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Genome-wide identification and expression analysis of the *Nonexpressor of pathogenesis-related* gene family in sweet potato

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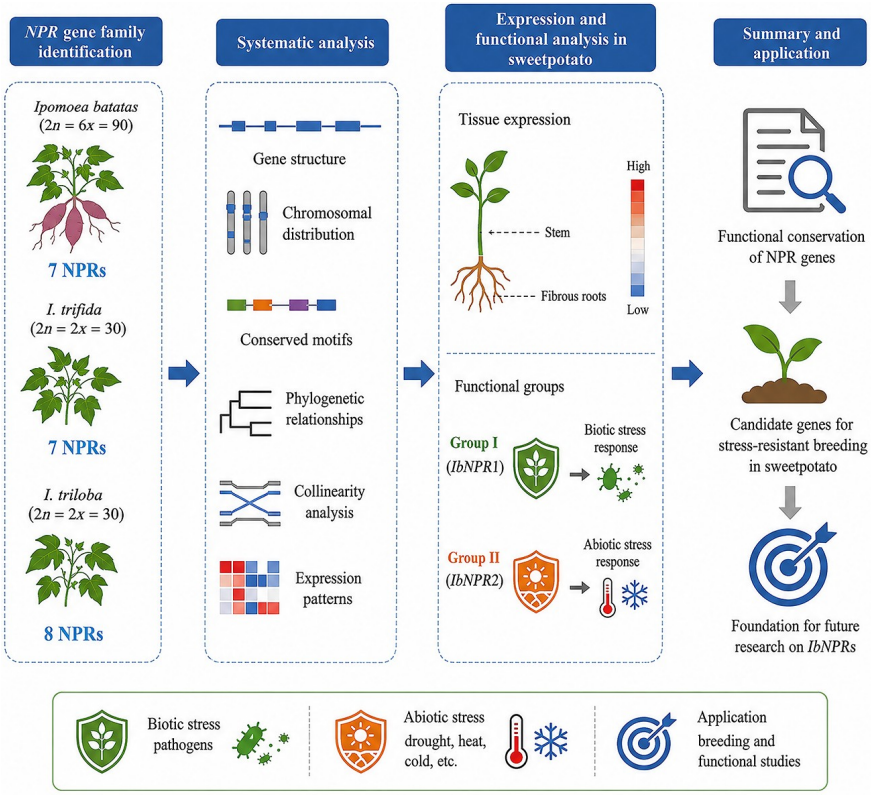
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In Brief

Salicylic acid (SA) receptor nonexpressor of pathogenesis-related (*NPR*) gene family participate in biotic stress and abiotic stress resistance in plants. Seven *IbNPR*s were identified in *Ipomoea batatas* (2*n* = 6*x* = 90). Conserved gene and protein structures suggested a high degree of functional conservation among *NPR* genes. The *IbNPR*s were highly expressed in stem and fibrous roots. The *IbNPR*s especially *IbNPR1* involved in Group I and *IbNPR2* belonged to Group II play a vital role in regulating the response to biotic and abiotic stresses in sweet potato.

Graphical abstract



Highlights

- A total of seven nonexpressor of pathogenesis-related (NPR) genes were identified in the sweet potato genome.
- The IbNPR family was classified into three phylogenetic subgroups with conserved gene structures and protein domains.
- Promoter analysis revealed abundant light-, hormone-, and stress-responsive *cis*-elements in IbNPRs.
- The IbNPRs especially IbNPR1 involved in Group I and IbNPR2 belonged to Group II play a vital role in regulating the response to biotic and abiotic stresses in sweet potato.

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Genome-wide identification and expression analysis of the *Nonexpressor of pathogenesis-related* gene family in sweet potato

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Abstract

The salicylic acid (SA) signaling pathway is a crucial biological process to regulate plants' immune response to pathogens and adverse environments, and the SA receptor nonexpressor of pathogenesis-related (*NPR*) gene family participates in biotic stress and abiotic stress resistance in plants. Although the *NPR*s have been identified in several plant species, their presence and functional roles in sweet potato (*Ipomoea batatas*) remain unexplored. In this research, seven, seven, and eight *NPR*s were identified in *I. batatas* (2*n* = 6*x* = 90), *Ipomoea trifida* (2*n* = 2*x* = 30), and *Ipomoea triloba* (2*n* = 2*x* = 30), respectively. A systematic analysis was performed, including assessments of gene structures, chromosomal distributions, protein physicochemical properties, conserved motifs, phylogenetic relationships, collinearity, and expression patterns. Conserved gene and protein structures suggested a high degree of functional conservation among *NPR* genes. The *IbNPR* genes were highly expressed in stems and fibrous roots. The *IbNPR* genes, especially *IbNPR1* in Group I and *IbNPR2* in Group II, play a vital role in regulating the response to biotic and abiotic stresses in sweet potato. In summary, this research provided a foundation for future research into *IbNPR*s and identified candidate genes for breeding for stress resistance in sweet potato.

Keywords: Sweet potato; Salicylic acid signaling pathway; *Nonexpressor of pathogenesis-related* gene; Biotic stress; Abiotic stress

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Introduction

Salicylic acid (SA) signaling is known to play an essential role in systemic acquired resistance (SAR) and induced systemic resistance (ISR), which can trigger a broad-spectrum and persistent immune response against pathogens and adverse environmental conditions[1,2]. As SA receptors, the *NPR* (*nonexpressor of pathogenesis-related* gene) family plays a master regulatory role in SA signaling pathways and is involved in both biotic and abiotic stress resistance in plants[3–5].

NPR genes encode proteins possessing two conserved functional domains: The ankyrin repeat domain (ANK, PF00023) and the BTB/POZ domain (broad complex, tramtrack, and bric-a-brac/pox virus and zinc finger, PF00651)[6,7]. Between these two domains, the BTB/POZ domain serves as the core functional element, being involved in facilitating NPR1 dimerization and interacting with the TGA domain of transcription factors to regulate downstream gene expression[8,9]. To date, the *NPR* gene family has been identified and characterized in diverse plant species, including *Arabidopsis thaliana* (6), Chinese pear (*Pyrus pyrifolia*) (9), *Camellia sinensis* (4), chili pepper (*Capsicum annuum*) (5), and wheat (*Triticum aestivum*) (17)[6,10–13]. Research on the functions of *NPR* family genes has primarily focused on their responses to biotic and abiotic stresses. In *A. thaliana*, AtNPR1 and AtNPR2 act as key positive regulators of the SA signaling pathway, participating in immune responses, whereas AtNPR3 and AtNPR4 exert opposing functions[5,14]. In rice (*Oryza sativa*), overexpression of *OsNPR1* effectively promotes resistance to rice blast[15]. In wheat, overexpression of *ScNPR1* improves resistance to red mold, whereas in cotton (*Gossypium hirsutum*), overexpression of *AtNPR1* enhances resistance to black root rot[16,17]. In apple (*Malus domestica*), overexpression of *MhNPR1* induces SAR and confers extended resistance to fungal diseases[18]. Knockdown of *SlNPR1* in tomato (*Solanum lycopersicum*) results in reduced drought tolerance[19]. The increase in the expression of SiNPR1 enhances the resistance of sesame bacterial wilt in *Sesamum indicum*[20]. GmERF1 positively regulates *GmNPR1* expression, thereby improving resistance to *Phytophthora* root rot in soybean (*Glycine max*)[21]. By contrast, knockdown of *TcNPR3* confers resistance against *Phytophthora tropicalis* in *Theobroma cacao*[22,23]. In conclusion, the *NPR* genes are crucial for plants' resistance to biotic and abiotic stress.

