Wang, H., Wan, Y., Buchner, P. H., King, R., Ma, H. and Hawkesford, M. J. 2020. Phylogeny and gene expression of the complete NITRATE TRANSPORTER 1/PEPTIDE TRANSPORTER FAMILY (NPF) in Triticum aestivum L. *Journal of Experimental Botany.* p. eraa210.

Summary of potential functions of identified *NPF* genes in *Arabidopsis* and rice and their phylogeny orthologs in wheat

NPF subfamily	Gene name (Old name)	Species	Gene expression responses	Substrates	Function in planta and phenotype	References	Wheat orthologs
1	*AtNPF1.1 (NRT1.12)*	**Arabidopsis thaliana**	No affection by N sources	NO3-, ABA, GA$_{1/3/4}$, Ja-Ile	Nitrate allocation to young leaves; *atnpf1.1,* impairs growth at high nitrate supply.	1	*TaNPF1.1*
	AtNPF1.2 (NRT1.11)	**Arabidopsis thaliana**	No affection by N sources	NO3-, GA$_{1/3/4}$, Ja-Ile	Nitrate allocation to young leaves; *atnpf1.12* impairs growth at high nitrate supply.	1	
	OsNPF1.3	**Oryza sativa**	Mycorrhiza inducible	ND	ND	65	
2	*AtNPF2.1*	**Arabidopsis thaliana**	ND	GA24	ND	64	*TaNPF2.10; TaNPF2.11; TaNPF2.12; TaNPF2.13; TaNPF2.14; TaNPF2.15; TaNPF2.16*
	AtNPF2.3	**Arabidopsis thaliana**	Barely affection by salt stress	NO3-, GA$_{1/3/4}$	Root-to-shoot nitrate transport under salinity; *atnpf2.3* reduces shoot biomass under salt stress.	2	
	AtNPF2.4	**Arabidopsis thaliana**	Repression by NaCl and ABA	Chloride, GA$_{1/3/4}$, Ja-Ile	Xylem loading of chloride under salinity; Knock down of *AtNPF2.4* reduces chloride accumulation in shoot.	3	
	AtNPF2.5	**Arabidopsis thaliana**	Induction by NaCl	ABA, GA$_{1/3/4}$	Chloride efflux from root.	4	
	AtNPF2.6	**Arabidopsis thaliana**	ND	GA1/4, Ja-Ile	ND	5	
	AtNPF2.7 (NAXT1)	**Arabidopsis thaliana**	Induction by low pH (pH=3) at protein level	NO3-, GA$_{1/3/4}$, Ja-Ile	Nitrate efflux in roots under acidic conditions.	6	
	AtNPF2.9 (NRT1.9)	**Arabidopsis thaliana**	Induction by long-term nitrate exposure	NO3-, 4MTB	Phloem loading of nitrate in root; *atnpf2.9* enhances plant growth under high-nitrate conditions.	7	*TaNPF2.1; TaNPF2.2; TaNPF2.3; TaNPF2.6; TaNPF2.7; TaNPF2.8; TaNPF2.9*
	AtNPF2.10 (GTR1)	**Arabidopsis thaliana**	Induction by wound and MeJA	NO3-, 4MTB, 8MTO, GA$_{1/3/4}$, Ja-Ile	GLS translocation to seeds. JA-Ile translocation to undamaged leaf; *atnpf2.10* reduces fertility, and *atnpf2.10, atnpf2.11* reduces seed weight and yield.	8-11	
	AtNPF2.11 (GTR2)	**Arabidopsis thaliana**	No affection by wound	NO3-, 4MTB, 8MTO, GA$_{3/4/24}$	GLS translocation to seeds; *atnpf2.10atnpf2.11* reduces seed weight and yield.	8, 9, 63	
	OsNPF2.2 (OsPTR2)	**Oryza sativa**	Induction by nitrate, mycorrhiza inducible	NO3-	Root-to-shoot nitrate transport; *osnpf2.2* shows severely dwarfism, short panicle, low seed setting, and abnormal seed development.	12, 65	
	AtNPF2.12 (NRT1.6)	**Arabidopsis thaliana**	Induction by N starvation	NO3-, GA$_{1/3/8/24}$	Nitrate transport to embryo. N cycling under low N stress; *atnpf2.12* reduces leaf area under low N condition and nitrate accumulation in seeds, and increases seed abortion rate.	13, 14, 63	*TaNPF2.4; TaNPF2.5*
	AtNPF2.13 (NRT1.7)	**Arabidopsis thaliana**	Induction by N starvation	NO3-, 4MTB, GA$_{1/3/4/19/24}$, Ja-Ile	Nitrate remobilization from old to young leaves; *atnpf2.13* shows retarded growth upon N starvation.	15, 63	
