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Study on the metabolic pathways of flavonoids in flax roots under salt stress

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ABSTRACT

Salt stress is a major constraint affecting crop productivity, and understanding plant metabolic responses is essential for improving tolerance. In this study, we examined the metabolic pathways of flavonoids in flax (*Linum usitatissimum* L.) roots using a salt-tolerant genotype (R40) and a salt-sensitive genotype (R24). Plants were subjected to 150 mmol L^{-1} NaCl, and changes in metabolites were analyzed using a widely targeted metabolomics approach. A total of 732 metabolites were detected, including 332 that increased and 400 that decreased under salt stress. Among these, 163 flavonoids were further analyzed to explore their role in stress response. KEGG pathway analysis revealed significant changes in flavonoid-related pathways, with 9 pathways upregulated, 10 down-regulated, and 4 showing mixed responses. Key metabolites with strong antioxidant properties, such as quercetin and epicatechin, were identified as important components of the plant's defense mechanism. Notably, clear differences were observed between the tolerant and sensitive genotypes in terms of flavonoid accumulation and metabolic patterns. These findings highlight the important role of flavonoids in helping flax cope with salinity stress and provide useful insights for developing salt-tolerant varieties.

Keywords: salt stress, flax, roots, flavonoids, metabolomics, stress tolerance

INTRODUCTION

Flax (*Linum usitatissimum* L.) belongs to the genus *Linum* of the family Linaceae (Zhang et al., 2019). It is the main edible oil for people in western China, an important source of omega-3 unsaturated fatty acids and is considered one of the healthiest edible oils (Dang et al., 2010). Flax in China is mainly distributed in arid and semi-arid provinces such as Gansu and Inner Mongolia, and the main flax-producing areas are all affected by varying degrees of saline-alkali damage (Wang et al., 2014). The area of saline soil in the world is about 1 billion hectares, and China's land salinization accounts for about one-tenth of the global area of saline soil (Zhao et al., 2006). The total area of saline-alkali land in Gansu Province is 1.414 million hectares, of which the area of severely saline-alkali land is 602,800 hectares, and there are 120,000 hectares of saline-alkali soil in cultivated land. Salt stress has become an important abiotic stress factor in current flaxseed production, seriously threatening the sustainable development of the flaxseed industry (Zhao Wei et al., 2019; Zhang et al., 2015).

Flavonoids are a class of plant secondary metabolites characterized by a C6–C3–C6 carbon skeleton as the basic carbon frame, mainly including flavonoids, flavanols, isoflavones, anthocyanins and proanthocyanidins. Flavonoids

are widely distributed in the plant kingdom. In plants, most of them exist in the form of glycosides or carboxyl groups combined with sugars, and some exist in the form of free ones (Zeng et al., 2023). Metabolomics is a downstream and final product of the genome. Through metabolomics studies, qualitative and quantitative analysis of changes in flaxseed metabolites under salt stress can be conducted to understand the relationship between metabolites and flaxseed salt stress responses (Wei et al., 2022; Wahocho et al., 2023). With the establishment of "high-throughput metabolite analysis methods", large-scale metabolomics studies have become possible. Studies have shown that the stress resistance of many plants is closely related to the content of flavonoids in their bodies because of their strong antioxidant capacity, which can eliminate the excess reactive oxygen species (ROS) produced by plants induced by abiotic stress (Tohge, 2013). Salt stress induces the accumulation of flavonoids in most plants (Saito et al., 2013). Flavonoids also play a significant role in plant resistance to abiotic stress. However, it is unclear how flavonoids are metabolized in plant salt stress resistance and the specific regulatory mechanisms, and their functions in plant adaptation to adverse stress have not been fully elucidated (Zhang et al., 2021). Therefore, this study aims to investigate flavonoid accumulation patterns and metabolic pathways in flax roots under salt stress using both tolerant and sensitive genotypes.