Sweet potato (*Ipomoea batatas* (L.) Lam., $2n = B_1B_1B_2B_2B_2B_2 = 6x = 90$) is a vital root and tuber crop for maintaining food security in China and is widely applied as food, industrial materials, and bioenergy resources[24,25]. In recent years, because of global climate change and increasing international exchanges, sweet potatoes have been increasingly challenged by biotic stresses (e.g., chlorotic stunt virus, feathery mottle virus, and *Fusarium oxysporum*) as well as abiotic stresses (heat, drought, and salt)[26]. Therefore, it is considered highly important to explore candidate genes that enhance stress resistance in sweet potato. The SA signaling pathway plays a crucial role in plants' immunity, providing resistance against pathogens and adverse environments for sweet potatoes. Moreover, as SA receptors, NPRs are involved in establishing resistance to both biotic and abiotic stresses in plants[1,4]. Consequently, the identification and analysis of the *NPR* gene family is essential for selecting stress-tolerant sweet potato varieties.

In this study, seven *NPR* genes were identified from the genome of *I. batatas*. For these putative genes, we assessed their gene structures and chromosomal distributions, examined their conserved motifs, and performed phylogenetic and collinearity analyses. In addition, their tissue-specific expression patterns and responses to biotic (virus and *Fusarium oxysporum*) and abiotic (heat, drought, and salt) stresses were characterized using quantitative real-time polymerase chain reaction (qRT-PCR) or RNA sequencing (RNA-seq). This research provides an invaluable clue for exploration of the

function of *IbNPR* genes in improving sweet potato's stress tolerance and for accelerating the breeding of stress-resistant sweet potato varieties.

Materials and methods

Identification of NPRs

Protein sequences of *Ipomoea trifida* and *Ipomoea triloba* were retrieved from the *Ipomoea* Genome Hub (https://sweetpotato.uga.edu, accessed on 18 December 2025), and protein sequences of *I. batatas* (cv. Taizhong6) were downloaded from the Sweet Potato Genomics Resource (https://sweetpotato.com/download_genome.html, accessed on 18 December 2025). Hidden Markov model (HMM) profiles of the ankyrin repeat domain (PF00023) and the BTB/POZ domain (PF00651) were obtained from the Pfam database (www.ebi.ac.uk/interpro, accessed on 18 December 2025) to screen for candidate NPR proteins in the three *Ipomoea* species. All putative NPR sequences were validated using NCBI Batch CD-Search programs (Conserved Domain Database [CDD], E value < $1e^{-2}$, www.ncbi.nlm.nih.gov/Structure/cdd/wrpsb.cgi, accessed on 18 December 2025) and SMART (http://smart.embl-heidelberg.de, accessed on 18 December 2025).

Chromosomal localization and property prediction of *NPR*s

The chromosomal positions of *IbNPR*s, *ItfNPR*s, and *ItbNPR*s were determined on the basis of annotated GFF3 files downloaded from the Ipomoea Genome Hub (www.ncbi.nlm.nih.gov/datasets/genome/GCA_002525835.2, accessed on 18 December 2025) and the Sweet Potato Genomics Resource (http://sweetpotato.plantbiology.msu.edu, accessed on 18 December 2025). Visualization was performed using TBtools v2.333 (South China Agricultural University, Guangzhou, China). Collinearity information among *IbNPR*s, *ItfNPR*s, and *ItbNPR*s was obtained using the 'One Step MCScanX Super Fast' module of TBtools[27].

The ExPASy tool (www.expasy.org, accessed on 18 December 2025) was used to compute molecular weight (MW), theoretical isoelectric point (*p*I), instability index, and grand average of hydropathicity (GRAVY) for NPR proteins. Subcellular localizations were predicted using WoLF PSORT (https://wolfpsort.hgc.jp/aboutWoLF_PSORT.html.en, accessed on 18 December 2025).

Phylogenetic analysis of NPRs

Protein sequences from *A. thaliana*, *I. batatas*, *I. triloba*, *I. trifida*, and *O. sativa* were aligned, and a phylogenetic tree was constructed using the neighbor-joining method with 1,000 bootstrap replicates[28]. The phylogenetic tree was visualized with iTOL (http://itol.embl.de, accessed on 19 December 2025).

Gene structures and conserved motifs analysis of *NPR*s

The conserved domain compositions of NPRs were identified using NCBI-CDD (www.ncbi.nlm.nih.gov/Structure/cdd/wrpsb.cgi, accessed on 19 December 2025). Conserved motifs were analyzed with MEME Suite (https://meme-suite.org/meme, accessed on 19 December 2025), with the maximum number of motifs set to 10[29]. TBtools software (v2.333) was used to visualize the conserved domain structures and exon–intron structures of *NPR*s (South China Agricultural University, Guangzhou, China).

Analysis of *cis*-acting elements in promoter regions of *IbNPR*s

Promoter regions approximately 2,000-bp upstream of *IbNPR*s were submitted to PlantCARE (http://bioinformatics.psb.ugent.be/webtools/plantcare/html, accessed on 20 December 2025) for predicting *cis*-elements[30]. TBtools software was used for visualization.

Expression patterns of *IbNPR*s

Transcriptome data of samples with different degrees of virus infection from 'Jishu 25' and 'Jishu 26' storage roots (BioProject number: PRJNA1381310)[31] and inoculation with *Fusarium oxysporum* in the disease-resistant variety 'Jishu 26' and the disease-susceptible variety 'Jishu 35' (unpublished data obtained at our laboratory) were used to calculate the expression patterns of *IbNPR*s. Additionally, transcriptome data of salt-tolerant ('Jishu 26') and salt-sensitive ('NL54') varieties under salt stress, as well as heat-treated 'Xuzishu 8', were obtained from previous studies[32,33]. Heatmaps were generated with TBtools software v2.333 (South China Agricultural University, Guangzhou, China).

The sweet potato variety 'Jishu 25' from the Crop Research Institute, Shandong Academy of Agricultural Sciences, China, was planted and collected for an analysis of tissue-specific expression and drought treatment expression. The primers used in this study are shown in Supplementary Table S1. The methods used for plant treatment and quantitative real-time polymerase chain reaction (qRT-PCR) were those described by Jiang et al.[34].