	AtNPF2.14	**Arabidopsis thaliana**	ND	4MTB	ND	5	
	OsNPF2.4	**Oryza sativa**	Affection by nitrate, ammonium and potassium differentially in tissues and by development	NO3-	Acquisition and long-distance transport of nitrate; *osnpf2.4* reduces plant height, panicle length, seed-setting rate and yield.	16	*TaNPF2.6*
3	*AtNPF3.1 (Nitr)*	**Arabidopsis thaliana**	Repression by GA, induction by ABA and *E. necator* pathogen inoculation	NO3-, NO2, ABA, GA$_{1/3/4/8/20/24}$, Ja-Ile	Nitrite accumulation in leaves. GA accumulation and responses; Overexpression of *AtNPF3.1* delays germination, and reduces plant growth. *Atnpf3.1* mutant is affected in hypocotyl elongation and germination under low N conditions.	17-19, 63	*TaNPF3.1*
4	*AtNPF4.1 (AIT3)*	**Arabidopsis thaliana**	ND	ABA,GA$_{1/3/4/8/19/20/24}$, Ja-Ile	ND	5, 63	*TaNPF4.1*
	AtNPF4.2 (AIT4)	**Arabidopsis thaliana**	ND	ABA, GA1/3	ND	5	
	AtNPF4.5 (AIT2)	**Arabidopsis thaliana**	ND	ABA	ND	5	
	AtNPF4.6 (NRT1.2/AIT1)	**Arabidopsis thaliana**	Repression by nitrate in short time (1h) and induction afterwards. Increased promoter activity by ABA	NO3-, ABA, GA$_{1/3/4/8/24}$, Ja-Ile	Nitrate uptake in roots. ABA-mediated inhibition of seed germination. N cycling under low N stress; *atnpf4.6* reduces leaf area under adequate N condition, and has more flower stalks under low N condition. Ait1/nrt1.2 mutants are less sensitive to exogenuously applied ABA. Excess water loss from open stomata.	14, 20-22, 63	
	OsNPF4.1 (SP1)	**Oryza sativa**	ND	ND	*osnpf4.1* severely reduces panicle length, seed size and number.	23	*TaNPF4.9*
	OsNPF4.12	**Oryza sativa**	Mycorrhiza inducible	ND	ND	65	*TaNPF4.10*
5	*AtNPF5.1*	**Arabidopsis thaliana**	ND	ABA, GA$_{1/3/4}$, JA-Ile	ND	5	*TaNPF5.1 TaNPF5.2*
	AtNPF5.2 (PTR3)	**Arabidopsis thaliana**	Induction by amino acids, wound, salt, SA, MeJA, ABA, *hrpA*	ABA, GA$_{1/3/4}$, di-peptides	Biotic and abiotic stresses response; *atnpf5.2* reduces tolerance to salt stress in germination rate, shows faster disease proceeding inoculated by *E. carotovora.*	24, 25	*TaNPF5.3-TaNPF5.7*
	AtNPF5.3	**Arabidopsis thaliana**	ND	ABA	ND	5	
	AtNPF5.5	**Arabidopsis thaliana**	ND	NO3-	N accumulation in embryo; *atnpf5.5* reduces N content in embryo.	26	*TaNPF5.8; TaNPF5.9*
	AtNPF5.6	**Arabidopsis thaliana**	ND	GA1/4	ND	5	
	AtNPF5.7	**Arabidopsis thaliana**	ND	ABA, GA$_{1/3/4}$, JA-Ile	ND	5	
	AtNPF5.10	**Arabidopsis thaliana**	ND	NO3-	ND	5	*TaNPF5.11-TaNPF5.34*
	AtNPF5.11	**Arabidopsis thaliana**	ND	NO3-	Vacuolar nitrate efflux (together with *AtNPF5.12* and *AtNPF5.16*) - modulation of nitrate allocation between roots and shoots via vacuolar nitrate release.	27	
	AtNPF5.12	**Arabidopsis thaliana**	ND	NO3-	Vacuolar nitrate efflux (together with *AtNPF5.11* and *AtNPF5.16*) - modulation of nitrate allocation between roots and shoots via vacuolar nitrate release.	27	
	AtNPF5.16	**Arabidopsis thaliana**	ND	NO3-	Vacuolar nitrate efflux (together with *AtNPF5.11* and *AtNPF5.12*) - modulation of nitrate allocation between roots and shoots via vacuolar nitrate release.	27	
6	*AtNPF6.2 (NRT1.4)*	**Arabidopsis thaliana**	No affection by nitrate	NO3-	Nitrate storage in petiole; *atnpf6.2* increases leaf width.	28	*TaNPF6.5*
