# NIN-Like Protein Transcription factors regulate leghemoglobin genes in legume nodules

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Leghemoglobins enable endosymbiotic $N_2$-fixation in legume nodules by channelling $O_2$ for bacterial respiration while maintaining a microoxic environment to protect $O_2$-sensitive nitrogenase. We show that the NIN-like Protein (NLP) transcription factors NLP2 and Nodule Inception (NIN) directly activate expression of leghemoglobins through a promoter motif resembling a 'double' version of the Nitrate Responsive Elements (NREs) targeted by other NLPs that has conserved orientation and position across legumes. CRISPR-KO of the NRE-like element resulted in strongly decreased expression of the associated leghemoglobin. Our findings indicate that the origins of the NLP-leghemoglobin module for $O_2$-buffering in nodules can be traced to an ancient pairing of NLPs with non-symbiotic hemoglobins that function in hypoxia.

**One Sentence Summary:** NLP regulation of leghemoglobins in N-fixing nodules descended from of an ancient NLP-hemoglobin regulatory module.

Most legume species can form an endosymbiosis with rhizobia bacteria, forming highly specialized root nodules containing cells in which rhizobial nitrogenase reduces dinitrogen to ammonia. Nitrogenase is rapidly and irreversibly deactivated by oxygen, while $N_2$-fixation is energy intensive, so the rate of $N_2$-fixation is a compromise between the $O_2$ required to support the energy demands of the symbionts and the poisoning of nitrogenase by $O_2$, the so-called "oxygen paradox" (1). To address this constraint, up to 40% of nodule protein is comprised of leghemoglobins (LgHbs), which contain an $O_2$-binding heme group that colors the nodule red. LgHbs feature an extremely fast $O_2$-association rate and a relatively slow $O_2$-dissociation rate, allowing them to buffer the free oxygen concentration at around 10 nM, and thereby maintain $O_2$ levels compatible with $N_2$-fixation. Notwithstanding the central role of LgHbs in $N_2$-fixation, their transcriptional regulation and the manner of their recruitment to nodulation have not been elucidated.

The founding member of the NIN-like Protein family, Nodule Inception (NIN), is required for infection by rhizobia as well as for nodule formation (*2*). In contrast, *Medicago truncatula* NLP1 and *Lotus japonicus* NLP4 are required for nitrate-suppression of nodulation (*3, 4*). *NIN* and *NLP2*, however, are the only NLPs expressed in medicago nodules (**Fig. 1A**; **fig. S1A**). The expression of *NLP2* and several *LgHbs* was strongly reduced in nodules induced by rhizobia mutants *bacA* and *fixJ* where $N_2$-fixation is defective due to lack of symbiosomes or nitrogenase activity, respectively, indicating a tight connection of *NLP2* with $N_2$-fixation (**Fig. 1B**).

To investigate NLP2's role, we evaluated nodulation on *NLP2*-knockout roots using an aeroponic system. The resultant nodules had normal zonation but were smaller and had reduced $N_2$-fixation potential (**Fig. 1C, D**). We then isolated two mutants, *nlp2-1* and *nlp2-2* (**fig. S1B**). The *nlp2-1* mutant had smaller nodules in aeroponics, matching the CRISPR knockout phenotype (**Fig. 1E)**, and had a greatly reduced plant biomass, but developed a normal number of nodules (**Fig. 1F)**. However, when grown in substrate the mutant developed normal sized nodules (**fig. S1C**). The increase in phenotype severity seen in aeroponics vs substrate conditions may reflect the much larger and more extensively nodulated root system that develops under aeroponics, which may exaggerate the N-fixation defect in *nlp2*. Nevertheless, the N-fixation potential of both *nlp2-1* and *nlp2-2* was also compromised, albeit to a lesser degree, when grown in substrate (**fig. S1D**), and could be partially complemented by expression of *NLP2* from its native promoter, but not by a mutant version of *NLP2* (**fig. S1E, F**). Furthermore, $^{15}N_2$ assimilation was compromised in *nlp2-1* plants nodulated in substrate, (**Fig. 2A)**, which corresponded to a decrease in N-content in nodules and shoot, while %N was unchanged (**Fig 2A; fig. S2D**). Evaluation of *nlp2* mutants under inhibitory nitrate regimes indicate that loss of NLP2 does not affect N-suppression of nodulation (**fig. S2A to C**). Together these results suggest a positive role for NLP2 in $N_2$-fixation.

