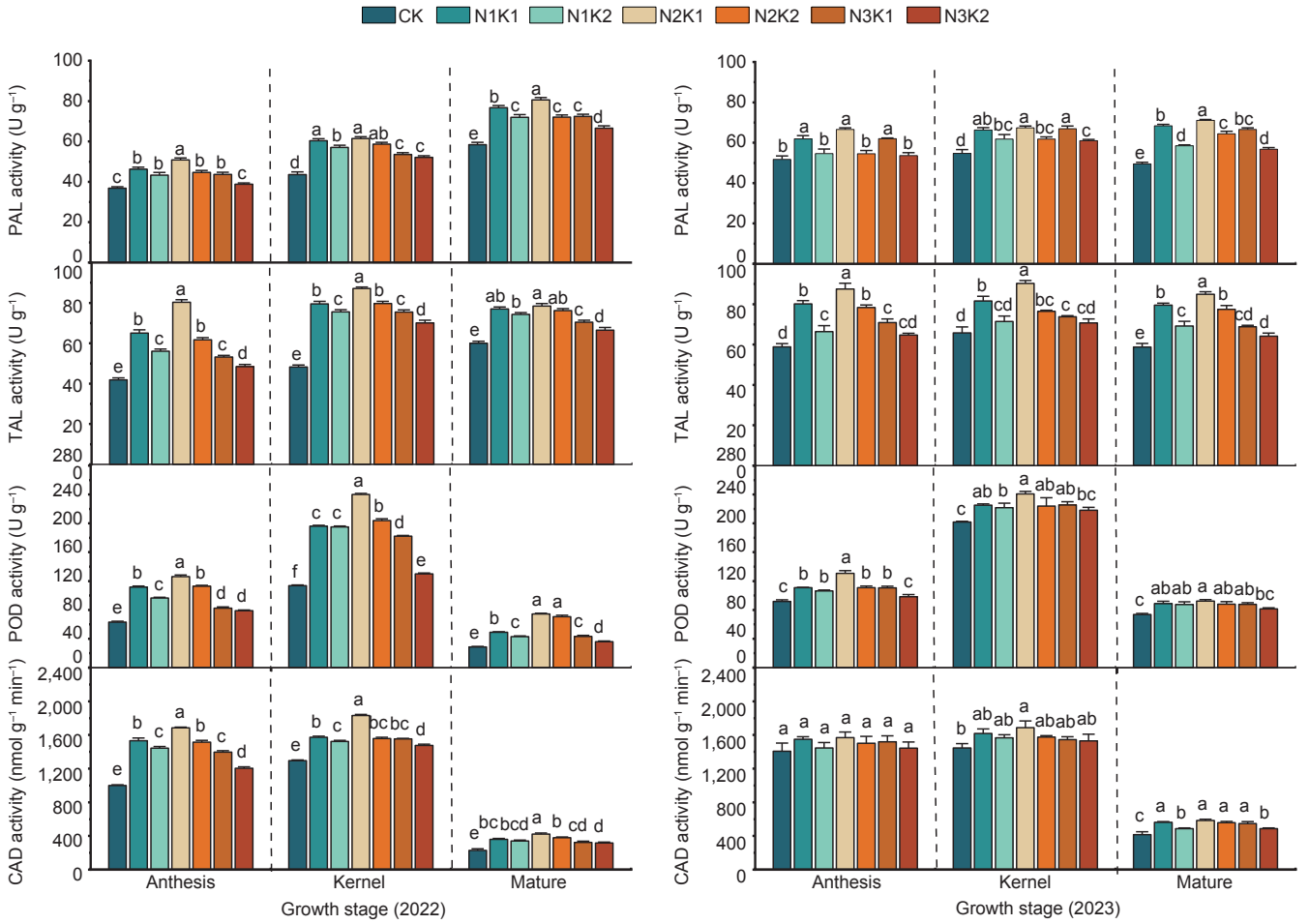


Fig. 2 Changes in the relative activity of lignin biosynthetic enzyme in the stems of oil flax under different nitrogen (N) and potassium (K) fertilizer treatments. CK, control; N1–N3, 75, 150, and 225 kg N ha^{-1}, respectively; K1 and K2, 60 and 90 kg K_2O ha^{-1}, respectively. Bars mean SE (n=3). Different small letters show significant differences according to the least-significant difference (LSD) test at P<0.05 level.

were significantly increased by 43.23, 26.20, and 17.41%, respectively, compared to CK in 2023. These findings indicate that N1K1 and N2K1 treatments significantly enhanced PAL activity, while TAL, POD, and CAD activities reached their maximum values — providing a strong enzymatic foundation for lignin biosynthesis. Furthermore, both unfertilized and excessively fertilized conditions were unfavorable for enhancing the relative activities of enzymes in the lignin synthesis pathway in stems.

Lignin content As nitrogen application increased, lignin content initially rose and then declined from anthesis to maturity (Fig. 3). The peak occurred at the N2 level, showing a 12.60–16.63%, 4.60–7.81%, and 5.40–8.57% increase compared to other nitrogen rates (two-year average). At the K1 level, lignin content was significantly higher than at K2. During anthesis, the N2K1 treatment consistently exhibited greater lignin content than other treatments across both years. At the kernel stage, under K1 conditions, the N2 treatment increased lignin content by 5.02 and 3.96% compared to N1. By the mature stage, N2K1 led to a significant rise of 8.60–27.22% and 2.42–5.61% over other fertilizer combinations. From anthesis to maturity, lignin content under combined nitrogen and potassium fertilization markedly exceeded that of the CK, increasing by 14.98–71.01%, 8.81–31.24%, and 21.68–43.56% at each respective stage. ANOVA revealed that the interaction between nitrogen and potassium fertilizers had a highly significant effect on stem lignin content, with the application of 150 kg N ha^{-1} and 60 kg K_2O ha^{-1} most effectively promoting lignin synthesis and accumulation.