Statistical analysis

All data were analyzed with a two-tailed Student's *t*-test using SPSS 26.0 (www.ibm.com/support/pages/downloading-ibm-spss-statistics-26). Data are shown as the means ± standard deviation (SD). Transcriptomic data were normalized between 0 and 1 using min–max normalization[35] in heatmaps, which involves subtracting the minimum value of the dataset, dividing the result by the max–min difference, and scaling the data proportionally for better presentation. Heatmaps were generated using TBtools software v2.333[27].

Results

Identification of *NPR*s in sweet potato and its two wild diploid relatives

Three complementary strategies (BLASTp search, HMMER search, and CD-search) were used to comprehensively identify *NPR*s in cultivated sweet potato and its two wild diploid relatives (*I. trifida* and *I. triloba*). We identified seven, seven, and eight *NPR*s in *I. batatas*, *I. trifida*, and *I. triloba*, respectively, designated as *IbNPR*, *ItfNPR*, and *ItbNPR*. Collinearity analysis revealed that all *ItfNPR*s and *ItbNPR*s had orthologous pairs in *I. batatas* (Fig. 1a). Notably, *ItbNPR5* and *ItbNPR6* on Chr 01 shared the same orthologous counterparts in both *I. batatas* and *I. trifida*, suggesting gene loss during evolution. These findings indicate that *NPR* genes are evolutionarily conserved from diploid to hexaploid status and that *I. batatas* exhibits a closer orthologous relationship with *I. trifida* than with *I. triloba*.

The basic characteristics of *IbNPR*s are summarized in Table 1. In *I. batatas*, the coding sequence (CDS) lengths of *IbNPR*s ranged from 1,353 to 1,887 bp, and the genomic lengths varied from 2,318 to 6,926 bp. The deduced proteins contained 450–628 amino acids, with molecular weights of 48.39–62.29 kDa and theoretical *p*I values

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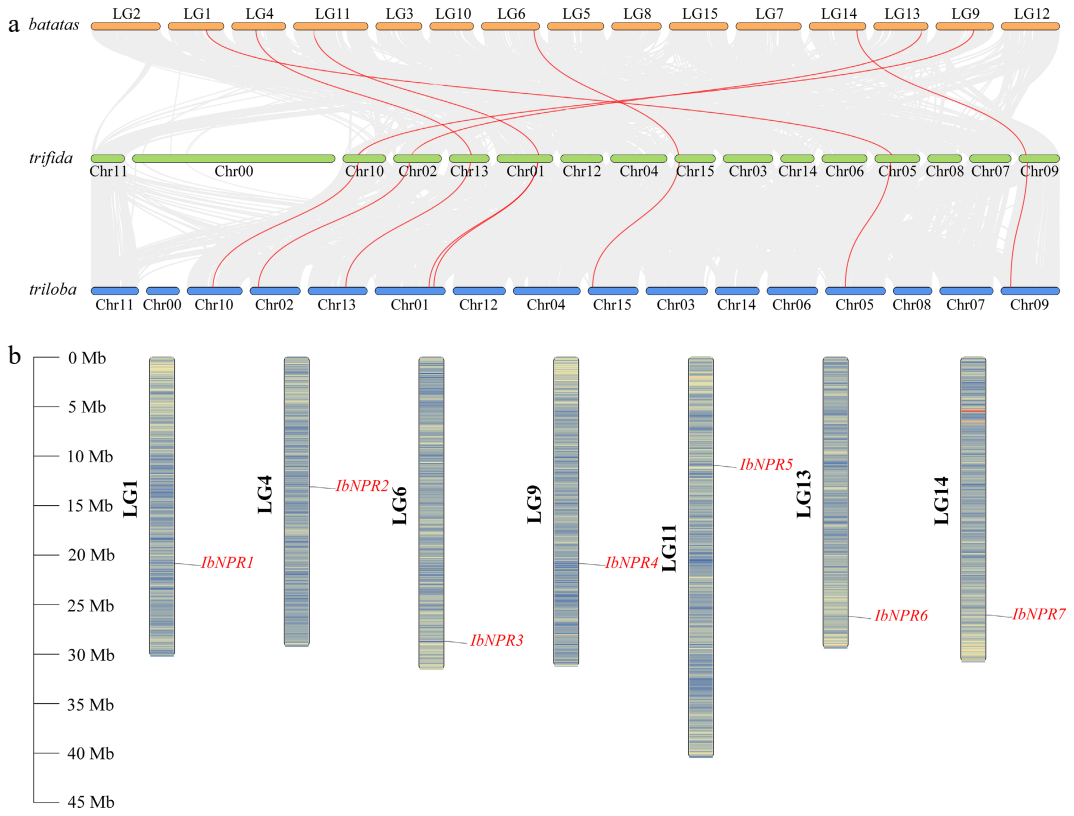


Fig. 1 Chromosomal localization and syntenic relationships of *NPR*s. (a) Syntenic analysis of *NPR*s in *I. batatas*, *I. trifida*, and *I. triloba*. Chromosomes of *I. batatas*, *I. trifida*, and *I. triloba* are shown in different colors. Red curves denote the syntenic relationships among *I. batatas*, *I. trifida*, and *I. triloba NPR*s. (b) Chromosomal localization and distribution of *NPR*s in *I. batatas*. The chromosome numbers are displayed on the left side, and the gene names are displayed on the right side. The relative chromosomal localization of each *NPR* gene is marked on the black line of the right side and indicated in units of Mbp. The stripes on chromosomes represent the density of chromosomes.

Table 1. Characteristics of NPRs in *I. batatas*.

Gene ID	Gene name	Genomic length (bp)	CDS (bp)	Protein size (aa)	MW (kDa)	*p*I	Instability	GRAVY	Subcellular location
g2961.t1	*IbNPR1*	4,577	1,602	533	59.1	6.03	49.12	−0.134	Cytoplasm (10)
g14548.t1	*IbNPR2*	4,136	1,887	628	69.29	6.53	36.88	−0.18	Nucleus (6) and cytoplasm (5)
g24785.t1	*IbNPR3*	3,040	1,353	450	48.39	6.5	48.71	−0.169	Cytoplasm (9)
g36877.t1	*IbNPR4*	5,567	1,614	537	60.21	6.22	35.45	−0.177	Nucleus (5) and cytoplasm (5)
g42979.t1	*IbNPR5*	4,735	1,467	488	52.97	6.22	46.48	−0.117	Nucleus (5) and the cytoplasm (6)
g54830.t1	*IbNPR6*	2,318	1,701	566	62.86	5.69	45.31	−0.178	Cytoplasm (9)
g59006.t1	*IbNPR7*	6,926	1,623	540	60.33	5.58	45.85	−0.199	Nucleus (5.5) and the cytoplasm (6.5)

CDS, coding sequence; MW, molecular weight; *p*I, isoelectric point; GRAVY, grand average of hydropathicity. The numbers between brackets represent the reliability thresholds of the prediction software.

of 5.58–6.53. Most IbNPRs were unstable (instability index > 40), except IbNPR2 and IbNPR4. GRAVY values ranged from −0.117 to −0.199, indicating hydrophilic character. Subcellular localization predictions showed that IbNPR2, IbNPR4, IbNPR5, and IbNPR7 were present in both nucleus and cytoplasm, whereas IbNPR1, IbNPR3, and IbNPR6 were exclusively cytoplasmic (Table 1). Chromosomal localization revealed that IbNPRs were distributed on LG1, LG4, LG6, LG9, LG11, LG13, and LG14, with one gene per chromosome; no NPRs were detected on LG2, LG3, LG5, LG7, LG8, LG10, LG12, or LG15 (Fig. 1b).