In addition to reduced N-fixation, *nlp2* nodules appeared less pink (**fig. S2E**), which was reflected in lower LgHb expression and heme levels (**Fig. 2B, C; fig. S2F**). We then profiled gene expression of *nlp2-1* nodules under different N-regimes using substrate where the mutant forms normal sized nodules, rather than using aeroponics where the smaller nodules on the mutant would confound the analysis. Results revealed nitrate-dependent effects on gene expression (**Fig. 2D**; full data set **Auxiliary File 1**). Genes encoding LgHbs, heme biosynthesis enzymes, and nitrate uptake transporters were strongly downregulated in *nlp2-1* (**Fig. 2E**, **F**; **Supplemental Table S1**) while jasmonate-related genes were upregulated (**Supplemental Table S2**) as previously reported in root hairs of *M. truncatula nin* (*5*). Expression of *NLP2* from its own promoter partially rescued gene expression in *nlp2*, but a mutant version did not (**Fig. 2G**). *In silico* promoter analysis revealed that 28 of the 55 genes with the largest overall decrease in expression in *nlp2* nodules contained Nitrate Responsive Elements (NREs), which are required for transcriptional activation by NLPs (*6*), including known genes required for N-fixation like *SymCRK*, *SEN1*, and Nodule Cysteine-Rich (NCR) secreted peptides (*7*, *8*; **Supplemental Table S3**). In addition, a larger motif consisting of two partly overlapping NREs was detected in the *LgHb* genes. We designated these as 'double-NREs' (dNREs), in which the second half of the first semi-palindrome (NRE1) overlaps with the first half of the second element (NRE2) (**Fig. 3A**). The dNREs all have the same orientation and are positioned between -100 and -300 bp upstream of the TSS (**Fig. 3B**). dNREs were also detected at same position and orientation in promoters of *LgHbs* of soybean and common bean, indicating their conservation across papilionoid legumes (**fig. S3A**). Examination of dNREs in promoters of soybean and medicago *LgHbs* suggests that those strongly differing from the consensus motif have lower expression in nodules (**fig. S3B, C**), suggesting the direct involvement of dNREs in the regulation of *LgHb* expression. Our transcriptomic data verified that *NLP2* and *NIN* are the primary *NLPs* expressed in medicago nodules (**fig. S1A**, **fig. S4)**, and since NIN binding sites strongly resemble NREs (*9*, *10*; **fig. S5**) we speculated that both NLP2 and NIN may directly promote *LgHb* expression. Using an EMSA we found that truncated NLP2 and NIN proteins containing their RWP-RK DNA binding domains could bind to dNRE-containing DNA fragments but not to those with mutated dNREs (**Fig. 3C**, **D;** details in **fig. S6, S7**). To test its importance for *LgHb* expression we mutated the dNRE element in the *LgHb1* promoter using CRISPR/CAS9. This resulted in strongly decreased expression of *LgHb1*, but not *LgHb2*, whose promoter contained the gRNA target sequence but lacked the PAM (**Fig. 3E; fig. S8**). When expressed in *Nicotiana benthamiana* leaves, both NIN and NLP2 activated reporter activity when driven by a dNRE-containing fragment of the *LgHb7* promoter, but not by a dNRE-deleted version (**Fig. 3F**). Versions of NIN and NLP2 with mutations in their RWP-RK domains were unable to activate the reporter (**fig. S9A**). Co-infiltration of *NIN* and *NLP* constructs resulted in higher reporter gene activity than either construct alone (**fig. S9B**). These results support a role for NLP2 and NIN in activation of *LgHb* expression in nodules. Since *nin* loss-of-function mutants do not form nodules, we used a CRISPR/CAS9-based strategy to selectively knockout *NIN* in a tissue-specific manner by expressing *CAS9* in the nodule interzone/nitrogen fixation zone of WT and *nlp2-1* nodules. Successfully edited nodules showed decreased *LgHb* expression suggesting that NLP2 and NIN act redundantly to regulate the transcription of nodule *LgHbs* (**fig. S10**).

We then investigated if the above regulation was a legume innovation or predated the symbiosis. Phylogenetic analysis showed that close homologs of NLP2 are found only in legumes, and group separately from their next closest homologs, most of which are expressed in seeds (**fig. S11, S12)**, while NIN was reported to be present in legumes and nodulating non-legumes (*11*). The absence of NLP2 in *Prosopis alba,* a Caesalpiniod legume, suggests that NLP2 arose before the divergence of Papilionoid legumes. LgHbs evolved from non-symbiotic hemoglobins (nsHbs) involved in energy maintenance under hypoxia and $O_2$ transport (*12, 13*), with class I nsHbs acting in the nsHB-Nitric Oxide cycle (*14-15*). Analysis of *nsHb* promoter sequences across angiosperms revealed that they frequently harbor NRE elements, suggesting they may be NLP targets (**fig. S13A, B**). Mining of data from a genome-wide ChIP analysis revealed binding of *L. japonicus* NIN to a class I *nsHB* (*16*). In addition, *nsHB1* was identified as a direct target of AtNLP7 in an Arabidopsis DAPseq study (*17*), while its expression was shown to be dependent on NLP7 or NLP8 in three transcriptomic studies (*18*, *19, 20*). Our own investigation of medicago *nsHB1* showed its expression is dependent on NLP1, and that it may be a direct target (**fig. S14**). These findings suggest that NLPs were recruited to nodulation as part of an ancient NLP-nsHb regulatory module. The dNRE element was detected in *Hb* promoters of a mimosoid legume, and thus appears to predate NLP2, but was absent in nodulating non-legumes (**fig. S13C;** these and other promoter sequences used are provided in the **Appendix** in the Supplemental materials). It therefore seems likely that regulation of hemoglobins by NLPs served as a basis for recruitment of NIN in nodulating non-legumes, then later NLP2, to enhance LgHb expression in legume nodules.

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**Author contributions:** The experiments were conducted by SJ, M-FJ, J-PG, YP, JW, FL, CSC, QL, YT, and MZ. KM and JW generated the *Tnt1* insertion mutants. Experiments were designed by SJ, M-FJ, J-PG, PX, PG and JDM. PX, PSP, EW, PG, and JDM wrote the manuscript.