3.3. Bending strength and lodging resistance index

Compared with CK, nitrogen and potassium fertilizer levels and their interaction significantly increased stem bending strength in oil flax (Fig. 4). At the anthesis to mature stage, the K1 treatment increased stem bending strength by 8.39, 15.01, and 11.72% (two-year average) relative to K2. Under N1 and N2 treatments, stem bending strength was significantly higher than CK by 29.85–40.55%, 27.44–38.86%, and 42.91–54.72%, respectively (two-year average). During the kernel stage, the N2 treatment under K1 conditions increased stem bending strength by 40.55 and 60.49% over CK across the two years. Under consistent potassium supply, the lodging resistance index initially increased and then declined with increasing nitrogen application. The index peaked at the anthesis to mature stage under N2. At the anthesis stage, the N1 and N2 treatments showed significantly higher lodging resistance index than N3 at K1. Under K2, no significant difference was observed between N1 and N3, though both were significantly lower than N2. During the kernel stage, the N2K1 treatment exhibited a significantly higher lodging resistance index than CK, with increases of 3.34 and 2.90, respectively. At the mature stage, under K1 conditions, the N1 and N2 treatments increased the index by 1.50- and 1.70-fold in 2022, and by 2.27- and 3.25-fold in 2023. Based on two-factor analysis of nitrogen and potassium fertilizers, the combination of 75–150 kg N ha^{-1} and 60 kg K_2O ha^{-1} significantly enhanced both stem bending strength and lodging resistance index in oil flax across both growing seasons.

3.4. Structural equation model

To better integrate the complex relationships between lignin biosynthesis, accumulation, and lodging resistance, a structural equation model (SEM) was developed (Fig. 5). Both potassium and nitrogen fertilizers significantly influenced

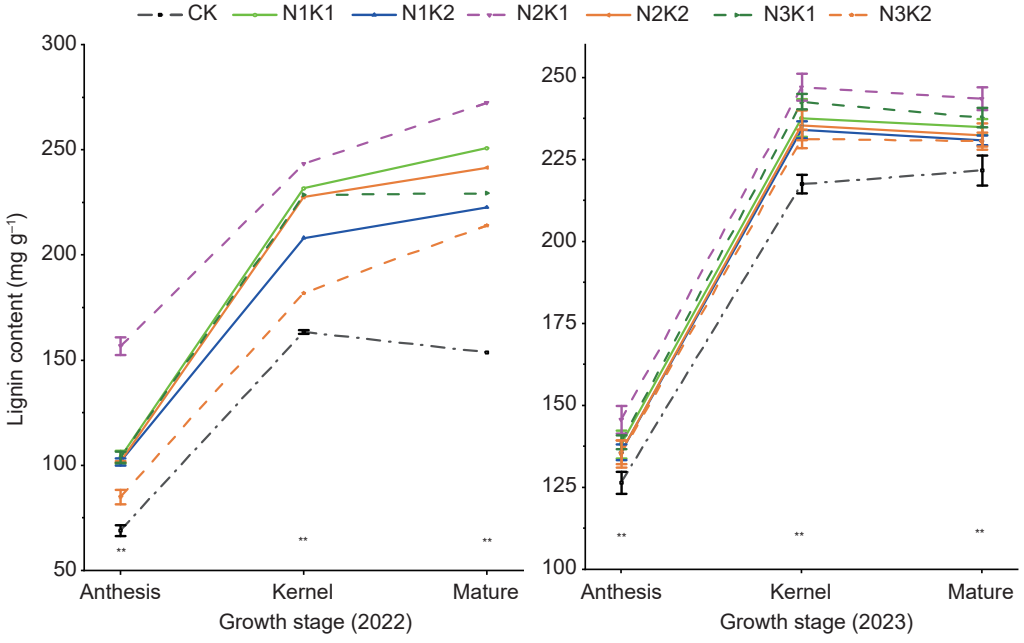


Fig. 3 Changes in lignin content in the stems of oil flax under different nitrogen (N) and potassium (K) fertilizer treatments. CK, control; N1–N3, 75, 150, and 225 kg N ha^{-1}, respectively; K1 and K2, 60 and 90 kg K_2O ha^{-1}, respectively. Bars mean SE (n=3) **, significant at P<0.01.