MATERIALS AND METHODS

Test material

Flax genotypes R40 (salt-tolerant) and R24 (salt-sensitive), provided by the Gansu Academy of Agricultural Sciences, were used in this study. Plants at the 8–10 leaf stage were treated with 150 mmol L^{-1} NaCl in a hydroponic system for 12 hours. Root samples were then collected with three biological replicates and stored for further analysis. Table 1 displays the grouping of samples and corresponding information

Table 1. The experimental material

Tissue site	Treatment description	Sample name
Flax root	R40 No stress	40ck1d
Flax root	R40 No stress	40ck2d
Flax root	R40 No stress	40ck3d
Flax root	R40 Stress	40xp1d
Flax root	R40 Stress	40xp2d
Flax root	R40 Stress	40xp3d
Flax root	R24 No stress	24ck1d
Flax root	R24 No stress	24ck2d
Flax root	R24 No stress	24ck3d
Flax root	R24 Stress	24xp1d
Flax root	R24 Stress	24xp2d
Flax root	R24 Stress	24xp3d

Sample testing procedures

Biological samples were initially subjected to vacuum freeze-drying to remove moisture while maintaining metabolic integrity. The lyophilized samples were then homogenized into a fine powder using a MM 400 ball mill (Retsch, Germany) at a frequency of 30 Hz for 1.5 min. For the extraction process, 100 mg of the resulting powder was accurately weighed and suspended in 1.0 mL of the extraction solvent. The mixtures were placed in a refrigerator at 4 °C for overnight extraction. To maximize the extraction yield, samples were vortex-mixed three times throughout the incubation period.

Sample clarification and storage

Following overnight extraction, the samples were centrifuged at 10.000 × g for 10 min. The resulting supernatant was carefully aspirated and filtered through a 0.22 μm microporous membrane to remove any remaining debris. The clarified extracts were then transferred into auto-sampler injection bottles and stored under appropriate conditions prior to LC-MS/MS analysis.

Group principal component analysis

Principal component analysis was performed on the samples (including the quality control samples) to provide an initial understanding of the overall metabolic differences among the groups of samples and the extent of variation among the samples within the groups. The PCA results showed a metabolome segregation tendency among the groups, indicating clear differences in metabolite profiles among the sample groups. The results showed that the PCA scores of the four treatments MIX, CK1d, STd, CK2d, and

SSd, which were repeated three times, showed that the treatment groups were aggregated with significant differences and met the test requirements (Figure 1).

RESULTS AND ANALYSIS

Metabolite detection results and analysis

The S plot visually represents the contribution rate of each metabolite to the group. The horizontal axis represents the variable. The farther the data point is from the origin, the greater the contribution of that point to the separation between sample groups. The vertical axis represents the correlation between samples, that is, the reliability of the distinguishing variable. The farther the data point is from the origin, the better the correlation between samples. The points on the "S" curve that are farther from the origin have a greater VIP value and contribute more to classification. In the graph, red indicates metabolites with VIP≥1 and green indicates metabolites with VIP<1. The results show that there are 5 metabolites with a variable greater than 100 and 5 metabolites with a variable less than -100 (Figure 2).

Metabolite types and quantities analysis

The test results showed that a total of 741 metabolites were cumulatively enriched by various treatments, among which the metabolites of CK1-vs-STD, STD-vs-SSD, and CK1-vs-CK2 flavonoids were all the most abundant. STD-vs-SSD had a total of 281 differential metabolites, including 62 flavonoids, the group with the highest number of differential metabolites in the comparison experiment, including 38 flavonoids and 24 flavonols, anthocyanins, isoflavones, and other flavonoids. CK1-vs-STD matched a total of 246 differential metabolites, including 48 flavonoids, which ranked second in the comparison group, including 24 flavonoids and 24 other flavonoids; CK1-vs-CK2 matched a total of 117 differential metabolites, including a total of 41 flavonoids, ranking third in the group, including 27 flavonoids and a total of 17 other flavonoids. In addition, CK2-vs-SSD matched a total of 97 differential metabolites, including a total of 9 flavonoids, including 4 flavonoids and 5 other flavonoids. The top metabolites are flavonoids (including flavonols, anthocyanins, isoflavones, and related compounds) organic acids and their derivatives, amino acids and their derivatives, lipids and phenylpropyl (Table 2).

The flavonoid enrichment quantity of the salt-tolerant resource R40 roots (CK1-vs-STD) before and after salt stress treatment was 5.3 times that of the sensitive resource R24 roots (CK2-vs-SSD). After salt stress, the flavonoids in R40 roots and R24 roots (STD-vs-SSD) were 1.5 times more than those in CK1-vs-CK2 before stress (Table 3).