**Competing interests:** Authors declare no competing interests.

**Data and materials availability:** All data is available in the main text or the supplementary materials.

**Supplementary Materials:**
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Tables S1-S5
References (*22-35*)

**Fig. 1. Expression of *NLP2* in *M. truncatula* nodules and *nlp2* nodulation phenotypes.**

**(A)** Nodule expression of *NLP2*. Histochemically stained nodule cross-section (15 dpi with *S. meliloti* Rm2011) expressing *pMtNLP2:GUS*. Bar, 100 µM. (**B**) Expression (qRT-PCR) of *NLP2*, *NIN, LgHb2, LgHb7,* and *LgHb8* relative to reference genes in nodules of WT plants inoculated with *S. meliloti* Rm2011 grown in attapulgite substrate with no nitrogen. n=3. **(C)** Representative DAPI-stained 70 µm nodule sections of *NLP2* knockout (*NLP2*-KO) and control (EV) roots grown using aeroponics with no nitrogen. Bar, 100 µM. Nodules were evaluated 11 dpi with *S. meliloti* Rm2011 carrying a *pNifH:GFP* reporter. **(D)** ARA of nodules of *NLP2* CRISPR-edited roots grown aeroponically without nitrogen. WT *M. truncatula* seedlings (A17) were transformed with a gRNA targeting *NLP2* and roots were genotyped. The mean number of nodules from edited and non-edited roots were compared (n=19) with a Kruskall non-parametric test, α=0.05. **(E)** Nodules of *nlp2-1* and WT nodules grown aeroponically without nitrogen; 18 dpi with *S. meliloti* Rm2011. (**F**) Biomass of inoculated, 18 dpi with *S. meliloti* Rm2011 (nod), and uninoculated plants. Right side: nodule number. Plants were grown aeroponically without nitrogen. n=10 for WT, 11 for *nlp2-1*. In (B, E and F), bars indicate ±SD. In (B and F), means were compared with Student's *t*-test α=0.05.

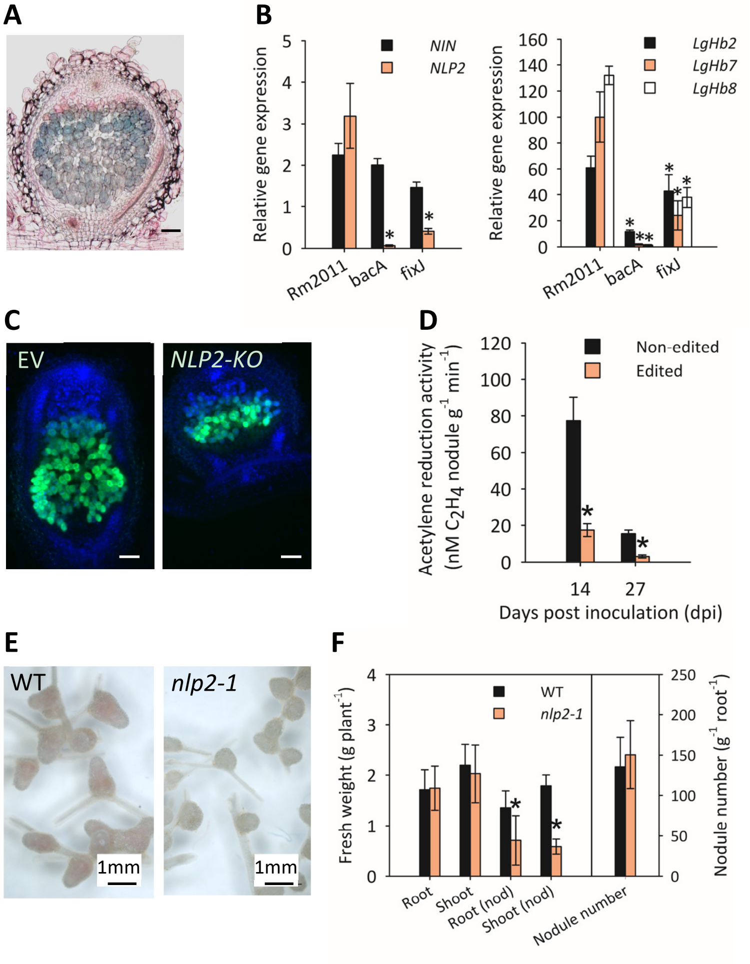
**Fig. 2. Loss of NLP2 reduces N-fixation, plant N-content, LgHb and heme levels.**

**(A)** Total N (Kjeldahl's) and $N_2$-fixation [d$^{15}$N (‰)] in *nlp2-1* and WT nodules. Plants were nodulated under 0.5 mM $KNO_3$. **(B)** LgHb content of WT and *nlp2-1* nodules. Western blot using α-LgHb antibodies to detect LgHb levels in nodules of WT and *nlp2-1* under different nitrogen regimes. The two bands reflect the presence of different sized LgHb isoforms. **(C)** Heme content of *nlp2-1* and WT nodules under different N-regimes. **(D)** Average fold changes for genes with changed expression in *nlp2-1* nodules at 2.0 mM $KNO_3$ (656 decreased, 915 increased) at different N-treatments. **(E)** Relative expression of *UROM1/2* in *nlp2-1* and WT nodules under 2.0 mM KCl (0), 0.5 mM $KNO_3$ (0.5), and 2.0 mM $KNO_3$ (2.0). **(F)** Expression of *LgHbs* in nodules in WT and *nlp2-1* under 2.0 mM $KNO_3$. **(G)** Complementation of gene expression in *nlp2-1* nodules under 2.0 mM $KNO_3$. Relative expression of *NLP2, LgHb1, LgHb2*, and *NiR* in nodules of the *nlp2-1* transformed with *pNLP2-NLP2, pNLP2-NLP2m* or EV (empty vector) using *A. rhizogenes* hairy-root transformation. *EF* was used as a reference. For (A), n=10, for (C, E, F and G), n=3. All plants were evaluated at 21 dpi with *S. meliloti* Rm2011. Means were compared with a Student's *t*-test, α=0.05. For (E and F) bars indicate 95% CI. For (A, C, and G) bars indicate ±SD.