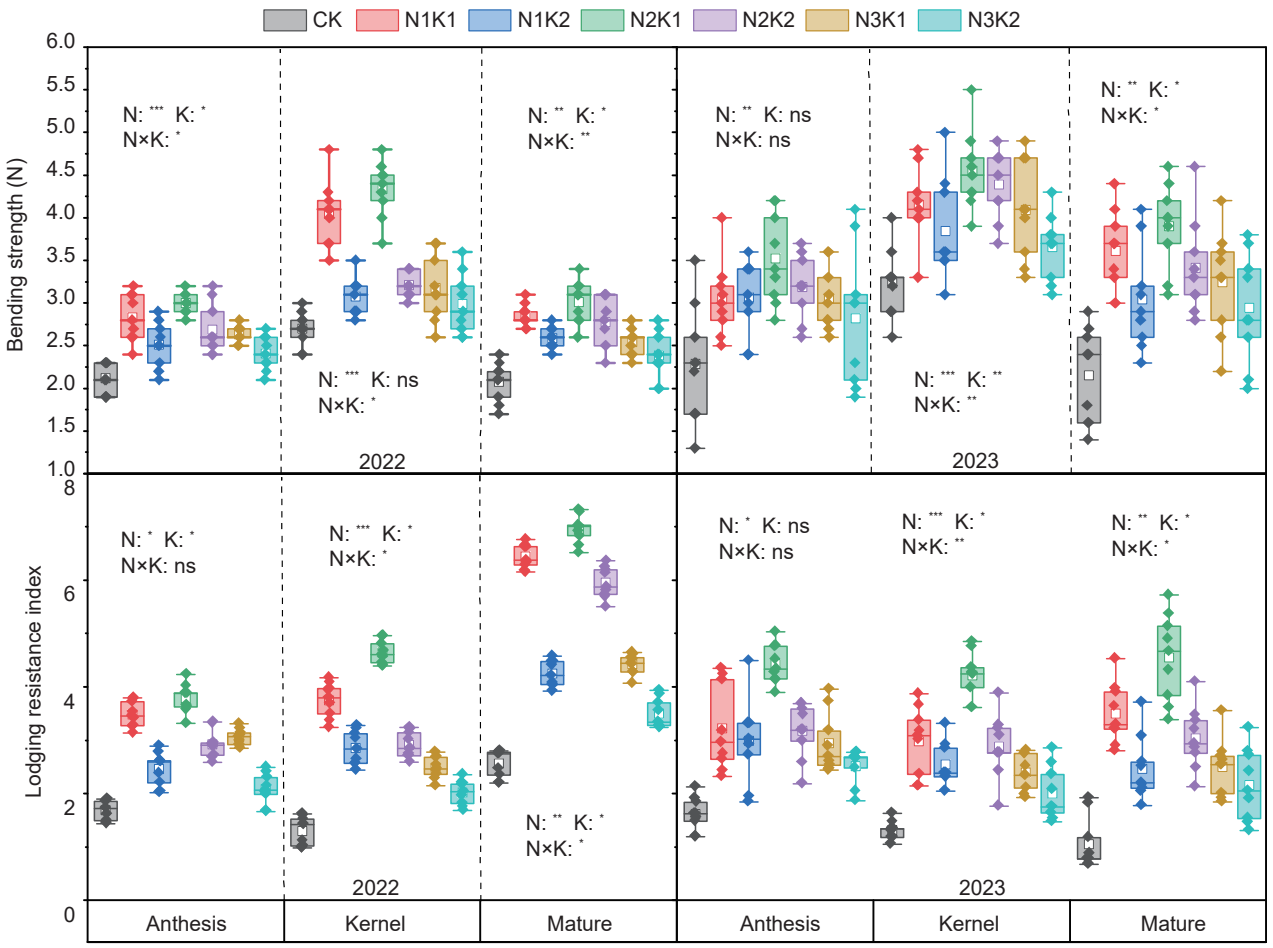


Fig. 4 Changes in the lodging resistance at mid-to-late stages in the stems of oil flax under different nitrogen (N) and potassium (K) fertilizer treatments. CK, control; N1–N3, 75, 150, and 225 kg N ha^{-1}, respectively; K1 and K2, 60 and 90 kg K_2O ha^{-1}, respectively. *, **, and ***, significant at $P<0.05$; $P<0.01$, and $P<0.001$, respectively; ns, not significant.

lodging resistance and grain yield in oil flax. In 2022, nitrogen fertilizer exerted stronger positive effects than potassium fertilizer on gene expression, lodging resistance, and grain yield, with Path coefficients (λ) of 0.427, 0.831, and 0.875, respectively. In 2023, nitrogen fertilizer again showed greater positive effects than potassium fertilizer on gene expression, enzymatic activity, lodging resistance, and grain yield, with λ of 0.372, 0.621, 0.914, and 0.894, respectively. Positive associations among gene expression, enzymatic activity, lodging resistance, and grain yield were observed in both growing seasons.

3.5. Redundancy analysis

Redundancy analysis (RDA) revealed positive associations between nitrogen and potassium fertilizers and the relative expression of *4CL1* and *F5H3*, as well as with PAL, TAL, CAD, and POD enzyme activities, lodging resistance, grain yield, and its components across both growing seasons (Fig. 6). The relative expression of *F5H3* was more strongly influenced by nitrogen and potassium fertilization than that of *4CL1*. Nitrogen and potassium fertilizers were also positively correlated with TAL, PAL, CAD, and POD enzyme activities. Lignin content showed a stronger positive association with nitrogen fertilizer than with stem bending strength or the lodging resistance index. However, lignin content was positively correlated with both bending strength and lodging resistance index in both years. Furthermore, nitrogen and potassium fertilizers were positively associated with grain yield and its components. The contribution of yield components to grain yield followed this order: number of grains>number of effective capsules>number of branches>thousand-kernel weight.

4. Discussion

4.1. Nitrogen and potassium fertilizers optimized on mechanical properties of oil flax stems

Crop yield improvement is severely constrained by lodging. Implementing appropriate cultivation practices can enhance plant stem characteristics and significantly improve the lodging resistance of oil flax, making it a critical strategy for achieving high yields (Cui *et al.* 2022). Appropriate application of nitrogen and potassium fertilizers increases plant biomass, strengthens mechanical parameters such as basal internode thickness and bending strength, reduces the lodging index, modifies physiological attributes of stems, elevates lignin and cellulose content, and enhances other