The results showed that the main organic compounds of flavonoids were glycoside compounds, with 23 STD-vs-SSD glycoside compounds, accounting for 67.6% of the flavonoid metabolites, ranking first among the four groups; 23 CK1-vs-CK2 glycoside compounds, 92.0% of flavonoid metabolites, ranked second; In the CK1-vs-SSTD comparison, there are 14 glycoside compounds in flavonoids, accounting for 58.3% of flavonoid metabolites; CK2-vs-SSD 3 glycoside compounds, 75% of flavonoid metabolites (Table 4).

Flavonoid metabolic pathway diagram

Salt stress treatment enriched 732 metabolites in flax roots, with 332 upregulated and 400 downregulated. Through screening 163 flavonoids, a KEGG pathway map was constructed, highlighting significantly enriched flavonoid pathways under salt stress: 9 were upregulated, 10 downregulated, and 4 contained both upregulated and

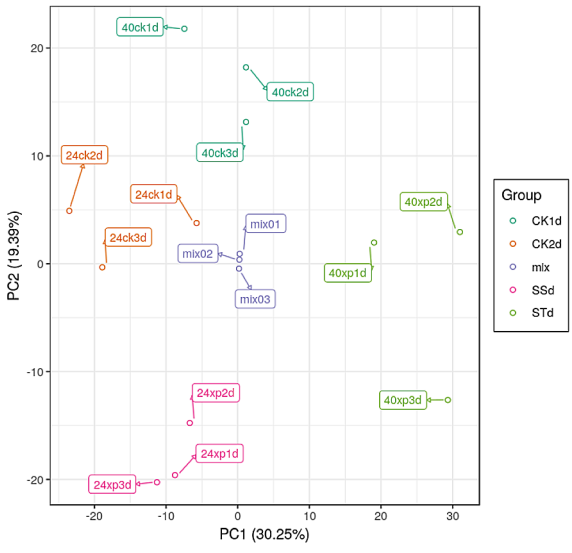

Figure 1. Three-dimensional diagram of principal component analysis of the groups