**Fig. 3. NLP2 directly activates *LgHb* expression via NRE-like promoter elements.**

(**A**) 'dNRE' motif detected in promoters of *M. truncatula nlp2-1* downregulated genes compared with NREs detected in *NiRs* across angiosperm plants (this study). The gapped semi-palindrome is indicated by arrows. The overlapping NREs are indicated by brackets. The matches of the NRE consensus to the dNRE are indicated by asterisks, and mismatches by hyphens. **(B)** The position of the dNRE sequence in promoters of *M. truncatula LgHbs* (NRE1 in orange, NRE2 in white).

The bold line indicates the 5'UTR. TSS: transcription start site, ATG: start codon. **(C)** EMSA to test for interaction between a truncated NLP2 protein containing the RWP-RK domain with an N-terminal His-tag and the CY5-labeled *LgHb7* promoter fragment containing the dNRE. M: *LgHb7* promoter with a mutated dNRE. **(D)** EMSA to test for interaction between a truncated NIN protein containing the RWP-RK domain with an N-terminal HIS tag and the CY5-labeled *LgHb7* promoter fragment containing the dNRE. M: *LgHb7* promoter with deleted dNRE. (**E**) Relative expression (qRT-PCR) of *LgHb1 and LgHb2* in nodules of *M. truncatula* plants transformed with a CRISPR construct with two gRNAs targeting the dNRE of *LgHb1*. gRNA1 also matches the dNRE sequence in the *LgHb2* promoter but there is no corresponding PAM site. The vector was introduced by hairy-root transformation and gene expression was evaluated at 21 dpi with *S. meliloti* Rm2011. *EF* was used as a reference gene. **(F)** Trans-activation assay for NLP2 and the *LgHb7* promoter driving *GUS* in *Agrobacterium tumefaciens* co-infiltrated *Nicotiana benthamiana* leaves. EV1: empty vector no-promoter control, EV2: empty vector no-*NLP2* control. *pLgHb7*:*LgHb7* promoter fragment (-342 to -1 bp) containing the dNRE, *LgHb7m*: *LgHb7* promoter fragment with the dNRE deleted. *NIN* and *NLP2*: p35S promoter driving full-length *NLP2* or *NIN*. For (E) and (F) means are shown ±SD, and compared with Student's *t*-test, α=0.05. For (E), n=3. For (F) each replicate consisted of six leaves. For NLP2 experiments (left side) n=3-4, for NIN experiments (right side) n=6-8.