	AtNPF6.4 (NRT1.3)	**Arabidopsis thaliana**	Induction by nitrate	NO3-	Polyamine resistance	29, 66	*TaNPF6.6; TaNPF6.7*
	AtNPF6.3 (NRT1.1)	**Arabidopsis thaliana**	Induction by nitrate, acidic pH	NO3-, IAA, 2,4-D	Nitrate uptake, root-to-shoot transport and transceptor in sensing/signaling. Lateral root growth by nitrate-regulated auxin transport. N signaling control of PSR. Abiotic stresse responses; *atnpf6.3* reduce growth of nascent roots, stems, leaves, flower buds, and delay flowering time.	20-40, 62	*TaNPF6.1; TaNPF6.2; TaNPF6.3; TaNPF6.4*
	OsNPF6.1	**Oryza sativa**	Induction by nitrate	NO3-	Nitrate uptake and utilization; The elite haplotype B confer high NUE under low N supply and increasing grain yield.	67	*TaNPF6.8*
	OsNPF6.3 (OsNRT1.1A)	**Oryza sativa**	Induction by ammonium (not nitrate)	NO3-	Tonoplast localization.N utilization and flowering time regulation; Overexpression of *OsNPF6.3* significantly promote NUE, grain yield and early maturation in field conditions, while mutation of *OsNPF6.3* reduce both nitrate and ammonium utilization, and lead to severe yield loss and late flowering.	41	*TaNPF6.1*
	OsNPF6.4	**Oryza sativa**	Mycorrhiza inducible	ND	ND	65	*TaNPF6.4*
	OsNPF6.5 (OsNRT1.1B)	**Oryza sativa**	Induction by nitrate (not ammonium)	NO3-	Functional homologue of *AtNPF6.3* in nitrate uptake, transport, and signaling. Component of signaling crosstalk of nitrate and phophate. Modulate root microbiome; *OsNPF6.5* diverge between *indica* and *japonica* rice subspecies, and *indica*-type allele improve NUE and actual yield.	42-44	*TaNPF6.2; TaNPF6.3*
7	*AtNPF7.1 (NRT1.7)*	**Arabidopsis thaliana**	Induction by low N	ND	N cycling under low N stress; flowwer - anther specific; *atnpf7.1* reduce leaf area under adequate N condition, have more and longer flower stalks under low N condition.	14	*TaNPF7.2; TaNPF7.10*
	AtNPF7.2 (NRT1.8)	**Arabidopsis thaliana**	Induction by nitrate; Upregulation by Cd and salt stress	NO3-	Nitrate retrieval from xylem; knockout mutants show enhanced sensitivity to abiotic stress.	45, 70	*TaNPF7.1; TaNPF7.10*
	AtNPF7.3 (NRT1.5)	**Arabidopsis thaliana**	Induction by nitrate and phosphate starvation, repression by pH increase and potassium limitation, salt, drought and cadmium stress	NO3-, K+	Xylem loading of nitrate and potassium. Involve in phosphate deficiency response.	46, 47, 68, 69	
	OsNPF7.1 (OsPTR4)	**Oryza sativa**	Affection by nitrate and/or ammonium differentially in tissues	ND	Involve in nitrate uptake and axillary buds growth; Overexpression of *OsNPF7.1* increase biomass, tiller number and grain yield, while knock down of *OsNPF7.1* has opposite effect.	48	*TaNPF7.8; TaNPF7.10*
	OsNPF7.2	**Oryza sativa**	Induction by high nitrate concentration	NO3-	Intracellular nitrate allocation in roots. Regulation of cell proliferation in tiller bud; Tonoplat localization. Overexpression of *OsNPF7.2* promote growth and increase tiller number and grain yield, while mutation of *OsNPF7.2* has opposite effect.	49, 50	*TaNPF7.9; TaNPF7.10*