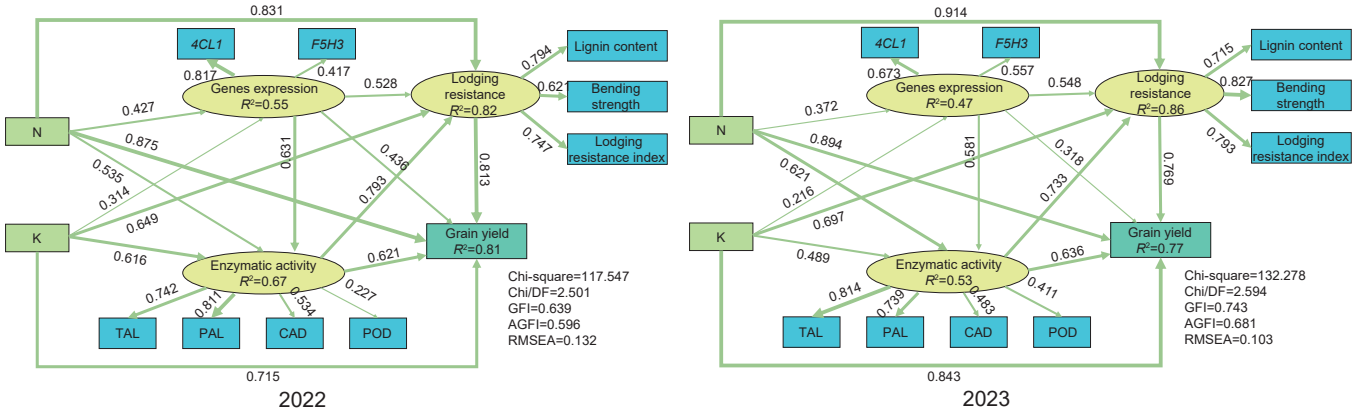


Fig. 5 Structure equation models fitted to linear relationships among potassium (K) and nitrogen (N) fertilizers, *F5H3* and *4CL1* relative expression, phenylalanine ammonia-lyase (PAL), tyrosine ammonia-lyase (TAL), cinnamyl alcohol dehydrogenase (CAD), and peroxidase (POD) enzyme activities, lignin content, bending strength, lodging resistance index, and grain yield in 2022 and 2023. Thickness of the arrows is proportional to the strength of the causal effect; numbers adjacent to the arrows represent standardized Path coefficients or covariates; R^2 values indicate the proportion of variance explained by each endogenous variable.

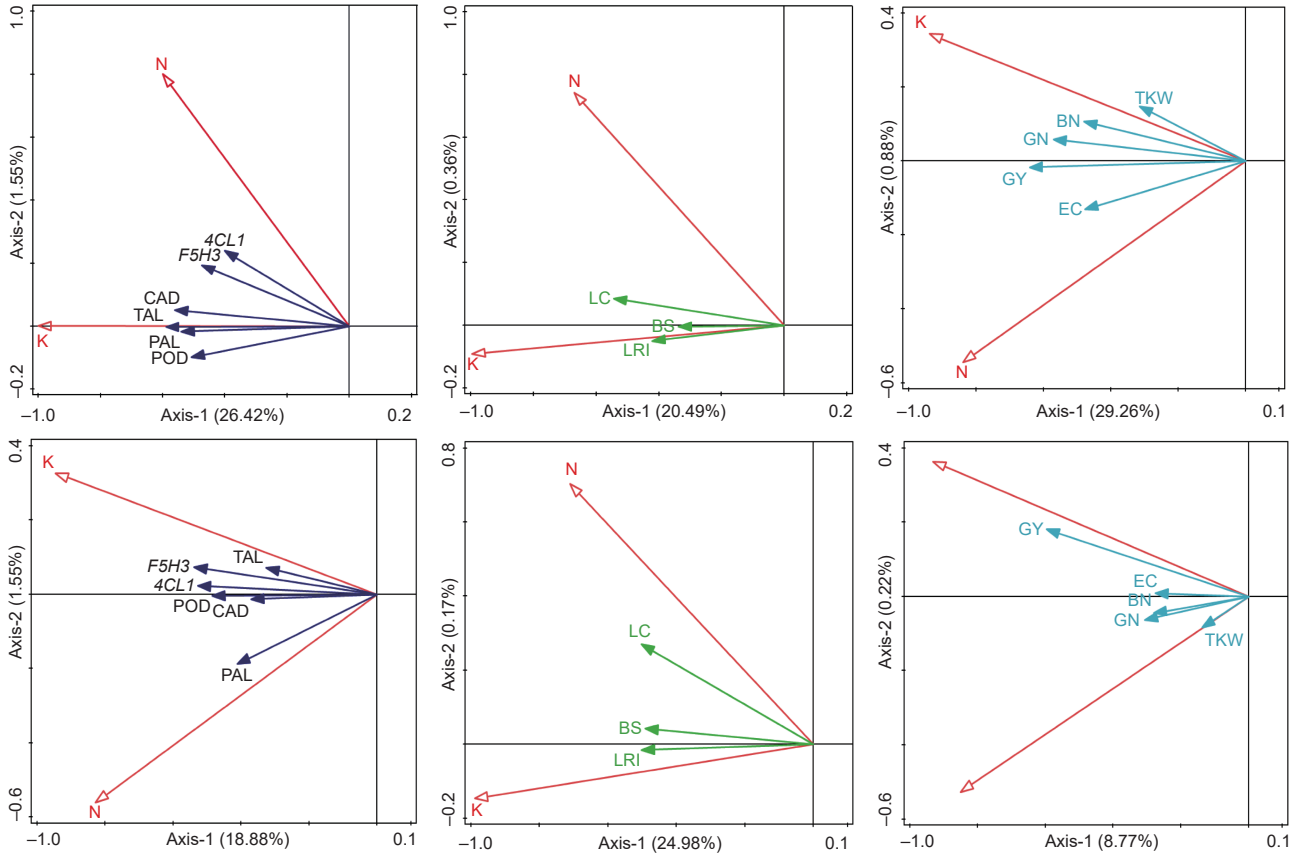


Fig. 6 Redundancy analysis (RDA) of lodging resistance and yield of oil flax by nitrogen (N) and potassium (K) fertilizer. The top and bottom parts of the figure represent the RDA results for 2022 and 2023, respectively. TAL, tyrosine ammonia-lyase; PAL, phenylalanine ammonia-lyase; CAD, cinnamyl alcohol dehydrogenase; POD, peroxidase. LC, lignin content; BS, bending strength; LRI, lodging resistance index; GY, grain yield; TKW, thousand-kernel weight; BN, branch number; EC, effective capsule; GN, grain number. Red arrows indicate nitrogen and potassium fertilizer applications; the vertical projection of the arrows between variables reflects the magnitude of correlation; longer lines indicate stronger correlations; acute angles between indicators denote positive correlations, while obtuse angles indicate negative correlations.