A
B
Relative gene expression
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4
3
2
1
0
NIN
NLP2
Rm2011
bacA
fixJ
*
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Relative gene expression
160
140
120
100
80
60
40
20
0
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LgHb7
LgHb8
Rm2011
bacA
fixJ
C
EV
NLP2-KO
D
Acetylene reduction activity
(nM C2H4 nodule g-1 min-1)
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100
80
60
40
20
0
Non-edited
Edited
14
27
Days post inoculation (dpi)
E
WT
nlp2-1
1mm
1mm
F
Fresh weight (g plant-1)
4
3
2
1
0
WT
nlp2-1
250
200
150
100
50
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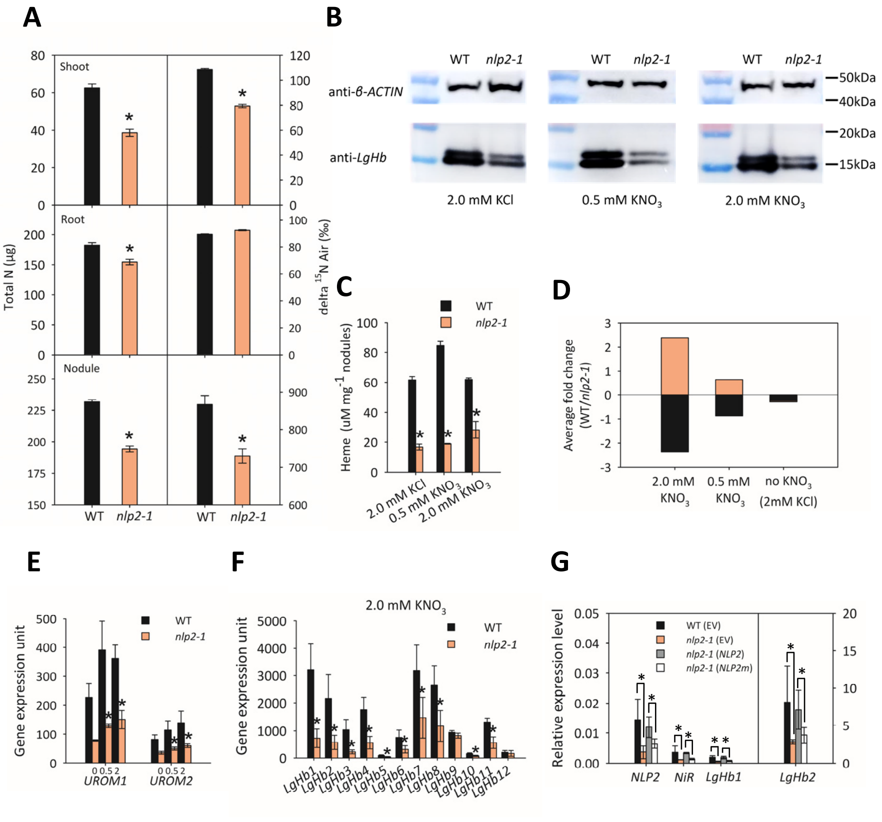
Root
Shoot
Root (nod)
Shoot (nod)
Nodule number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Shoot
Root
Nodule
Total N (µg)
delta $^{15}$N Air (‰)
WT
nlp2-1
B
anti-β-ACTIN
anti-LgHb
50kDa
40kDa
20kDa
15kDa
2.0 mM KCl
0.5 mM KNO$_3$
2.0 mM KNO$_3$
C
Heme (uM mg$^{-1}$ nodules)
D
Average fold change (WT/nlp2-1)
2.0 mM KNO$_3$
0.5 mM KNO$_3$
no KNO$_3$ (2mM KCl)
E
Gene expression unit
UROM1
UROM2
F
2.0 mM KNO$_3$
LgHb1
LgHb2
LgHb3
LgHb4
LgHb5
LgHb6
LgHb7
LgHb8
LgHb9
LgHb10
LgHb11
LgHb12
G
Relative expression level
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NiR
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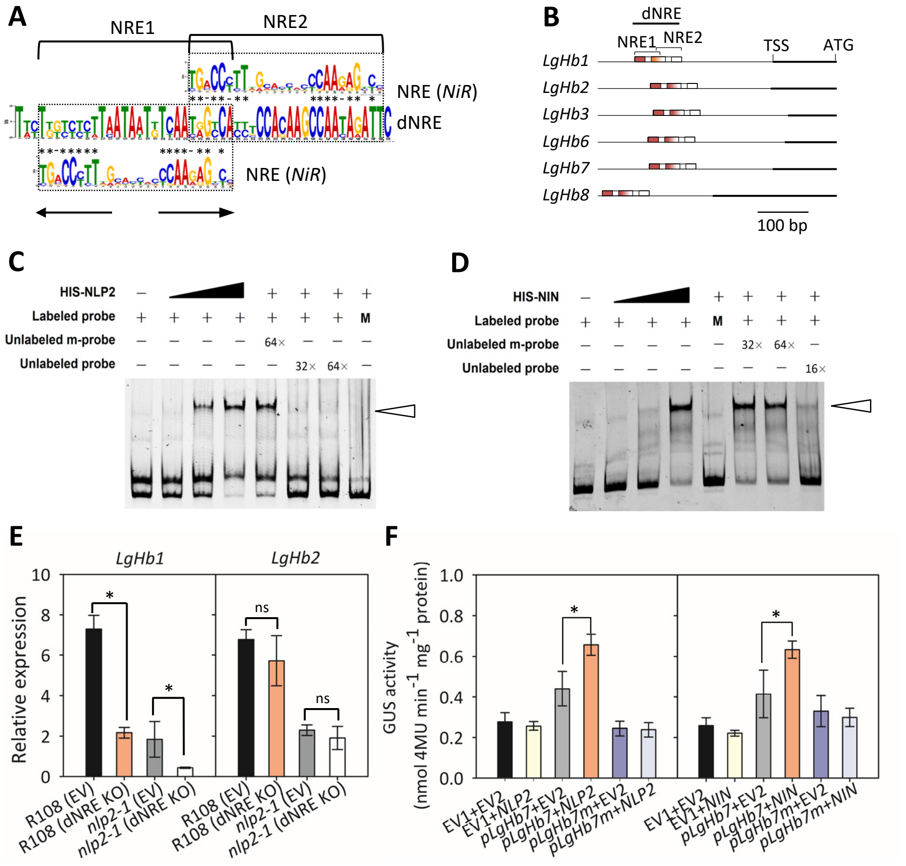
LgHb2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NRE2
NRE (NiR)
dNRE
NRE (NiR)
B
dNRE
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NRE2
TSS
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LgHb1
LgHb2
LgHb3
LgHb6
LgHb7
LgHb8
100 bp
C
HIS-NLP2
Labeled probe
Unlabeled m-probe
Unlabeled probe
64×
32×
64×
M
D
HIS-NIN
Labeled probe
Unlabeled m-probe
Unlabeled probe
M
32×
64×
16×
E
LgHb1
LgHb2
Relative expression
10
8
6
4
2
0
*
*
ns
ns
R108 (EV)
R108 (dNRE KO)
nlp2-1 (EV)
nlp2-1 (dNRE KO)
F
GUS activity
(nmol 4MU min-1 mg-1 protein)
1.0
0.8
0.6
0.4
0.2
0.0
*
*
EV1+EV2
EV1+NLP2
pLgHb7+EV2
pLgHb7+NLP2
pLgHb7m+EV2
pLgHb7m+NLP2
EV1+EV2
EV1+NIN
pLgHb7+EV2
pLgHb7+NIN
pLgHb7m+EV2
pLgHb7m+NIN

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# Supplementary Materials for

## NIN-Like Protein Transcription factors regulate leghemoglobin genes in legume nodules

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## Materials and Methods

### Gene sequences

All accession numbers for genes mentioned in this paper are listed in **Table S4.**

### Plant materials

*M. truncatula* wild type R108-C3 and A17 were used in this study. Plants homozygous for a *Tnt1* transposon insertion in *NLP2* were isolated from lines NF7812 and NF8520 and were designated as *nlp2-1*, and *nlp2-2*, respectively. Genotyping primers are provided in **Table S5**. *M. truncatula NLP1 Tnt1* insertion mutants *nlp1-1* (NF12956) and *nlp1-2* (NF14709) were kindly provided by Fang Xie (CEMPS).

### Growth conditions

For plants grown in aeroponic conditions, seeds were first scarified and sterilized and then grown in caisson units where they were initially provided 5 mM $NH_4NO_3$, then grown in nitrate-free medium before being inoculated with rhizobia as previously described in The Medicago Handbook, Growing *Medicago truncatula*: choice of substrates and growth conditions (ISBN 0-9754303-1-9. http://www.noble.org/MedicagoHandbook/, 2007) (***22***). For plants grown in substrate, seeds were scarified and sterilized with NaClO, rinsed thoroughly, plated on deionized water-agar plates, and then grown inverted for 7 days in the dark at 4 °C. Seedlings were then transferred to cells in a tray (32 per tray) containing vermiculite: perlite substrate (1:1, v:v) and cultivated in a growth chamber (22 °C, 16 h/8 h day/night, ~70 % humidity) with weekly provision of Fahräeus Plant (FP) medium supplemented with the indicated concentrations of $KNO_3$. For the plants inoculated with the *fixJ* and *bacA* rhizobia mutants, the plants were grown on attapulgite with caisson medium without N, then inoculated with 200 µl (per plant) of a solution of *Sinorhizobium meliloti* Rm2011 $OD_{600nm} = 1$ and provided only $H_2O$.