Phylogenetic relationship analysis of NPRs in sweet potato and its two diploid wild relatives

A phylogenetic tree included 33 NPRs of five species (i.e., 7 in *I. batatas*, 7 in *I. trifida*, 8 in *I. triloba*, 6 in *A. thaliana*, and 5 in *O. sativa*) was constructed to explore the phylogeny of the NPRs. According to the neighbor-joining method with 1,000 bootstrap replicates, three relatively independent branches existed in the phylogenetic tree. Each branch was determined as one group and all the NPRs were divided into three groups. The specific distributions of NPRs were as follows (presented as total: *I. batatas*, *I. trifida*, *I. triloba*, *A.thaliana*, and *O. sativa*): Group I (6:1, 1, 1, 2, 1), Group II (16:4, 4, 4, 2, 2), and Group III (11:2, 2, 3, 2, 2) (Fig. 2). On the basis of the functions of AtNPRs, we named Group I, Group II, and Group III the AtNPR1/2 group, AtNPR3/4 group, and AtNPR5/6 group, respectively (Fig. 2). Previous studies have reported that AtNPR1 and AtNPR2 are the positive regulators of SAR, and IbNPR1 belongs to the AtNPR1/2 group. On the contrary, AtNPR3 and AtNPR4 act as negative regulators of SAR, and IbNPR2, IbNPR4, IbNPR6, and IbNPR7 are contained in the AtNPR3/4 group[5,14]. In addition, AtNPR5 and AtNPR6

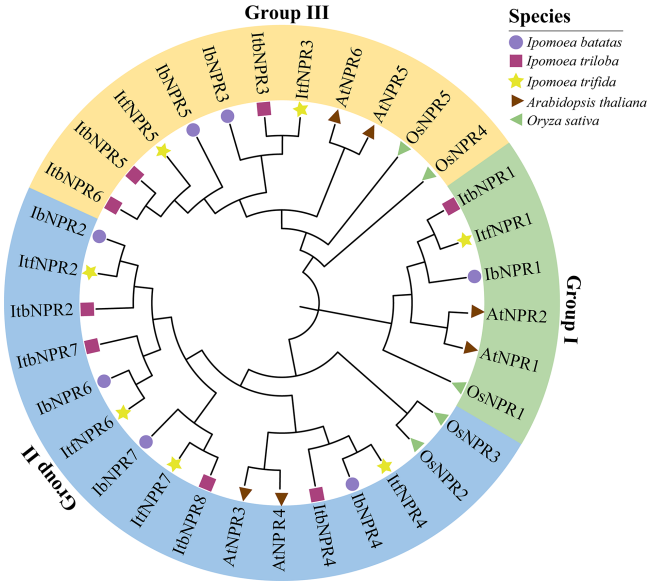


Fig. 2 Phylogenetic analysis of NPRs. Phylogenetic analysis of NPRs in *I. batatas*, *I. triloba*, *I. trifida*, *A. thaliana*, and *O. sativa*. According to the neighbor-joining method with 1,000 bootstrap replicates and the function of AtNPRs, the total of 33 NPRs were divided into three groups (Groups I, II, and III, filled with green, blue and yellow, respectively). The purple circles represent seven IbNPRs in *I. batatas*. The claret squares represent seven ItfNPRs in *I. trifida*. The yellow stars represent eight ItbNPRs in *I. triloba*. The brown triangles represent six AtNPRs in *A. thaliana*. The green triangles represent five OsNPRs in *O. sativa*.

participate in plant development, and IbNPR3 and IbNPR5 are part of AtNPR5/6 group[36]. These results indicated the functional diversification of NPRs and provided preliminary function annotation for these genes.

Conserved motif and exon–intron structure analysis of NPRs

We also examined the conserved domains and motifs to infer the potential functions of NPRs in the three *Ipomoea* species. All NPR proteins contain an *N*-terminal BTB/POZ domain and a central ankyrin repeat domain. Additionally, a PR1-like *C*-terminal region was present only in Group I and Group II proteins (Fig. 3a). Using MEME, we identified 10 conserved motifs in IbNPRs, ItfNPRs, and ItbNPRs (Fig. 3b, Supplementary Fig. S1). All NPRs contained these 10 motifs, but Group I and Group II proteins possessed additional motifs (especially Motifs 7, 8, and 9) compared with Group III.

Exon–intron distribution analysis (Fig. 3b) showed limited variation among *NPR*s. All Group I and Group II *NPR* genes contained four exons, whereas Group III genes had three exons. Importantly, homologous *NPR*s across the three species shared identical exon numbers (Fig. 3c), indicating strong conservation during sweet potato's evolution and suggesting that the NPR1-like *C*-terminal region may play a critical role in stress resistance regulation.

Cis-element analysis in the promoters of *NPR*s in sweet potato

Promoter *cis*-elements are closely linked to gene function. We extracted the 2,000-bp upstream regions of *IbNPR*s and classified