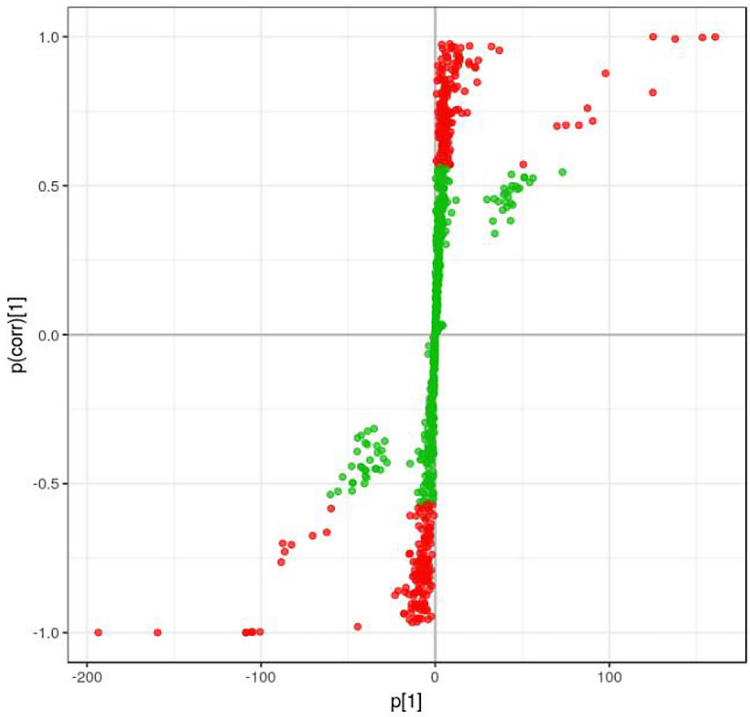

Figure 2. OPLS-DA S-plot

Table 2. The testing results of the metabolites

CK1-vs-STD	Quantity	STD-vs-SSD	Quantity	CK1-vs-CK2	Quantity	CK2-vs-SSD	Quantity
Organic acids and derivatives	36	Organic acids and derivatives	46	Flavonoids	27	Amino acids and derivatives	19
Amino acids and derivatives	33	Flavonoids	38	Phenylpropyl	18	Organic acids and their derivatives	15
Lipids	29	Lipids	33	Organic acids and derivatives	18	Nucleotides and derivatives	12
Flavonoids	24	Phenylpropyl	30	Amino acids and derivatives	7	Lipids	9
Phenylpropanin	18	Amino acids and derivatives	21	Anthocyanins	6	Phenylpropanin	8
Nucleotides and derivatives	14	Nucleotides and derivatives	20	Flavonols	5	Sugar	6
Sugars	11	Alkaloids	13	Polyphenols	4	Others	5
Alkaloids	11	Flavonoids	9	Flavonoids	4	Phenolamine	4
Flavonoids	9	Terpenoids	9	Vitamins and derivatives	4	Flavonoids	4
Flavanone	8	Vitamins and derivatives	9	Lipids	4	Vitamins and Derivatives	4
Vitamins and Derivatives	7	Flavonols	7	Others	4	Flavonoids	3
Others	7	Flavanone	7	Nucleotides and derivatives	3	Alkaloids	3
Phenolamine	7	Polyphenols	6	Quinones	3	Alcohols	1
Terpenoids	6	Phenolamine	6	Alcohols	2	Polyphenols	1
Flavonols	6	Others	6	Phenolamine	2	Anthocyanins	1
Anthocyanin	5	Alcohols	5	Alkaloids	2	Flavonols	1
Polyphenols	5	Anthocyanins	5	Isoflavones	2	Terpenoids	1
Isoflavones	4	Sugars	5	Flavanone	1		
Quinones	4	Quinones	3	Terpenoids	1		
Alcohols	2	Isoflavones	3				

Table 3. Quantities of flavonoid metabolites

CK1-vs-STD	Quantity	STD-vs-SSD	Quantity	CK1-vs-CK2	Quantity	CK2-vs-SSD	Quantity
Flavonoids	24	Flavonoids	38	Flavonoids	27	Flavonoids	4
Other flavonoids	9	Other flavonoids	9	Anthocyanin	6	Other flavonoids	3
Flavonols	6	Flavonols	7	Flavonols	5	Anthocyanins	1
Anthocyanin	5	Anthocyanin	5	Other flavonoids	4	Flavonols	1
Isoflavones	4	Isoflavone	3	Isoflavone	2		