chemical constituents (Pitre *et al.* 2007; Wei *et al.* 2008; Liang *et al.* 2021). Additionally, these nutrients improve vascular bundle characteristics in the basal internode, thereby enhancing the plant's lodging resistance (Xu *et al.* 2018). In this study, nitrogen fertilizer application at 75–150 kg ha^{-1} increased stem bending strength and lodging resistance

index by 6.20–17.83% and 16.82–54.26% in 2022, and by 10.54–15.87% and 25.73–53.09% in 2023. Furthermore, potassium fertilizer applied at 60 kg ha^{-1} enhanced stem bending strength, contributing to improved lodging resistance. The combination of 75–150 kg N ha^{-1} with 60 kg K_2O ha^{-1} significantly improved stem lodging resistance, indicating that within an optimal range, increasing nitrogen and potassium inputs enhances lodging resistance. However, further increases in fertilizer rates did not improve resistance, likely due to excessive vegetative growth, reduced light penetration at the base, increased plant height, elevated center of gravity, reduced lignin accumulation, and consequently higher lodging risk (Wei *et al.* 2008; Zhang *et al.* 2017; Wu *et al.* 2019; Li *et al.* 2021). Treatments with combined nitrogen and potassium fertilization showed significantly higher stem bending strength and lodging resistance index than the CK, attributed to the fact that deficiencies in either nutrient result in weaker stems, reduced internode length, diameter, and wall thickness, and impaired root development, all of which compromise lodging resistance (Zhang *et al.* 2016; Shah *et al.* 2017).

4.2. Nitrogen and potassium fertilizers facilitated on lignin accumulation in oil flax stems

Lignin is a complex phenolic polymer, and its content in plant stems is closely associated with lodging resistance (Peng *et al.* 2014). Previous studies have shown that balanced nitrogen and potassium supply significantly increases the expression of lignin-related genes and enzyme activities, promoting lignin biosynthesis and enhancing mechanical strength and lodging resistance (Lu *et al.* 2014; Kuai *et al.* 2016; Wu *et al.* 2023). Both insufficient and excessive nitrogen or potassium application hinder lignin synthesis and accumulation (Liu X Y *et al.* 2007; Chen *et al.* 2018). At a fixed potassium rate of 60 kg K_2O ha^{-1}, nitrogen application promoted stem lignin accumulation, which peaked under the 75–150 kg N ha^{-1} with 60 kg K_2O ha^{-1} treatment before declining at higher rates. This study identified a rapid phase of lignin accumulation from anthesis to kernel development. During late growth stages, as grains develop and canopy density increases, plants redirect nutrients to stems to maintain structural integrity, resulting in increased lignin content that enhances stem stiffness and hardness, thereby reducing lodging risk (Kost *et al.* 2002). Gene expression levels and enzyme activities are key regulators during lignin biosynthesis (Wang *et al.* 2009; Chen *et al.* 2018; Kamran *et al.* 2018a). The 75–150 kg N ha^{-1} with 60 kg K_2O ha^{-1} treatment significantly upregulated the relative expression of *4CL1* and *F5H3* genes by 72.91–85.54% and 39.39–44.42%, respectively, compared to CK. Enzyme activities of TAL, POD, and CAD reached their maximum under 150 kg N ha^{-1} combined with 60 kg K_2O ha^{-1}. PAL activity was significantly higher in the 75–150 kg N ha^{-1} with 60 kg K_2O ha^{-1} treatments compared to others. Thus, optimal nitrogen and potassium fertilization enhances the expression of lignin-related genes and associated enzyme activities, promoting lignin biosynthesis. Insufficient nitrogen or excessive potassium application is detrimental to lignin accumulation (Martz *et al.* 1998; Kumar *et al.* 2003; Christin *et al.* 2010; Chen *et al.* 2018).

SEM analysis revealed that the activities of lignin biosynthetic enzymes (TAL, PAL, POD, and CAD) and the expression of related genes (*4CL1* and *F5H3*) were positively correlated with lignin content in both growing seasons. This indicates that elevated gene expression and enzyme activity effectively promote lignin synthesis and accumulation (Wang *et al.* 2009; Kamran *et al.* 2018a). Correlation analysis showed that nitrogen and potassium fertilizers significantly regulated lodging resistance and grain yield. Lignin content, stem bending strength, and lodging resistance index exhibited highly significant positive correlations with lodging resistance. A significant positive relationship also existed between lodging resistance and grain yield. These findings suggest that, within an optimal range, nitrogen and potassium fertilization enhances the expression of lignin-related genes and enzyme activities, thereby promoting lignin accumulation. High stem lignin content, coupled with multiple layers of mechanical tissue and abundant, large vascular bundles, contributes simultaneously to strong lodging resistance and high grain yield (Chen *et al.* 2011).

4.3. Nitrogen and potassium fertilizers raised on grain yield by oil flax populations

In field production, research has focused on balancing grain yield and stem quality (Xu *et al.* 2017). Grain yield and its components are influenced by various factors, including nitrogen fertilizer type and rate, fertilizer use efficiency, application timing, and basal-to-topdressing ratio (Clement *et al.* 2007; Sawan *et al.* 2008). Appropriate cultivation methods improve stem quality and increase grain yield. Timely fertilization enhances monosaccharide and polysaccharide content in stems, promotes internode plumpness, stimulates cellulose and lignin biosynthesis, and increases bending strength, thereby improving both lodging resistance and grain yield (Yang *et al.* 2009; Ahmad *et al.* 2020). In this study, nitrogen, potassium, and their interaction had significant positive effects on thousand-kernel weight, branch number, and effective capsule count. Grain yield initially increased and then declined with increasing nitrogen and potassium rates. The highest yield was achieved with 150 kg N ha^{-1} and 60 kg K_2O ha^{-1}, which was 45.45 and 21.77% higher than the control in the two growing seasons, respectively. Moderate nitrogen and potassium application likely increased grain yield by enhancing photosynthesis and respiration, providing more ATP for protein and seed formation, and improving carbohydrate translocation to seeds (Tikkoo *et al.* 2013). In practical production, optimized nitrogen and potassium application can synergistically improve individual plant performance and population quality, supporting high-yield oil flax cultivation.