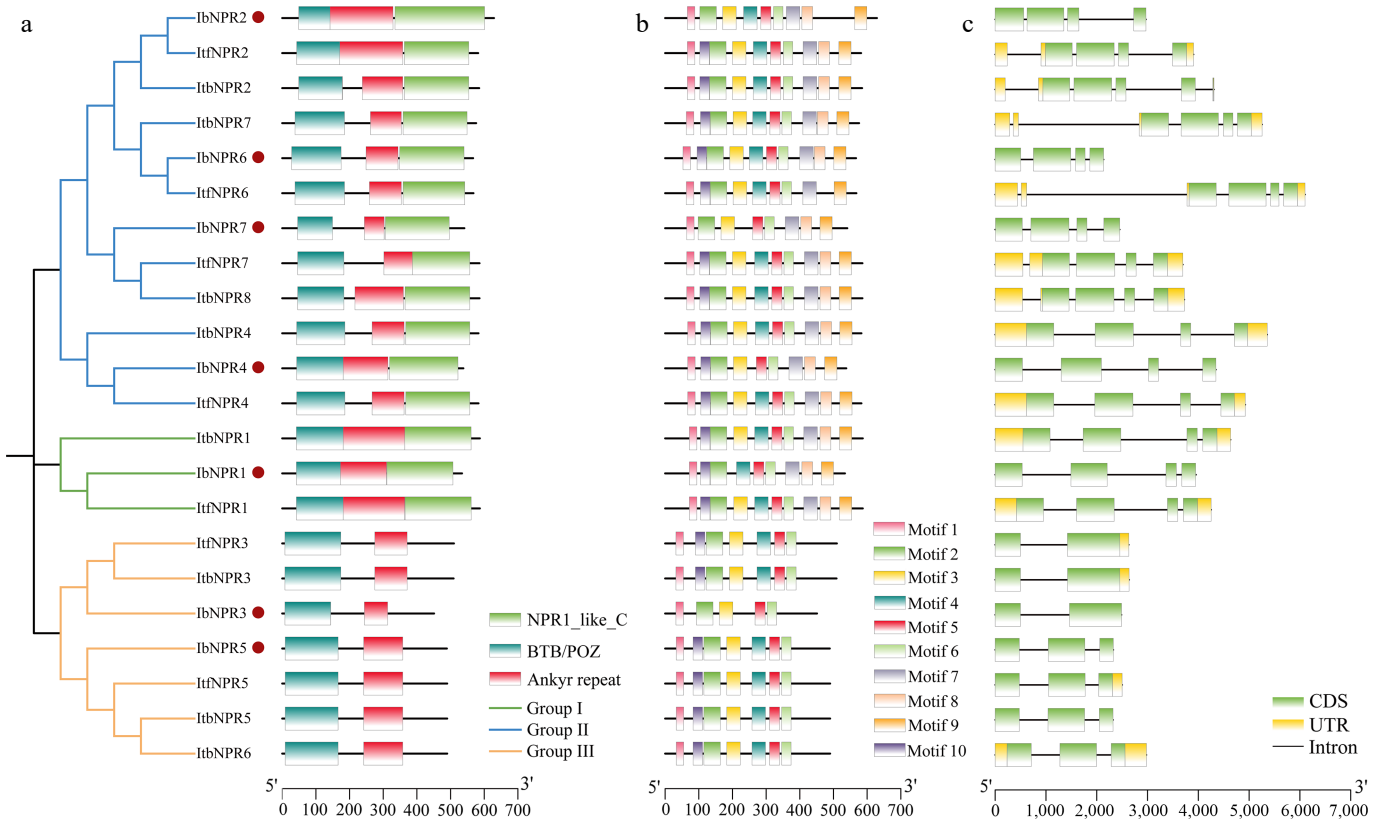


Fig. 3 Conserved motifs and exon–intron structure analysis of *NPR*s in *I. batatas*, *I. trifida*, and *I. triloba*. (a) The phylogenetic tree shows that NPRs are divided into three subgroups, and the three conserved structural domains are shown in different colors. The red circles represent IbNPRs. (b) Ten conserved motifs, shown in different colors. (c) Exon–intron structures of *NPR*s. The green boxes, yellow boxes, and black lines represent untranscribed regions (UTRs), exons and introns, respectively.

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the predicted *cis*-elements into five categories: Core/binding, development, light, hormone, and abiotic/biotic elements (Fig. 4). First, core/binding elements (TATA-box, CAAT-box) were abundant in all *IbNPR* promoters. The promoters of *IbNPR3*, *IbNPR4*, *IbNPR5*, and *IbNPR7* also contained numerous AT-TATA-boxes. Light-responsive elements (AE-box, Box 4, GATA-motif, G-box, TCT-motif) were present in most *IbNPR* promoters. Development-related elements were scarce, suggesting limited roles in growth regulation. Hormone-responsive elements were abundant in *IbNPR* promoters, including abscisic acid (ABA)-responsive (ABRE, ABRE3a, ABRE4), gibberellin (GA)-responsive (P-box, TATC-box), jasmonic acid (JA)-responsive (CGTCA-motif, TGACG-motif), and SA-responsive (TCA-element) motifs (Fig. 4). Most *IbNPR* promoters also harbored abiotic/biotic stress-related elements, such as drought-responsive (MYB, MYC), antioxidant-responsive (ARE, STRE), low-temperature-responsive (ERE, WRE3), and biotic stress-responsive (as-1) elements. Collectively, these findings indicate that *IbNPR*s are primarily involved in regulating hormone crosstalk and abiotic/biotic stress defense in sweet potato.

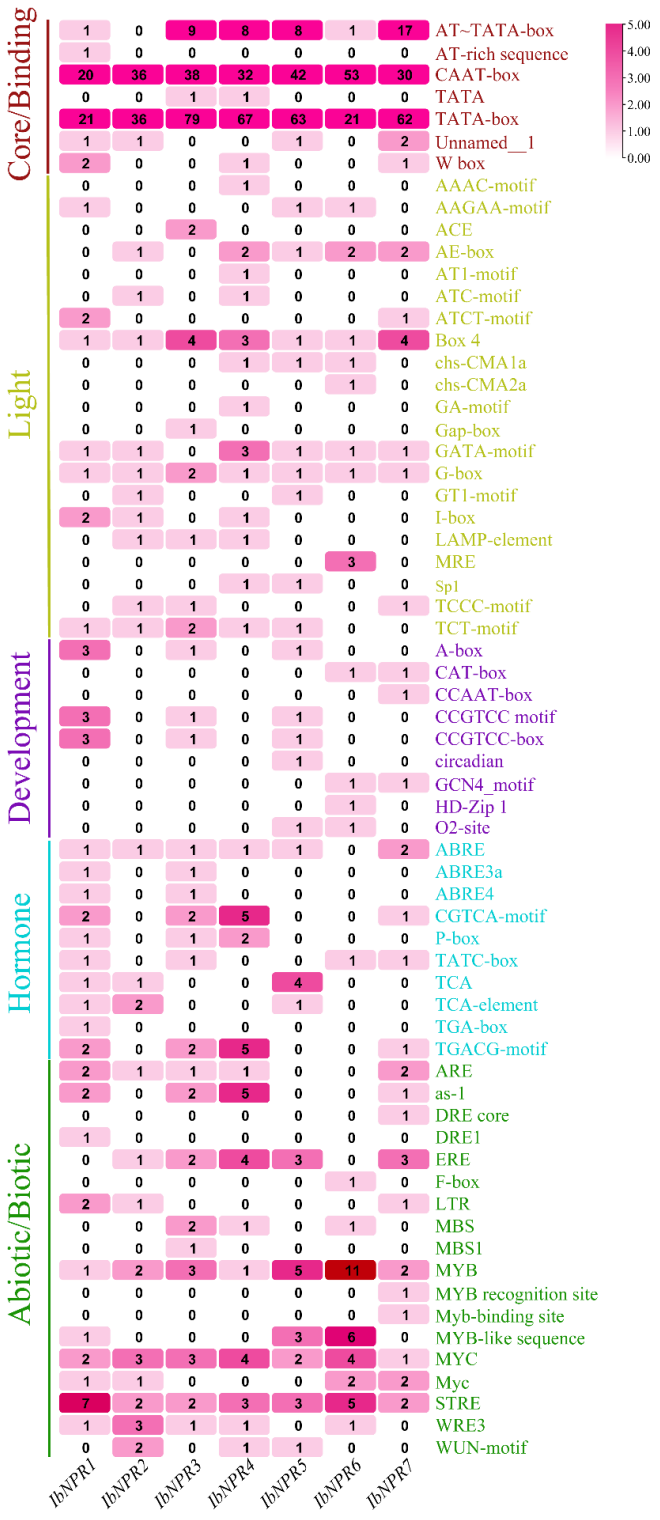


Fig. 4 *Cis*-element analysis in the promoters of *NPR*s from *I. batatas*. The *cis*-elements were divided into five broad categories. The degree of red colors represents the number of *cis*-elements in the promoters of *NPR*s.