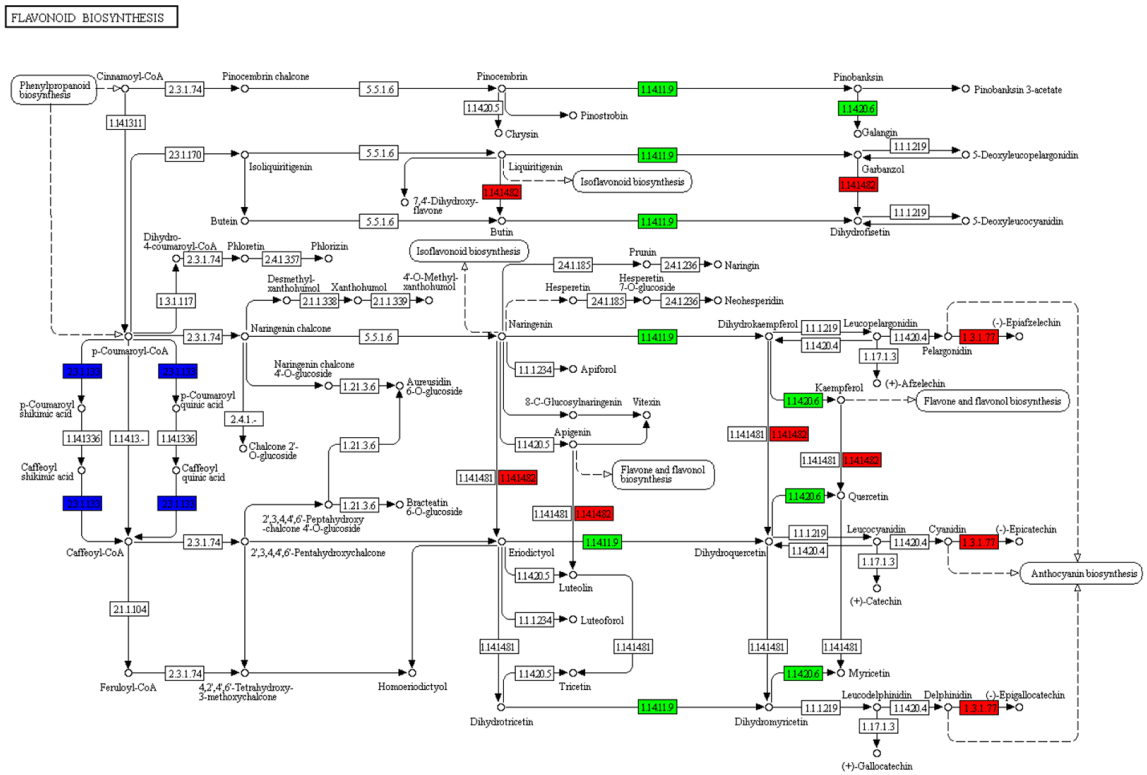

Figure 3. Map of significantly enriched KEGG pathways. KO nodes containing only upregulated differentially expressed genes are marked in red, KO nodes containing only downregulated differentially expressed genes are marked in green, and KO nodes containing both upregulated and downregulated genes are marked in blue

downregulated metabolites (Figure 3). Through screening and integration, we identified 13 flavonoid metabolic pathways, 9 of which were upregulated pathways, and 7 key node metabolic compounds. They are dihydrofisetin, butin, Quercetin, Luteolin, Eriodictyol, Dihydroquercetin, Epiafzelechin (Table 5).

DISCUSSION

Research on flavonoid metabolism in different plants under salt stress

Flavonoids are a class of natural pigments that are widely present in the plant kingdom and have the basic carbon framework of C6-C3-C6 (Choi et al., 2009). Most flavonoids have phenolic hydroxyl groups and are thus acidic, and the strength of the acidity depends on the number and position of the phenolic hydroxyl groups, such as alkyl polyglycosides, which have low surface tension, strong decontamination power, strong broad-spectrum antibacterial activity, and strong salt resistance (Clayton et al., 2018). A systematic study of hydroponic maize under salt stress using biochemical and metabolomic methods has shown that biosynthesis of flavonoids is associated with the removal of reactive oxygen species under salt stress and is the most important metabolic pathway against salt stress, indicating that flavonoids play a very important role in plant salt stress resistance (Rao et al.,