### Nodulation assays

*M. truncatula* seedlings were transferred to soil, watered with distilled water, and grown for one week. One seedling was then inoculated with *S. meliloti* Rm2011 (1 mL, $OD_{600nm}=0.8$). One day after inoculation they were watered with Modified Fahräeus Plant (MFP) with different N-regimes. They were initially provided with 2 L medium per tray, and then were provided 1 L per tray every week afterwards. FP contains 0.7 mM $KH_2PO_4$, 0.5 mM $MgSO_4$, 1 mM $CaCl_2$, 50 µM Fe-EDTA, 0.8 mM $Na_2HPO_4$, 0.1 µg $L^{-1}$ $H_3BO_3$, 0.1 µg $L^{-1}$ $MnSO_4 \cdot H_2O$, 0.1 µg $L^{-1}$ $ZnSO_4 \cdot 7H_2O$, 0.1 µg $L^{-1}$ $CuSO_4 \cdot 5H_2O$, and 0.1 µg $L^{-1}$ $Na_2MoO_4$. MFP is FP with different levels of $KNO_3$ added. Four different N-regimes were used: 2 mM KCl (no nitrate control), 0.5 mM $KNO_3$, 2.0 mM $KNO_3$ and 5.0 mM $KNO_3$. The nutrient solutions were adjusted to a pH of 6.5 ± 0.05 using $H_2SO_4$ or NaOH. Nodules were harvested 21 days post inoculation (dpi).

### Acetylene reduction assays

For determination of acetylene-reduction activity (ARA), plants were either assayed 21 dpi with *S. meliloti* (Rm2011) with weekly provision of either $KNO_3$ or KCl as described above or were nodulated under 1 mM $KNO_3$. Additional treatments with 500 mLof either 1mM $KNO_3$ or 5 mM $KNO_3$ per tray were carried out and ARA was evaluated 48-h later. For the ARA assay, ≥4 biological replicates with each comprised of 3 nodulated roots were analyzed for each genotype. The nodulated roots were introduced into 20 mL glass vials sealed with rubber stoppers. After injection of 1 mL acetylene, they were subsequently incubated for 1.5~2.5 h at room temperature. Samples of 200 µL of gas from each bottle were used to measure ethylene production using a gas chromatograph (7820A, Agilent Technology, Shanghai, China) and the roots were weighed. The nodules were then excised and weighed, and the total nitrogenase activity was calculated as nanomoles of ethylene per min per gram nodule.

### Complementation of *nlp2-1*

Plasmids were constructed using either Gateway or Golden Gate techniques in combination with Gibson cloning. For the *nlp2-1* complementation analysis, fragments of the *NLP2* promoter (2874 bp, *pNLP2*) and the *NLP2* CDS were amplified using the polymerase chain reaction (PCR) from genomic DNA and cDNA of *M. truncatula*, and the products were cloned into pL0V-PU-41295 and pL0V-SC-41308, respectively, using Gibson cloning (NovoRec plus One step PCR Cloning Kit, Novoprotein, Shanghai, China). The resultant L0 vectors containing the *pNLP2* and *NLP2* CDS were recombined with a L0 containing the T-Adh terminator to create pL1V-F2-47742 (*pNLP2-NLP2*). pL1V-F2-47742 was recombined with pL1V-R1-47802 containing the *dsRed* CDS under ~1.1kb of the *Lotus japonicus Ubiquitin* promoter. The NLP2m vector with a mutation in the RWP-RK domain was constructed in the same way after PCR mutagenesis of the L0. The resultant L2 constructs (pNLP2-NLP2-Adh-F2-47742-pLjUBQ-dsRed-NOS-R1-47802-ELE2) and the mutated version were introduced into the *nlp2-1* mutant background by *Agrobacterium rhizogenes* (Arqua-1) hairy-root transformation and an empty vector was used as a control.

### CRISPR/Cas9 knockouts

For CRISPR/Cas9-mediated gene editing of *NLP2*, five guide RNAs (gRNA) were designed with CRISPR webtool (version 4.8, http://crispor.tefor.net/, 20bp-NGG-Sp Cas9, SpCas9-HF1, eSpCas9 1.1) using the INRA A17r5.0 r1.6 *M. truncatula* genome release (NLP2_gRNA_1 GAGGAAGGACAAGGTATATC, NLP2_gRNA_2 GTTTCAGAAGCTGAACTAAG, NLP2_gRNA_3 GAAACGAACCTAAAAAATAG, NLP2_gRNA_4 GAAAGCAGGCTGAGAAAAAG, NLP2_gRNA_5 GGATGCTGCAAAAAAAATAG). Plasmids required for all the following assemblies were provided by the ENSA project (Engineering Nitrogen Symbiosis for Africa) (https://www.ensa.ac.uk) and the Golden Gate cloning strategy was systematically applied (***23***). Synthetic polycistronic genes containing two gRNAs (NLP2_gRNA_1 and NLP2_gRNA_2) and three gRNAs (NLP2_gRNA_3, NLP2_gRNA_4, NLP2_gRNA_5) interspersed by tRNAs were pre-assembled by PCR using pGTR plasmid as template and Golden Gate cloning and placed under the control of *MtU6.1* (MtrunA17Chr3g0136831) and *MtU6.6* (MtrunA17Chr7g0251721) promoters respectively (***24***). The gRNAs expression modules and a *Cas9* cassette (pLjUbi:Cas9-SV40:T35S (EC15251), (EC41414), (EC15747), with SV40 NLS C-fused by PCR to the AtCAS9 sequence) were then integrated into a binary vector (EC50506) in between a kanamycin resistance cassette (p35S:KanR:TNos (EC15529)), and a *dsRed* marker cassette (pAtUbi10:DsRed:TOcs (EC15062, EC15073 and EC41432)). The engineered binary vector was introduced into *A. rhizogenes strain* (Arqua-1) that was then used to transform *M. truncatula* A17 roots. Out of 227 transformed root systems inoculated with *S. meliloti* Rm2011 and genotyped using genomic PCR and amplicon sequencing, 64 were found to be homozygous for *NLP2* gene editions.