5. Conclusion

The study demonstrated that applying 75–150 kg N ha^{-1} significantly increased the lodging resistance index in oil flax stems compared to other nitrogen levels. Similarly, the expression of *4CL1* and *F5H3* genes, along with

PAL and TAL enzyme activities, and lignin accumulation responded positively to nitrogen application within this range. Application of 60 kg K_2O ha^{-1} enhanced lignin-related enzyme activities and gene expression, effectively promoting lignin biosynthesis and accumulation. The combination of 75–150 kg N ha^{-1} with 60 kg K_2O ha^{-1} resulted in significantly higher lignin content, stem bending strength, and lodging resistance index compared to other treatments and their interactions. SEM indicated significant positive correlations among gene expression, enzyme activities, and lodging resistance. In conclusion, the 75–150 kg N ha^{-1} with 60 kg K_2O ha^{-1} treatment is an effective strategy for enhancing lodging resistance and achieving efficient oil flax production in the study region. However, regional soil fertility, environmental conditions, varietal traits, and other factors should be comprehensively considered when implementing such fertilization strategies.

Acknowledgements

This research was funded by the National Natural Science Foundation of China (31760363), the Earmarked Fund for CARS (CARS-14-1-16), the Gansu Education Science and Technology Innovation Industry Support Program, China (2021CYZC-38), the Gansu Provincial Key Laboratory of Arid Land Crop Science, Gansu Agricultural University, China (GSCS-2020-Z6).

Declaration of competing interest

The authors declare that they have no conflict of interest.

Declaration of generative AI and AI-assisted technologies in the writing process

The authors declare that they did not use AI in the preparation and writing of this manuscript.

References

Ahmad I, Meng X P, Kamran M, Ali S, Ahmad S, Liu T N, Cai T, Han Q F. 2020. Effects of uniconazole with or without micronutrient on the lignin biosynthesis, lodging resistance, and winter wheat production in semiarid regions. *Journal of Integrative Agriculture*, **19**, 62–77.

Alexandra B, Igor C, Adriana B S, Renato V, Juliana L S M, Ruben V, Kris M, Geert G, Jullyana C M S M, Paula M N, Sandra M C G, Ivan A A, Silvana C, Wout B, Marcos G A L, Paulo M. 2013. Lignification in sugarcane: Biochemical characterization, gene discovery, and expression analysis in two genotypes contrasting for lignin content. *Plant Physiology*, **163**, 1539–1557.

Baucher M, Monties B, Montagu M V, Boerjan W. 1998. Biosynthesis and genetic engineering of lignin. *Critical Reviews in Plant Sciences*, **17**, 125–197.

Chen X G, Shi C Y, Yin Y P, Lin W Z, Shi Y H, Peng D L, Li Y. 2011. Relationship between lignin metabolism and lodging resistance in wheat. *Acta Agronomica Sinica*, **37**, 1616–1622. (in Chinese)

Chen X G, Wang J, Wang Z L, Li W Y, Wang C Y, Yan S H, Li H M, Zhang A J, Tang Z H, Wei M. 2018. Optimized nitrogen fertilizer application mode increased culms lignin accumulation and lodging resistance in culms of winter wheat. *Field Crops Research*, **228**, 31–38.

Christin F, Carsten M, Bettina H, Peter-Robert L, Christoph B, Jürgen S, Thomas V. 2010. Tapetum-specific location of a cation-dependent O-methyltransferase in *Arabidopsis thaliana*. *The Plant Journal*, **56**, 132–145.

Christopher J S, Ryan L, Douglas D C. 2019. Maize stem buckling failure is dominated by morphological factors. *BioRxiv*, **17**, 833863.

Clement B J, Gwathmey C O. 2007. Potassium effects on partitioning, yield, and earliness of contrasting cotton cultivars. *Agronomy Journal*, **99**, 1130–1136.

Cosgrove D J. 2005. Growth of the plant cell wall. *Nature Reviews Molecular Cell Biology*, **6**, 850–861.

Cui Z J, Yan B, Gao Y H, Wu B, Wang Y F, Wang H D, Xu P, Zhao B Q, Cao Z, Zhang Y. 2022. Agronomic cultivation measures on productivity of oilseed flax: A review. *Oil Crop Science*, **7**, 53–62.

Gao Y, Chen X B, Long S H, Deng X, Zhou J, Liu A L. 2008. Cloning and sequence analysis of partial fragments of critical genes involved in flax lignin synthesis. *Acta Agronomica Sinica*, **34**, 337−340. (in Chinese)

Gao Y, Jiang H, Wu B, Niu J, Li Y, Guo F, Wang L, Blakney A J. 2018. The effects of planting density on lodging resistance, related enzyme activities, and grain yield in different genotypes of oilseed flax. *Crop Science*, **58**, 2613–2622.

Gao Z N, Guo L Z, Li L, Guo F, Niu J Y. 2014. Effects of nitrogen on oilseed flax stem lignin and relative enzyme and lodging resistance. *Chinese Journal of Oil Crop Sciences*, **36**, 610–615. (in Chinese)

Gao Z N, Zhao L, Guo L Z, Huang B X, Li Y, Niu J Y. 2015. Effects of irrigation and nitrogen fertilizer rates on oilseed flax stem lodging resistance and yield. *Chinese Journal of Eco-Agriculture*, **23**, 544–553. (in Chinese)

Gong R L, Song B, Yang Z Y, Lu L J, Dong J G. 2023. Effects of sowing date and density on lodging resistance and yield of different rapeseed cultivars. *Acta Agronomica Sinica*, **49**, 2777–2792. (in Chinese)

Guo Y, Hu Y, Chen H, Yan P, Du Q, Wang Y, Wang H, Wang Z, Kang D, Li W X. 2021. Identification of traits and genes associated with lodging resistance in maize. *The Crop Journal*, **9**, 1408–1417.