Table 4. Names of flavonoids

CK1-vs-STD	STD-vs-SSD	CK1-vs-CK2	CK2-vs-SSD
6-C-hexam-apigenin O-ferulic hexam-glycoside	6-C-hexanoid-apigenin O-ferulic hexanoside	6-C-hexanoid-apigenin O-ferulic hexanoside	8- c-hexanooside - luteolin o-hexanoside
8-C-hexoside - apigenin O-hexoside - o-hexoside	8-C-hexam-apigenin O-hexam-o-hexamside	8-C-hexose Fund Saint grass flavin o-hexoside	Wheat flavone 5-O-hexanoside
Acillin c-hexanoside	8- c-hexanooside - luteolin o-hexanoside	C-hexosinyl-oxaflutein O-glucosyl hexosaccharide	C-pentosyl apigenin O-salicylhexanoside
C-hexylapigenin O-cafeylhexose	C-hexosinyl-jinshengoxafin O-glucosinyl-glucoside	C-hexosaccharide luteolin O-hexoside	Others (other than glycosides)
C-pentose apigenin O-salicyl-hexosaccharide	C-hexosaccharide luteolin O-hexoside	Acillin c-hexanoside	Poplar
Amycin c-hexaglycoside	Jinshengoxafin 6-c-hexosaccharide 8-c-hexosaccharide o-hexosaccharide	Jinshengoxanthin 6-c-hexyl-8-c-hexyl-O-hexglycoside	
Jinshengoxafin O-malonylhexanoside	Jinshengoxafin 7-O-hexanoside	Jinshengoxanthin 7-O-hexanoside	
Wheat flavone 5-O-hexanoside	Jin Sheng Cao Huang Su 8-C-hexaglycoside	Jinshengoxafin 8-c-hexanoside	
Luteolin o-glucosinylhexanoside	Jinshengoxafin O-malonylhexanoside	Jin Sheng Cao Huang Su O-malleylhexanoside	
8-C-hexosinyl-luteolin O-pentoside	C-hexosyl-luteolin c-pentoside	C-hexosyl-luteolin C-pentoside	
C-hexosyl-apigenin O-pentoside	Wheat flavone 5-O-hexanoside	Wheat flavone 5-O-hexanoside	
Luteolin o-hexosino-O-pentoside	Luteolin C, c-dihexylglycoside	Luteolin C, c-dihexanoside	
Apigenin c-hexosaccharide c-pentoside	Luteolin o-hexglycosyl-O-pentoside	Luteolin O-hexosino-O-pentoside	
Apigenin-6, 8-dic-glucoside	Apigenin c-glucoside	Apigenin c-glucoside	
Others (other than glycosides)	Allonaringin	Allonaringoside	
Nobiletin	8-C-hexose Fund Saint grass flavin o-hexose glycoside	Poplar O-malonyl hexanoside	
Purple ritin	C-hexosy-apigenin O-p-coumaryl hexoside	Acillin O-acetylhexanoside	
Acillin	Luteolin O-glucoside	Wheat flavone o-glycerylhexanoside	
Wheat flavonoids O-erucic acid	Hydroxymethyl flavonoid O-malonylhexanoside	Hydroxymethyl flavonoid 5-O-hexanoside	
Luteolin	Sinophenol c-hexosino-o-hexoside	Naringenin c-hexanoside	
Naringin brassica	8-C-hexosinyl-luteolin O-pentoside	Apigenin 8-c-pentoside	
Acillin	Golden Saint Grass flavin O-glucuronic acid	Apigenin 5-O-glucoside	
Wheat flavone o-erucic acid	Apigenin-6, 8-dic-glucoside	Golden Saint grass flavin o-hexglycosyl-O-rutin	
Luteolin	Others (except glycosides)	Other (other than glycosides)	
Naringin	Nobiletin	Heterophyll	
	Purple rivet	Luteolin	
	Jasminoside		
	Luteolin		
	4,2',4',6' -tetrahydroxychalketone		
	C-hexosyl-luteolin O-erucic acid		
	C-pentosyl-c-hexose apigenin		
	Wheat flavone		
	Luteolin		
	Jinsheng Oxaflutein O-glucuronic acid		
	Camellia officinalis O-glucuronic acid		

2020). Some studies also explored the salt tolerance mechanism of *Lycium barbarum* under salt stress, analyzed the metabolomics changes of *Lycium barbarum*, and found that when exposed to salt stress, the flavonoid content in *Lycium barbarum* increased significantly, indicating that flavonoids have a positive effect on the salt tolerance of *Lycium barbarum* (Li et al., 2018). Some studies found that after 3 days of salt stress treatment, the content of flavonoids apigenin, genistein and genistein in the wood bean increased significantly, suggesting that apigenin, genistein and genistein are involved in the salt stress response process (Chen et al., 2019).

Flavonoid salt resistance mechanism

Most flavonoids bind to glucose or rhamnose to form glycosides, and some exist in a free state or in combination with tannins. Glycosides, also known as glycosides, are generally acetal derivatives formed when the hemiacetal hydroxyl group of a monosaccharide reacts with the hydroxyl group of an alcohol or phenol and loses water. Glycosides are widely distributed in the roots, stems, leaves, flowers and fruits of plants (Watkins et al., 2017). The results of this study show that the main organic compounds of flavonoids in the roots of flax under salt stress are glycoside compounds, accounting for more than 60% of the flavonoid metabolites. A 14 glycoside compounds were enriched in root flavonoids before and after salt stress in the salt-tolerant material R40, which was 4.67 times that of the sensitive material R24 before and after salt stress. This may be one of the key factors for the strong salt tolerance of R40. Flavonoid components are non-enzymatic antioxidants that can effectively enhance the adaptability of plants to adverse stress. Flavonoid components enhance plant resistance to drought and salt stress by blocking oxidation processes, osmotic regulation, and improving photosynthetic efficiency. Abiotic stress causes the production, accumulation and signaling of reactive oxygen species (ROS), and therefore the removal of ROS is a necessary process for plants to respond to abiotic stress. Because most flavonoids have a strong antioxidant scavenging effect on free radicals, they play an effective role in eliminating and preventing ROS production (Li et al., 2019).