	OsNPF7.3 (OsPTR6)	**Oryza sativa**	Induction by both organic and inorganic N		Vaolar membrane localization; N allocation - N-recycling from leaf to panicle. Overexpression of *OsNPF7.3* promote growth, tiller number, grain N content and yield, while knock down of *OsNPF7.3* has opposite effect. N-recycling from leaf to panicle.	51, 52	*TaNPF7.4; TaNPF7.10*
	OsNPF7.4 (OsPTR5)	**Oryza sativa**	Affection by nitrate and/or ammonium differentially in tissues	ND	Involve in nitrate uptake and axillary buds growth; *osnpf7.4* increase biomass, tiller number and grain yield, while overexpression of *OsNPF7.4* has opposite effect.	48	
	OsNPF7.7	**Oryza sativa**	The two splicing forms response differentially to nitrate and/or ammonium in tissues		N allocation and axillary buds growth; Overexpression of the two splicing variants of *OsNPF7.7* both increase tiller number, effective panicle number, filled grain number, grain yield and NUE, while knock down of *OsNPF7.7* has opposite effect.	53	*TaNPF7.6; TaNPF7.10*
8	*AtNPF8.1 (PTR1)*	**Arabidopsis thaliana**	ND	di-peptides, Ja-Ile	Peptide uptake by root.	54-56	*TaNPF8.1~ TaNPF8.8*
	AtNPF8.2 (PTR5)	**Arabidopsis thaliana**	ND	di-peptides, ABA, GA$_{1/4}$, Ja-Ile	Peptide transport into germinating pollen; Overexpression of *AtNPF8.2* enhances shoot growth.	55, 56	
	AtNPF8.3 (PTR2)	**Arabidopsis thaliana**	No affection by cold stratifcation during germination	di-peptides, Histidine	Involve in water uptake during seed germination; *atnpf8.3* delays seed germination.	57	*TaNPF8.9-TaNPF8.29*
	OsNPF8.1 (OsPTR7)	**Oryza sativa**	Induction by As(Ⅲ)	DMA	Dimethylarsenate accumulation in rice grain; *osnpf8.1* reduces As in brown rice without influence on grain yield and N content	58	*TaNPF8.1-TaNPF8.4*
	OsNPF8.9 (OsNRT1)	**Oryza sativa**	No affection by short term nitrate presence	NO3-	Overexpression of *OsNPF8.9* and its 6 transmembrane splicing variant *OsNPF8.9b* both promote shoot growth.	59, 60	*TaNPF8.13; TaNPF8.14*
	OsNPF8.20 (OsPTR9)	**Oryza sativa**	Induction by inorganic N sources	ND	Involve in ammonium uptake, N assimilation and root development; Overexpression of *OsNPF8.20* promotes plant growth, increases tiller number and grain yield, while mutation of *OsNPF8.20* has opposite effect.	61	*TaNPF8.26; TaNPF8.27; TaNPF8.28; TaNPF8.29*

Note: Based on reviews by Wang *et al* (2018) and Corratge and Lamonbe (2017) and with the exception of recently reported or new discovery of *NPF* genes of *AtNPF2.12*, *AtNPF4.6* and *AtNPF7.1* (Babst *et al*., 2019), AtNPF3.1 (David et al., 2016), *AtNPF6.3* (Fang *et al*., 2016; Jian *et al*., 2018,2019; Medici *et al*., 2019; Pan *et al*., 2020; Teng *et al*., 2019; Zhu *et al*., 2019), *AtNPF7.3* (Cui *et al*., 2019; Li *et al*., 2017), OsNPF6.1 (Tang et al., 2019),*OsNPF6.3* (Wang *et al*., 2018), *OsNPF6.5* (Hu *et al*., 2019; Zhang *et al*.,2019), *OsNPF7.1* and *OsNPF7.4* (Huang *et al*., 2019), *OsNPF7.7* (Huang *et al*., 2018).

Abbreviations: ABA, bscisic acid; As, arsenic; DMA, Dimethylarsenate; 2,4-D, 2,4-dichlorophenoxyacetic acid; GA, gibberellin; GLS, glucosinolate; *hrpA*, hypersensitive response and virulence; IAA, Indole-3-Acetic Acid; JA-Ile, jasmonoyl-isoleucine; MeJA, methyl jasmonate; MTB, methylthiobutyl glucosinolate; MTO, methylthiooctyl glucosinolates; N, nitrogen; ND, not determined; NUE, nitrogen use efficiency; PSR, phosphate starvation response.