Expression analysis in various tissues in sweet potato

In order to obtain insights about the functions of *IbNPR*s in different tissues, qRT-PCR was carried out to calculate the expression patterns of leaves, shoot apices, stems, fibrous roots, and storage roots of sweet potato. The results showed that all *IbNPR*s had highest expression levels in the stems (*IbNPR1*, *IbNPR3* and *IbNPR6*) or fibrous roots (*IbNPR2*, *IbNPR4*, *IbNPR5*, and *IbNPR7*). In addition, *IbNPR2*, *IbNPR6*, and *IbNPR7* also showed strong expression values in shoot apices, and both *IbNPR1* and *IbNPR2* were expressed highly in storage roots (Fig. 5).

Expression analysis of *IbNPR*s in response to biotic stress

To determine the potential effects of *IbNPR*s in response to biotic stress, the RNA-seq data with different degrees of virus infection in 'Jishu 25' and 'Jishu 26' storage roots (BioProject number: PRJNA1381310)[31] and inoculation with *F. oxysporum* in the disease-resistant variety 'Jishu 26' and the disease-susceptible variety 'Jishu

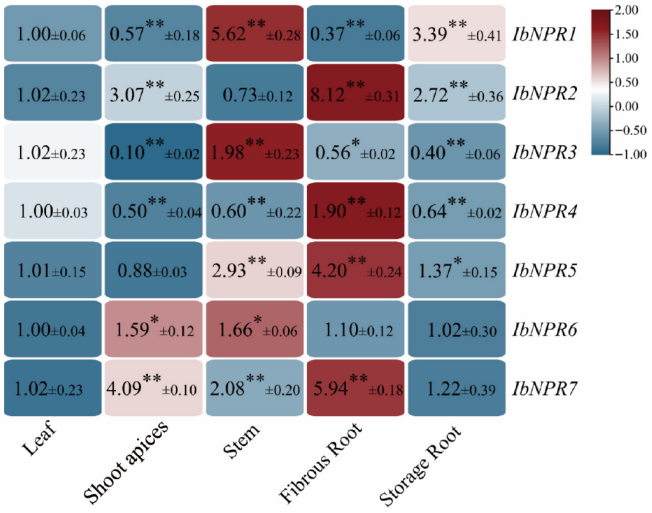


Fig. 5 Expression analysis of *NPR*s in different tissues of *I. batatas*. Expression analysis of *IbNPR*s in the leaves, shoot apices, stems, fibrous roots, and storage roots of *I. batatas*. The values were determined by qRT-PCR from three biological replicates consisting of pools of three plants, and the results were analyzed using the comparative C_T method. The expression level of leaves is set as '1'. Fold change ± SD is shown in the boxes. Asterisks (**) and (*) indicate significant differences at $p < 0.01$ and $p < 0.05$, respectively, based on Student's *t*-test compared with leaves.

35' (unpublished data obtained at our laboratory) were analyzed. In the transcriptomes with different virus content, *IbNPR1*, *IbNPR2*, *IbNPR3*, and *IbNPR5* were highly expressed in 'Jishu 25' and 'Jishu 26' storage roots with a low degree of viral infection. *IbNPR4*, *IbNPR6*, and *IbNPR7* showed higher expression levels in 'Jishu 25' and 'Jishu 26' storage roots with a high degree of viral infection (Fig. 6a). In the transcriptome after inoculation with *F. oxysporum*, all *IbNPR*s were upregulated in the disease-resistant variety 'Jishu 26'. *IbNPR1* and *IbNPR4* exhibited significantly higher expression levels in 'Jishu 26' and 'Jishu 35' compared with the control. *IbNPR2*, *IbNPR3*, and *IbNPR6* were only highly expressed in the disease-resistant line 'Jishu 26' compared with the control. *IbNPR5* and *IbNPR7* showed lower expression levels or had no obvious trend in expression in 'Jishu 26' and 'Jishu 35' compared with the control (Fig. 6b). The results suggest that *IbNPR*s partake in resistance to viruses and *F. oxysporum*.

Expression analysis of *IbNPR*s under drought, salt, and heat stresses

To investigate the potential roles of *IbNPR*s in the response to drought, salt, and heat stress, the expression patterns of *IbNPR*s were analyzed using qRT-PCR in 'Jishu 25' under polyethylene glycol (PEG) 6000 stress at 0, 3, 6, 12, 24, and 48 h after drought treatment. The RNA-seq data of the salt-sensitive variety 'NL54' and the salt-tolerant line 'Jishu 26' under NaCl stress at 0, 0.5, 6, and 12 h after salt treatment, and of 'Xuzishu 8' after heat stress treatment were used to calculate the expression of *IbNPR*s[32,33]. Under PEG6000 stress, *IbNPR1*, *IbNPR2*, *IbNPR5*, *IbNPR6*, and *IbNPR7* were upregulated and *IbNPR3* and *IbNPR4* were downregulated in 'Jishu 25' (Fig. 7a). Under NaCl stress, *IbNPR6* was upregulated in both 'Jishu 26' and 'NL54', *IbNPR4* and *IbNPR5* were upregulated only in 'Jishu 26', *IbNPR1* and *IbNPR7* were downregulated in both 'Jishu 26' and 'NL54' and others showed no significant trend (Fig. 7b). Under heat stress, *IbNPR1*, *IbNPR2*, *IbNPR3*, and *IbNPR7* were upregulated compared with the control, and others showed a downregulated trend compared with the control (Fig. 7c). The results implied that *IbNPR*s take a more important part in the response to drought and heat stresses than in that to salt stress.