Table 5. Upregulates flavonoid metabolic pathways

S#	Metabolic pathways	Status
1	Garbanzol -- dihydrofisetin	Upregulated
2	liquiritigenin - butin	Upregulated
3	naringenin ligand - Eriodictyol	Upregulated
4	kaempferol - Quercetin	Upregulated
5	Apigenin - Luteolin of digitalis	Upregulated
6	Luteolin-5-glucoside dihydrokaempferol-dihydroquercetin	Upregulated
7	Pelargonidin -- Epiafzelechin (C)	Upregulated
8	Delphinidin - Epigallocatechin	Upregulated
9	Cyanidin - Epicatechin	Upregulated

Metabolic mechanism of flavonoids in flax roots under salt stress

Seven key metabolites were identified from the upregulated metabolic pathway in this study: saponin, chrysanthocyanin, quercetin, digitalis flavonoids, and epicatechin, all of which have strong oxidizing properties and thus can provide theoretical support for the salt-alkali resistance pathway. Related studies showed that xanthophyllene has antioxidant activity; the flavonoids rich in purple ritin flavonoids extract are natural antioxidants that can effectively inhibit the generation of free radicals; Dihydroquercetin is a powerful antioxidant that boosts plant immunity and activity and enhances stress resistance; Holy grass phenol is a flavonoid with an o-diphenol hydroxyl group on the B ring, so holy grass phenol is a potentially highly active natural antioxidant; Quercetin, as a good antioxidant, effectively eliminates free radicals, delays cell aging, and provides some protection against oxidative damage to the body; Antioxidant effect of digitalis flavonoids is more than twice that of vitamin E, and it has a strong effect in eliminating superoxide free radicals; Epicatechin has antioxidant, free radical scavenging, and enhanced metabolism functions, among which the antioxidant capacity of epicatechin is believed to be achieved by the combination of phenolic hydroxyl groups in the molecule and free radicals to eliminate free radicals (Yang et al., 2015; Yang et al., 2023). In summary, the upregulated enrichment of these antioxidant flavonoids may be a key factor contributing to the stronger salt tolerance observed in salt-tolerant flax genotypes compared with sensitive ones.

CONCLUSIONS

In this study, high-throughput metabolomic analysis was conducted using the salt-tolerant flax genotype R40 and the salt-sensitive genotype R24. Plants were stressed with 150 mmol L^{-1} NaCl, and root samples were collected after 12 hours. A total of 732 metabolites were detected, of which 332 were upregulated and 400 were downregulated under salt stress. KEGG pathway analysis based on 163 flavonoids revealed 9 upregulated pathways, 10 downregulated pathways, and 4 pathways exhibiting both up- and downregulation. Flavonoids, as non-enzymatic antioxidants, play an important role in enhancing plant adaptability to stress conditions. Seven key metabolites with strong antioxidant properties, including quercetin and epicatechin, were identified. These metabolites contributed to distinguishing between salt-tolerant and salt-sensitive genotypes and highlighted differences in flavonoid metabolism, accumulation, and salt resistance mechanisms.