Humphreys J M, Chapple C. 2002. Rewriting the lignin roadmap. *Current Opinionin Plant Biology*, **5**, 224–229.

Kamran M, Ahmad I, Wang H, Wu X, Xu J, Liu T, Ding R, Han Q. 2018a. Mepiquat chloride application increases lodging resistance of maize by enhancing stem physical strength and lignin biosynthesis. *Field Crops Research*, **224**, 148–159.

Kamran M, Cui W, Ahmad I, Meng X, Zhang S. 2018b. Effect of paclobutrazol, a potential growth regulator on stalk mechanical strength, lignin accumulation and its relation with lodging resistance of maize. *Journal of Plant Growth Regulation*, **84**, 317–332.

Kost B, Chua N H. 2002. The plant cytoskeleton: Vacuoles and cell walls make the difference. *Cell*, **108**, 9–12.

Kuai J, Sun Y Y, Zhou M, Zhang P P, Zuo Q S, Wu J S, Zhou G S. 2016. The effect of nitrogen application and planting density on the radiation use efficiency and the stem lignin metabolism in rapeseed (*Brassica napus* L.). *Field Crops Research*, **199**, 89–98.

Kumar A, Ellis B E. 2003. 4-Coumarate: CoA ligase gene family in *Rubus idaeus*: cDNA structures, evolution, and expression. *Plant Molecular Biology*, **51**, 327–340.

Li C H, Chang Y L, Luo Y L, Li W Q, Jin M, Wang Y Y, Cui H X, Sun S F, Li Y, Wang Z L. 2023. Nitrogen regulates stem lodging resistance by breaking the balance of photosynthetic carbon allocation in wheat. *Field Crops Research*, **296**, 108908.

Li L J, Wang Q, Han Y L, Tan J F. 2009. Study of effects of potassium levels on phenolic and lignin metabolism of wheat and dynamic of aphid population. *Chinese Agricultural Science Bulletin*, **25**, 143–148. (in Chinese)

Li Y H, Zheng J L, Wu Q, Lin W H, Chi D C. 2021. Zeolite alleviates potassium deficiency and improves lodging-related stem morphological characteristics and grain yield in rice. *Crop & Pasture Science*, **72**, 407–415.

Liang H Y, Li H, Ding C, Yang F, Song X Q, Deng Y R, Liu G S, Lin F X, Zhang X Y, Su Z M, Jiang C. 2021. Effects of potassium fertilizer on morphology, mechanical properties, physiological characteristics and lodging resistance of broom corn millet. *Crops*, **6**, 177–181. (in Chinese)

Liu F, Zhou F, Wang X, Zhan X, Guo Z, Liu Q, Wei G, Lan T, Feng D, Kong F, Yuan J. 2023. Optimizing nitrogen management enhances stalk lodging resistance and grain yield in dense planting maize by improving canopy light distribution. *European Journal of Agronomy*, **148**, 126871.

Liu T X, Guan C Y, Liang Y. 2007. Research progress of rapeseed lodging. *Crop Research*, **2**, 140–144. (in Chinese)

Liu X Y, Jin J Y, He P, Gao W, Li W J. 2007. Effect of potassium chloride

on lignin metabolism and its relation to resistance of corn to stalk rot. *Scientia Agricultura Sinica*, **40**, 2780–2787. (in Chinese)

Livak K J, Schmittgen T D. 2001. Analysis of relative gene expression data using real-time quantitative PCR and the $2^{-\Delta\Delta Ct}$ method. *Methods*, **25**, 402–408.

Lu K L, Yin Y P, Wang Z L, Li Y, Peng D L, Yang W B, Cui Z Y, Yang D Q, Jiang W W. 2014. Effect of nitrogen fertilization Timing on lignin synthesis of stem and physiological mechanism of lodging resistance in wheat. *Acta Agronomica Sinica*, **40**, 1686. (in Chinese)

Martz F, Stéphane M, Pinon G, Legrand M. 1998. cDNA cloning, substrate specificity and expression study of tobacco caffeoyl-CoA 3-O-methyltransferase, a lignin biosynthetic enzyme. *Plant Molecular Biology*, **36**, 427–437.

Mohammadi M, Kazemi H. 2002. Changes in peroxidase and polyphenol oxidase activities in susceptible and resistant wheat heads inoculated with *Fusarium graminearum* and induced resistance. *Plant Science*, **162**, 491–498.

Mónica Q, Consuelo G, Miguel B, Araceli B, Iraida A, María M, Francisco A, Silvia M F, Horacio T, Victoriano V. 2000. A tomato peroxidase involved in the synthesis of lignin and suberin. *Plant Physiology*, **122**, 1119–1128.

Muhammad K, Su W N, Irshad A, Meng X P, Cui W W, Zhang X D, Mou S W, Aaqil K, Han Q F, Liu T N. 2018. Application of paclobutrazol affect maize grain yield by regulating root morphological and physiological characteristics under a semi-arid region. *Scientific Reports*, **8**, 4818.

Nan M, Li J, Zhao G Q, Chai J K, Liu Y M. 2022. Relationship between lodging resistance of oats and the basal internode stem characteristics and lignin synthesis. *Acta Prataculturae Sinica*, **31**, 172–180. (in Chinese)

Peng D L, Chen X G, Yin Y P, Lu K L, Yang W B, Tang Y H, Wang Z L. 2014. Lodging resistance of winter wheat (*Triticum aestivum* L.): Lignin accumulation and its related enzymes activities due to the application of paclobutrazol or gibberellin acid. *Field Crops Research*, **157**, 1–7.