For CRISPR/Cas9-mediated gene editing of *NIN* a tissue-specific knockout strategy was used in which *Cas9* was expressed from the promoter of *Nodule-Cysteine Rich 158* (*NCR158*), which is specifically expressed in the interzone and $N_2$-fixation zone of nodules (**fig. S10A**). The CRISPR constructs were developed by modifying the previously described pKSE401 and pCDC-T1T2 vectors (***25***). The pKSE401 neomycin resistance gene was replaced by the *dsRed* CDS using the *Nco* I and *Rsr* II restriction sites. In addition, the *CaMV 35S* promoter upstream of *Cas9* was removed *by Bst*E II and *Xba* I double digestion and replaced by a 2112 bp fragment of the *NCR158* (Medtr7g027180) promoter using Gibson Assembly (NovoRec plus One step PCR Cloning Kit, Novoprotein, Shanghai, China). This vector was renamed as pKNF401.The gRNA vector pG-DT1T2.was synthesized containing the gRNA-Scaffold, *AtU6-26t*, transcriptional blocker sequence (***26***), and *AtU6-26pro* (synthesized by GenScript). We used CRISPR-P 2.0 for guide RNA design in this study (***27***). Two specific primers were synthesized, gRNA-T1-F and gRNA-T2-R, pG-DT1T2 were used as a template for amplification of the guide RNA cassette. The PCR product was recombined with the vector in a one-tube Golden Gate reaction using *Bsa* I (NEB) and T4 DNA ligase (NEB) (4 min at 37°C, 3 min at 16°C, 40 cycles), to make the CRISPR target vector pKGSD401-pNCR158:Cas9. Similar cloning strategy was used for constructing the binary vector for dNRE editing except *Cas9* expression was driven by the *CaMV 35S* promoter using the pKGSD401-p35S:Cas9 vector. The guide RNA sequences are listed in **Table S5**.

### Hairy-root transformations

The recombinant plasmids were introduced into *A. rhizogenes* Arqua-1. A single *A. rhizogene*s colony was picked and cultured overnight at 28°C with shaking. *M. truncatula* seeds were sterilized and germinated as described above. A 50 mL volume of the overnight culture was pelleted in a benchtop microfuge at 4,000×rpm speed for 5 min, supernatant was removed, and the pellet was resuspended in 2-5 mL autoclaved ddH$_2$O. About 3 mm of the root tip was removed from each seedling on a sterile flow bench, and then the end of wounded root tip was dipped in the *A. rhizogenes* Arqua-1 culture and seedlings were placed on FP plates. After a week of vertical growth on the plates in a growth chamber (22°C, 16-h light/8-h dark photoperiod), any extended roots were removed, and the seedlings were transferred to FP medium containing 0.5 mM KNO$_3$ and grown at 22°C under 16-h light/8-h dark photoperiod for 3 weeks. The dsRed positive roots were identified under a fluorescent microscope, and non-transgenic roots were removed. The plants were then transferred to pots containing a vermiculite: perlite substrate (1:1, v:v) and kept in a growth chamber at 22 °C under 16-h light/8-h dark photoperiod for 7-10 days before being inoculated.

### Western blot analysis

Fresh nodules (150-200 mg) were homogenized in liquid nitrogen with a cold mortar and pestle. 1 mL of extraction buffer (50 mM Tris-HCl, 150 mM NaCl, 1 mM proteinase inhibitor, 10 % glycerol and Triton X-100, pH=7.5) was added to each sample which were then vortexed, incubated on ice for 20 min, and then centrifuged at 12,000g for 20 min at 4°C. The supernatant was then collected in fresh tube and placed on ice. After total protein isolation, protein concentrations were quantified using the Bradford assay (***27***). For western blot analysis, protein samples were separated on 4-12 % gradient SDS-PAGE gel, then transferred to polyvinylidene difluoride membranes. For LgHb detection, an α-LgHb antibody made by ABclonal Co., Ltd. that was designed against a peptide sequence common to all *M. truncatula* LgHbs (Cat No. A20191, Wuhan, China) was used as a primary antibody and HRP-conjugated rabbit α-goat as a secondary antibody (ABclonal Co., Ltd.). Signals were acquired with Western ECL Substrate (Thermo Fisher, USA) under a ChemiScope western blot processor (Amersham Imager 600, GE healthcare, USA).

### Quantification of total heme

For heme extraction, nodules (~100 mg) were ground into a fine powder in liquid nitrogen and resuspended in 1 mL deionized water. After centrifugation (12,000g, 10 min), supernatants were incubated following the manufacturer's protocol (Heme Assay Kit, MAK316-1KT, Sigma-Aldrich, USA).