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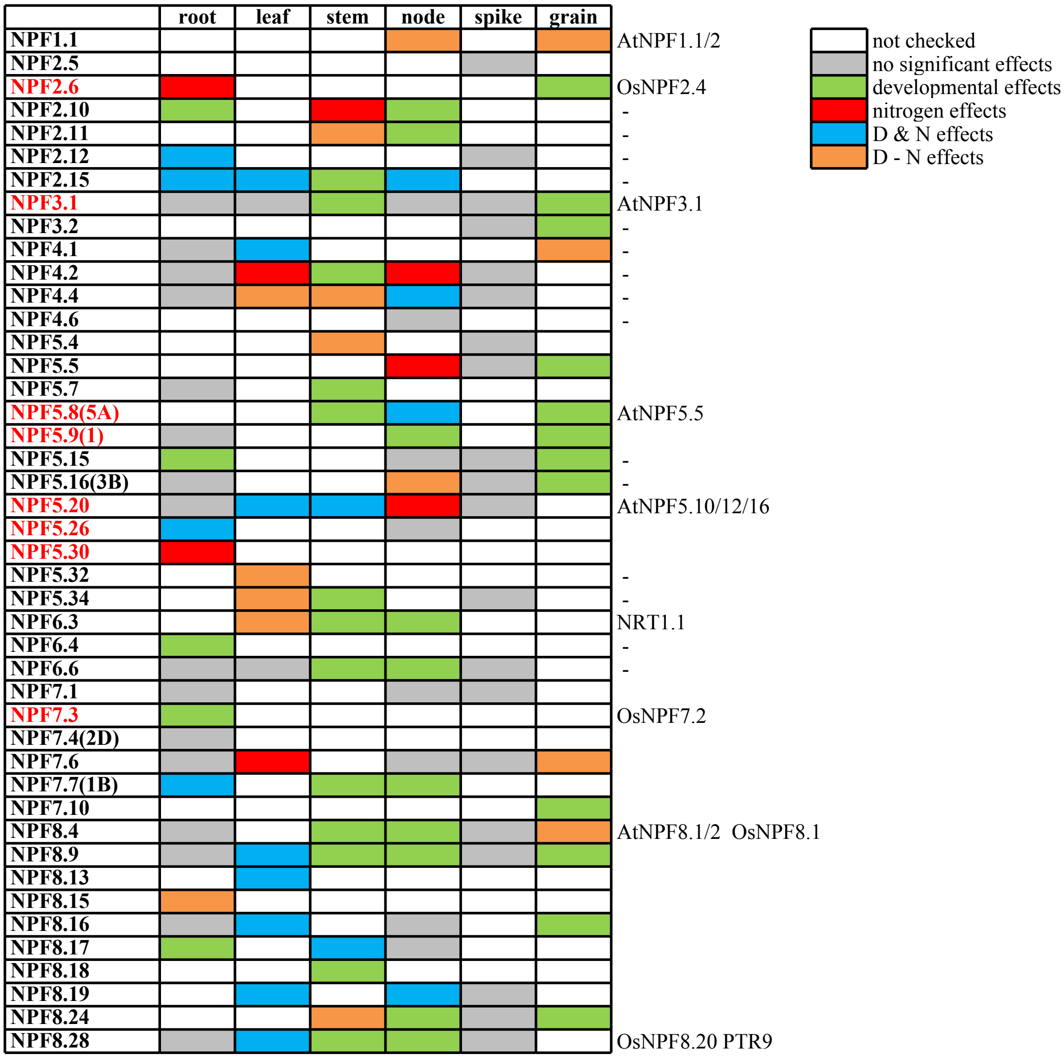
root
leaf
stem
node
spike
grain
NPF1.1
NPF2.5
NPF2.6
NPF2.10
NPF2.11
NPF2.12
NPF2.15
NPF3.1
NPF3.2
NPF4.1
NPF4.2
NPF4.4
NPF4.6
NPF5.4
NPF5.5
NPF5.7
NPF5.8(5A)
NPF5.9(1)
NPF5.15
NPF5.16(3B)
NPF5.20
NPF5.26
NPF5.30
NPF5.32
NPF5.34
NPF6.3
NPF6.4
NPF6.6
NPF7.1
NPF7.3
NPF7.4(2D)
NPF7.6
NPF7.7(1B)
NPF7.10
NPF8.4
NPF8.9
NPF8.13
NPF8.15
NPF8.16
NPF8.17
NPF8.18
NPF8.19
NPF8.24
NPF8.28
AtNPF1.1/2
OsNPF2.4
-
-
-
-
AtNPF3.1
-
-
-
-
-
AtNPF5.5
-
-
AtNPF5.10/12/16
-
-
NRT1.1
-
-
OsNPF7.2
AtNPF8.1/2 OsNPF8.1
OsNPF8.20 PTR9
not checked
no significant effects
developmental effects
nitrogen effects
D & N effects
D - N effects