Pitre F E, Cooke J E K, Mackay J J. 2007. Short-term effects of nitrogen availability on wood formation and fibre properties in hybrid poplar. *Trees*, **21**, 249–259.

Qu H Q. 2010. Preliminary report on the results of experiments on different potassium application rates in oil flax. *Information of Agricultural Science and Technology*, **13**, 31–32.

Ruegger M, Meyer K, Cusumano J C, Chapple C. 1999. Regulation of ferulate-5-hydroxylase expression in *Arabidopsis* in the context of sinapate ester biosynthesis. *Plant Physiology*, **119**, 101–110.

Sawan Z M, Mahmoud M H, El-Guibali A H. 2008. Influence of potassium fertilization and foliar application of zinc and phosphorus on growth, yield components, yield and fiber properties of Egyptian cotton (*Gossypium barbadense* L.). *Journal of Plant Ecology*, **1**, 259–270.

Shah A N, Tanveer M, Rehman A U, Anjum S A, Iqbal J, Ahmad R. 2017. Lodging stress in cereal — Effects and management: An overview. *Journal of Environmental Science and Health Part B-Pesticides Food Contaminants and Agricultural Wastes*, **24**, 5222–5237.

Shi D Y, Li Y H, Zhang J W, Liu P, Zhao B, Dong S T. 2016. Effects of plant density and nitrogen rate on lodging-related stalk traits of summer maize. *Plant Soil and Environment*, **62**, 299–306.

Stubbs C J, Kunduru B, Bokros N, Verges V, Porter J, Cook D D, DeBolt S, McMahan C, Sekhon R S, Robertson D J. 2023. Moving toward short stature maize: The effect of plant height on maize stalk lodging resistance. *Field Crops Research*, **300**, 109008.

Tikkoo A, Yadav S S, Kaushik N. 2013. Effect of irrigation, nitrogen and potassium on seed yield and oil content of *Jatropha curcas* in coarse textured soils of Northwest India. *Soil & Tillage Research*, **134**, 142–146.

Tripathi S C, Sayre K D, Kaul J N, Narang R S. 2004. Lodging behavior and yield potential of spring wheat (*Triticum aestivum* L.): Effects of ethephon and genotypes. *Field Crops Research*, **87**, 207–220.

Wang J, Chen X B, Gao Y, Zhang Y H, Long S H, Deng X, He D F, Wang Y F. 2009. Expression of critical lignin metabolism genes in flax. *Acta Agronomica Sinica*, **35**, 1468–1473. (in Chinese)

Wang Q, Xue J, Chen J L, Fan Y H, Zhang G Q, Xie R Z, Ming B, Hou P, Wang K R, Li S K. 2020. Key indicators affecting maize stalk lodging resistance of different growth periods under different sowing dates. *Journal of Integrative Agriculture*, **19**, 2419–2428.

Wei F Z, Li J C, Wang C Y, Qu H J, Shen X S. 2008. Effects of nitrogenous fertilizer application model on culm lodging resistance in winter wheat. *Acta Agronomica Sinica*, **34**, 1080–1085. (in Chinese)

Wu B, Cui Z J, Ma L J, Li X Q, Wang H D, Wang Y F, Yan B, Dong H W, Gao Y H. 2023. Effects of planting density-potassium interaction on the coordination among the lignin synthesis, stem lodging resistance, and grain yield in oil flax. *Agronomy Journal*, **13**, 2556.

Wu W, Ma B L, Fan J J, Sun M, Yi Y, Guo W S, Voldeng H D. 2019. Management of nitrogen fertilization to balance reducing lodging risk and increasing yield and protein content in spring wheat. *Field Crops Research*, **241**, 107584.

Xiang D B, Guo K, Lei T, Yu X B, Luo Q M, Yang W Y. 2010. Effects of phosphorus and potassium on stem characteristics and lodging resistance of relay cropping soybean. *Chinese Journal of Oil Crop Sciences*, **32**, 395–402. (in Chinese)

Xu C L, Gao Y B, Tian B J, Ren J H, Meng Q F, Wang P. 2017. Effects of EDAH, a novel plant growth regulator, on mechanical strength, stalk vascular bundles and grain yield of summer maize at high densities. *Field Crops Research*, **200**, 71–79.

Xu Z, Lai T, Li S, Si D, Zhang C, Cui Z, Chen X. 2018. Promoting potassium allocation to stalk enhances stalk bending resistance of maize (*Zea mays* L.). *Field Crops Research*, **215**, 200–206.

Xue J, Gou L, Zhao Y S, Yao M N, Yao H S, Tian J S, Zhang W F. 2016. Effects of light intensity within the canopy on maize lodging. *Field Crops Research*, **188**, 133–141.

Xun X H, Xie Y P, Niu J Y, Li A R. 2015. Effect of potassium application rate on uptake and distribution of potassium and grain yield in oil flax. *Acta Prataculturae Sinica*, **24**, 30–38. (in Chinese)

Yang S M, Xie L, Zhang S L, Li J, Yuan J C. 2009. Effects of nitrogen rate and transplanting density on physical and chemical characteristics and lodging resistance of culms in hybrid rice. *Acta Agronomica Sinica*, **35**, 93–103. (in Chinese)

Zhang W, Wu L, Wu X, Ding Y, Li G, Li J, Weng F, Liu Z, Tang S, Ding C, Wang S. 2016. Lodging resistance of *japonica* rice (*Oryza sativa* L.): Morphological and anatomical traits due to top-dressing nitrogen application rates. *Rice*, **9**, 31.

Zhang W J, Wu L M, Ding Y F, Yao X, Wu X R, Weng F, Li G H, Liu Z H, Tang S, Ding C Q. 2017. Nitrogen fertilizer application affects lodging resistance by altering secondary cell wall synthesis in *japonica* rice (*Oryza sativa*). *Journal of Plant Research*, **130**, 859–871.

Executive Editor-in-Chief Shaokun Li
Managing Editor Ning Wang