Discussion

NPRs were conserved during the evolution of sweet potato and had diversity with functionality

With the recent advances in genomics, identification and characterization of the *NPR* gene family have been performed in various plants; for example, 6 in *A. thaliana*, nine in Chinese pear, 4 in *Camellia sinensis*, 5 in chili pepper, and 17 in wheat[6,10–13]. In this research, we identified seven, seven and eight *NPR*s in *I. batatas*, *I. trifida*, and *I. triloba*, respectively. There was one more *ItbNPR*s than *IbNPR*s and *ItfNPR*s. Collinearity analysis found that gene loss occurred during the process of evolution, and *I. batatas* has a closer evolutionary relationship with *I. trifida* (Fig. 1a). Further chromosomal localization and the phylogenetic tree of *NPR*s revealed that all IbNPRs had pairs of orthologs in *I. trifida* and *I. triloba*, and the homologs among *I. batatas*, *I. trifida*, and *I. triloba* were located on similar sites (Figs. 1b and 2). Gene structures are typically conserved among homologous genes of a gene family[37]. Furthermore, the conserved structural domains, motifs, and exon–intron distributions indicated that all homologous NPRs had the similar distributions of conserved domains, motifs and exons–introns in *I. batatas*, *I. trifida*, and *I. triloba* (Fig. 3). These results suggested that sweet potato has conserved phylogenetic relationships with its diploid ancestors.

NPR family genes have been thoroughly studied in *A. thaliana*, with six members identified. Among them, *AtNPR1* and *AtNPR2* are key positive regulators in the SA signaling pathway, involved in immune responses in *A. thaliana*. In contrast, *AtNPR3* and *AtNPR4* play opposing roles[5,14]. *AtNPR5* and *AtNPR6* are involved in regulating the growth of lateral branches and floral organs in *A. thaliana*[36]. According to the functions of the AtNPRs, IbNPRs, ItfNPRs, and ItbNPRs were divided into three groups (Group I: AtNPR1/2 group; Group II: AtNPR3/4 group; Group III: AtNPR5/6 group), and Group III lacked the NPR1-like *C*-terminal region with less conserved motifs and exons (Figs. 2 and 3). These results proved that NPRs have functional diversity, and NPR1-like *C*-terminal region may play a crucial role in the regulation of stress resistance.

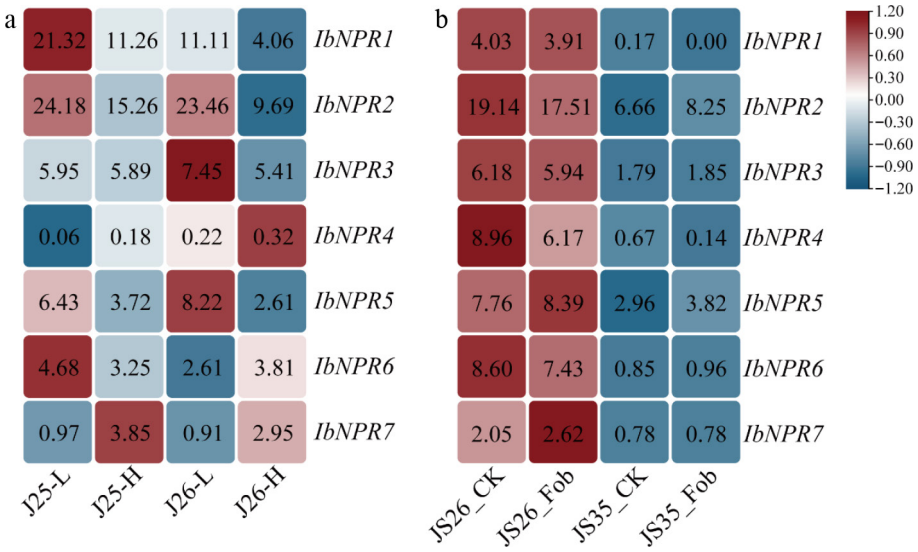


Fig. 6 Expression analysis of *IbNPR*s under biotic stresses. (a) Expression analysis of *IbNPR*s at different degrees of viral infection in 'Jishu 25' (J25) and 'Jishu 26' (J26) storage roots (L, low degrees of virus infection; H, high degrees of virus infection). The fragments per kilobase per million mapped reads (FPKM) values are shown in the boxes. (b) Expression analysis of *IbNPR*s with inoculation with Fob (*F. oxysporum*) in the disease-resistant variety 'Jishu 26' (JS26) and the disease-susceptible variety 'Jishu 35' (JS35). The FPKM values are shown in the boxes.

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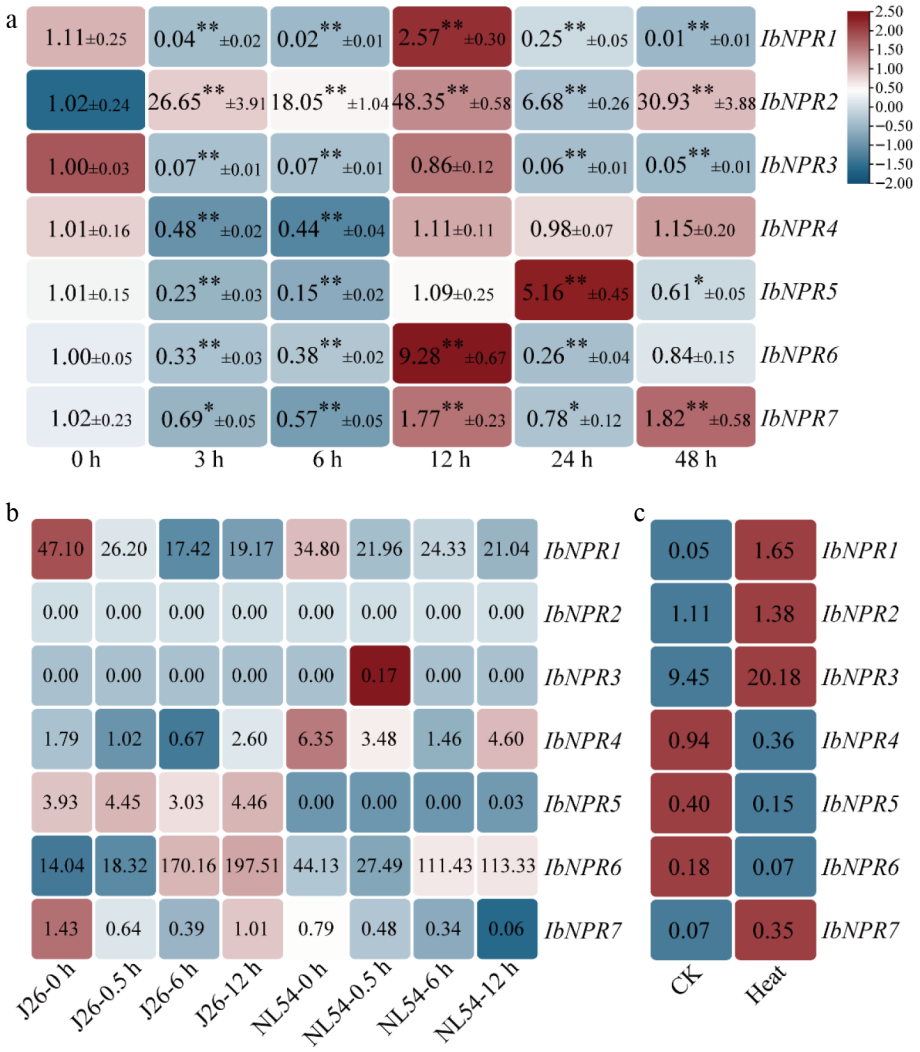


Fig. 7 Expression analysis of *IbNPR*s under drought, salt, and heat stresses. (a) Expression analysis of *IbNPR*s in 'Jishu 25' under PEG6000 stress. The values were determined by qRT-PCR from three biological replicates consisting of pools of three plants, and the results were analyzed using the comparative C_T method. The expression level of 0 h is set as '1'. Fold change ± SD is shown in the boxes. Asterisks (**) and (*) indicate significant differences at $p < 0.01$ and $p < 0.05$, respectively, based on Student's *t*-test compared with 0 h. (b) Expression analysis of *IbNPR*s in the salt-sensitive variety 'NL54' and the salt-tolerant line 'Jishu 26' (J26) under NaCl stress. (c) Expression analysis of *IbNPR*s in 'Xuzishu 8' under heat stress. The FPKM values are shown in boxes.