REFERENCES

1. Chen S., Wu F., Li Y., Qian Y., Pan X., Li F., Wang Y., Wu Z., Fu C., Lin H. (2019). NtMYB4 and NtCHS1 are critical factors in the regulation of flavonoid biosynthesis and are involved in salinity responsiveness. *Frontiers in Plant Science, 10*, 178.
2. Choi S.W., Kwon Y.R., Hossain M.A., Hong S.W., Lee B.H., and Lee H. (2009). A mutation in ELA1, an age-dependent negative regulator of PAP1/MYB75, causes UV- and cold stress-tolerance in Arabidopsis thaliana seedlings. *Plant Science, 176*(5), 678–686.
3. Clayton W.A, Albert N, Thrimawithana A.H, McGhie T.K, Deroles S.C, Schwinn K.E, Warren B.A, McLachlan A.R.G, Bowman J.L, Jordan B.R, and Davies K.M. (2018). UVR8-mediated induction of flavonoid biosynthesis for UVB tolerance is conserved between the liverwort Marchantia polymorpha and flowering plants. *Plant Journal, 96*(3), 503–517.
4. Zhanhai D., Rongying Z., Min W., Zhao D. (2010). Visual analysis of flax research from an international perspective. *Chinese Journal of Flax Industry, 32*(6), 305–307.
5. Jie L., Xiaohua Y. (2019). Multi-omics association analysis of crop stress tolerance. *Journal of Guangdong Agricultural Sciences, 46*(8), 22–28.
6. Li Q., Yu H.M., Meng X.F., Lin J.S., Li Y.J., Hou B.K. (2018). Ectopic expression of glycosyltransferase 76E11 increases flavonoid accumulation and enhances abiotic stress tolerance in Arabidopsis. *Plant Biology, 20*(1), 10–19.
7. Rao M.J., Xu Y., Tang X., Huang Y., Xu Q. (2020). CsCYT75B1, a Citrus cytochrome P450 gene, is involved in accumulation of antioxidant flavonoids and induces drought tolerance in Arabidopsis. *Oxidative Medicine and Cellular Longevity, 9*(2), 161.
8. Saito K., Yonekura-Sakakibara K., Nakabayashi R., Higashi Y., Yamazaki M., Tohge T., Fernie A.R. (2013). The flavonoid biosynthetic pathway in Arabidopsis: structural and genetic diversity. *Plant Physiology and Biochemistry, 72*, 21–34.
9. Tohge T, Watanabe M, Hoefgen R, Fernie AR. (2013). The evolution of phenylpropanoid metabolism in the green lineage. *Critical Reviews in Biochemistry and Molecular Biology, 48*(2), 123–152.
10. Wahocho, N. A., Laghari, R. M. U. R., Talpur, K. H., Jamali, M. F., Ahmad, W., Shah, A. N.,..., Wahocho, S. A. (2023). Seed germination and vegetative growth of petunia (Petunia hybrida) genotypes to salt stress. *Journal of Applied Research in Plant Sciences, 4*(2), 553–565.
11. Watkins J.M., Chapman J.M., Muday G.K. (2017). Abscisic acid-induced reactive oxygen species are modulated by flavonols to control stomatal aperture. *Plant Physiology, 175*(4), 1807–1825.
12. Hengsheng W., Zhimin D., Kelong C., Miaomiao S. (2014). The economic value of flax, its development and application prospects and its cultivation status in Qinghai. *Chinese Journal of Anhui Agricultural Sciences, 7*, 2093–2096.
13. Huanhuan Y. (2015). *Flavonols in plant salt stress responses.* Shandong University.
14. Jie Y. (2023). Metabolic regulation mechanism of flavonoids in mung bean and its biological function against salt stress. Northeast Forestry University, Doctoral Dissertation.
15. Yong Z., Huimin L. (2023). *Flavonoid-mediated analysis of plant stress tolerance*. Molecular Plant Breeding, online first publication.
16. Jinlin Z., Huiru L., Shuyuan G., Suomin W., Huazhong S., Qingqing H., Aike B., Qing M. (2015). Research progress on salt stress adaptation in higher plants. *Acta Prataculturae Sinica, 24*(12), 220–236.
17. Zhang S., Yang J., Li H., Chiang V.L., Fu Y. (2021). Cooperative regulation of flavonoid and lignin biosynthesis in plants. *Critical Reviews in Plant Sciences, 40*(2), 109–126.
18. Yanping Z., Wei Z., Yanni Q., Yaping X. (2019). Effects of NaCl stress on the growth of flax seedlings and their ion absorption and transport. *Gansu Agricultural Science and Technology,* (11), 26–31.

19. Li Z., Zhanhai D., Yi L., Jianping Z., Xiaolong X., Xisen W., Yanping H. (2006). Health benefits and development and utilization of flaxseed. *Chinese Oils and Fats, 31*(3), 71–74.
20. Wei Z., Yanni Q., Jianping Z., Li Z., Limin W., Yaping X., Bin W., Yanping Z. (2019). Comprehensive evaluation of salt tolerance during the germination period of flax resources. *Plant Research, 39*(6), 955–963.
21. Wei Z., Li Z., Jianping Z., Yanni Q., Limin W., Yaping X., Wenjuan L., Zhao P., Minglu Y., Yanping Z. (2022). Joint transcriptomic and metabolomic analysis of the response mechanism of flax roots to salt stress. *Acta Prataculturae Sinica, 39*(6), 1151–1164.
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