NPRs regulate the response to biotic and abiotic stresses in sweet potato

SA is a phenolic plant hormone that is widely present in plants and significantly regulates plants' stress defenses[38,39]. The genes of the *NPR* family act as genuine transcriptional co-factors in the SA signal transduction pathway to affect resistance against biotic and abiotic stresses[5].

In *A. thaliana*, overexpressing *AtNPR1* could enhance resistance against bacterial pathogens and oomycete pathogens such as *Pseudomonas syringae* and *Phytophthora infestans* (causing late blight). In crops, fungal diseases can seriously affect yield and even lead to crop failure, but *NPR* genes could enhance plants' immune response and resistance to diseases, thereby ensuring yield. In rice, overexpression of *OsNPR1* effectively promotes plants' resistance to rice blast[15]. Overexpressed *ScNPR1* in wheat could improve the resistance to red mold. In cotton, overexpression of *AtNPR1* enhanced the resistance to cotton black root rot[16,17]. In apple, overexpression of the *MhNPR1* gene induced SAR and exhibited extended resistance to fungal diseases[18]. Silencing *SlNPR1* in tomato led to a decrease in drought tolerance[19].

Viral diseases are significant pathogens affecting the yield and quality of sweet potatoes[40,41]. The accumulation of viruses leads to severe declines in both the yield and quality of seed roots and impair their sprouting capability[42]. *F. oxysporum* is a major pathogenic fungus that causes some diseases in sweet potato, which decrease the yield and quality of sweet potato[26]. In this research, *IbNPR1*, *IbNPR2*, *IbNPR3*, and *IbNPR5* were highly expressed in 'Jishu 25' and 'Jishu 26' storage roots with a low degree of virus infection (Fig. 6a). All *IbNPR*s showed higher expression in the disease-resistant variety 'Jishu 26' than in the disease-susceptible variety 'Jishu 35'. *IbNPR1*, *IbNPR2*, *IbNPR3*, *IbNPR4*, and *IbNPR6* were expressed highly in the disease-resistant line 'Jishu 26' compared with the control (Fig. 6b). Therefore, *IbNPR1*, *IbNPR2*, and *IbNPR3* play an important part in the response to biotic stress and provide the candidate genes for breeding disease-resistant sweet potato.

In recent years, sweet potato cultivation has shifted towards marginal lands and low-quality soils, making them more susceptible to abiotic stresses such as drought and salt[43]. Under PEG6000 stress, *IbNPR1*, *IbNPR2*, *IbNPR5*, *IbNPR6*, and *IbNPR7* were upregulated in 'Jishu 25' (Fig. 7a). Under NaCl stress, only *IbNPR6* was upregulated in both 'Jishu 26' and 'NL54' (Fig. 7b). Under heat stress,

IbNPR1, *IbNPR2*, *IbNPR3*, and *IbNPR7* were upregulated compared with the control (Fig. 7c). These results indicated that *IbNPR*s, especially *IbNPR1*, *IbNPR2*, and *IbNPR7*, have a significant influence on the response to drought and heat stress, and *IbNPR6* was effective in responding to drought and salt stress.

In summary, *IbNPR1*, which is in Group I (AtNPR1/2 group), plays an important role in positively regulating the response to biotic and abiotic stress in sweet potato, which was consistent with the positive regulation of plants' immune response by AtNPR1 and AtNPR2 in *A. thaliana*. It is an important candidate gene for breeding for resistance in sweet potato. Interestingly, although we grouped IbNPRs according to the functions of AtNPRs in the phylogenetic tree, the RNA-seq data and qRT-PCR analysis revealed that many *IbNPR*s belonging to Group II (AtNPR3/4 group) and Group III (AtNPR5/6 group) also enhanced sweet potato's resistance to biotic and abiotic stress, such as *IbNPR2* in Group II. This may be related to the changes in the promoter structure of *IbNPR*s during the evolutionary process. In our study, all promoters of *IbNPR*s contained abundant hormone-responsive elements and abiotic/biotic stress-responsive elements, which allowed *IbNPR*s to play a more active role in responding to biotic and abiotic stress. This research provides a foundation for future research and crop improvement strategies for sweet potatoes.

Conclusions

In this study, seven, seven and eight *NPR*s were identified in the cultivated sweet potato and its two diploid wild relatives *I. trifida* and *I. triloba*, respectively. A systematic analysis was performed on *IbNPR*s' gene structures and distributions, the proteins' physicochemical properties and conserved motifs, and the expression patterns, along with phylogenetic and collinearity analyses. All homologs of IbNPRs, ItfNPRs, and ItbNPRs showed the similar conserved domains and motifs in the proteins, and the same exon structures, which suggested functional conservation among the NPRs. The *IbNPR*s were upregulated in stems and fibrous roots. *IbNPR1*, *IbNPR2*, and *IbNPR3* played a crucial part in resistance to biotic stress, and *IbNPR1*, *IbNPR2*, and *IbNPR7* had a significant influence on the response to drought and heat stress. However, *IbNPR*s were not effective in salt stress resistance. In conclusion, *IbNPR1* in Group I and *IbNPR2* in Group II could be used as candidate genes to improve the resistance to biotic and abiotic stresses in sweet potato.

Author contributions

The authors confirm their contributions to the paper as follows: study conception and design: Jiang Z; data collection: Jiang Z, Du T; analysis and interpretation of the results: Jiang Z, Zhou Y; draft manuscript preparation: Jiang Z, Qin Z, Li A, Wang Q, Hou F; funding acquisition: Jiang Z, Hou F. All authors reviewed the results and approved the final version of the manuscript.

Data availability

The authors declare that the data supporting the findings of this study are available within the paper and the Supplementary Material. The RNA-seq data are available in the National Center for Biotechnology Information (NCBI). The RNA-seq data of inoculation with *F. oxysporum* in the disease-resistant variety 'Jishu 26' and the disease- susceptible variety 'Jishu 35', and the datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Conflict of interest

The authors declare that they have no conflict of interest.

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