### Leghemoglobin (LgHb) concentration

For the measurement of LgHb concentration in nodules, 100 mg of fresh nodules were ground and homogenized in 0.3 mL precooled PBS buffer ($Na_2HPO_4$-$NaH_2PO_4$ buffer at 5°C, pH=6.8). The resulting slurry was then centrifuged at 12,000g for 15 min prior to assaying the supernatant by spectrophotometry at wavelengths of 540, 520 and 560 nm. The LgHb concentration was calculated as described previously (***28***). Bovine Hb was used as a protein standard in this experiment.

### RNA extraction and real-time PCR analysis

Total RNA was extracted from nodules using an Ultrapure RNA kit (Tiangen, Beijing, China). First strand cDNA was synthesized and carried out using an EasyScript One-Step gDNA Removal and cDNA Synthesis SuperMix Kit (Tiangen, Beijing, China). The UltraSYBR Green Mixture qPCR kit (GenStar, Beijing, China; Yeasen, Shanghai, China) was used in the qPCR reaction. The real-time PCR was carried out using StepOne Plus (Applied Biosystems, USA). Either *M. truncatula Elongation Factor* (*EF*), or Helicase, UBIQ, Mt0085_00020, and Mt0004_00216 were used as reference genes. The sequences of primers are listed in **Table S5**. Standard errors and statistical significance based on three biological replicates were calculated using the 2-ΔΔCt method (***29***).

### Electrophoretic Mobility-Shift Assays (EMSA)

To create constructs for EMSAs, the partial-length CDS of *NLP2* (encoding C-terminal residues 560–913) and *NIN* (encoding C-terminal residues 566-993) were cloned into pDONR207 and then recombined into pHGWA and pBAD-DEST49 to create pHGWA-NLP2 and pDEST49-NIN, then introduced into *E. coli* BL21. The *pLgHb7* and *pLgHb1* probes were amplified and then labeled with Cy5 by PCR amplification. Primers used for probe synthesis are listed in **Table S5**. NIN and NLP2 proteins were expressed in *E. coli* transformed with pDEST49-NIN and pHGWA-NLP2 and then purified as described as below. The purified proteins were then incubated with the Cy5-labelled probe at 37 °C for 30 min in EMSA buffer (20 mM Tris, pH=7.9, 5 % glycerol, 40 ng $\mu L^{-1}$ BSA, 50 mM $MgCl_2$ and 5 mM dithiothreitol). After incubation, the reaction mixture was electrophoresed on a 6 % native polyacrylamide gel with running buffer (25 mM Tris, 192 mM glycine, 0.1 % SDS) and then imaged with a Starion FLA-9000 imager (Fujifilm).

For the EMSA using the pLgHb7 promoter fragment the mutated variant pLgHb7m had three two bp mutations as shown below: the conserved dNRE indicated in bold, deleted bases are indicated with hyphens the corresponding bases in WT are shown in red, the consensus dNRE is shown for reference.

| | |
|---|---|
| pLgHb7 | TA**TTGTCTC**T**TTAA**TAATGT**CAACAGCCATTTC**CACAAG**CCAATAGATT**CTT |
| pLgHb7m | TA--**GTCTCTTTAA**TAATGT**C--CAGCCATTTC**CACAAG**CC--TAGATT**CTT |
| consensus dNRE | TK**KYYYY-WTMA**NNNNNNN**Y**AA**YRGYCAYYBC**NNNNNN**CC**AA**YARATT** |

For the *nsHB1* EMSA the following version of the *M. truncatula nsHB1* promoter sequence containing two copies (2X) of the NRE was used:

*original WT nsHB1 promoter sequence:*
GAATGAATGAAAGTATGAATGACTCCCCATTGGTATGAAGGGTCAATTTCATCTTCAATTAA

*pnsHB1 2×NRE probe used for EMSA- 126bp:*
cggtacctcgcgaatgcaGAATGAATGAAAGTATGAATGACTCCCCATTGGTATGAAGGGTCAAATGACTCCCCATTGGTATGAAGGGTCAATTTCATCTTCAATTAAatcccgggcccgtcgact

The NREs are indicated in red and green. Adaptor primers are shown in lowercase.

## Protein Purification

The constructed recombinant plasmid was transformed into *E. coli* BL21 competent cells, and plated on LB solid medium containing appropriate antibiotics, and the positive transformants were identified. Single colonies were inoculated into LB liquid medium with antibiotic and incubated at 37°C overnight. The next day, the cultures were inoculated into 10 mL antibiotic-containing LB medium with 1:100 dilution and incubated at 37°C for about 1-2 h until $OD_{600nm}$ ~ 0.4 to 0.5, and then induced with 0.8mM IPTG. A culture without IPTG was used as a control. The bacteria were incubated at 28°C with shaking for 6 h and then were kept at 4°C for 10-30 min. Then the bacteria were centrifuged at 4,000 rpm for 5 min at 4°C to form a pellet. Then 3~6 mL of pre-cooled HIS Lysis Buffer (with 50 mM $NaH_2PO_4$ and 300 mM NaCl, pH=8.0) was used to resuspend the bacteria and the liquid was transferred into a 5 mL centrifuge tube. The tubes were then placed on ice and sonicated (Noise Isolating Chamber, Ningbo Scientz Biotechnology Co. Ltd) until the bacteria solution clarified. The supernatant was then centrifuged at 12,000g for 5 min on a microcentrifuge (Eppendorf) at 4°C and the supernatant was then transferred to a new tube after. Then 5 mL of HIS Lysis Buffer was used to wash the protein purification column, and 20-50 µL of Ni-NTA Agarose beads was added. The column containing beads was washed three times using HIS Lysis Buffer. The lysate supernatant was added to the column and was allowed to flow through for 1-2 h at 4°C. The column was then washed twice using HIS Lysis Buffer and once using a wash buffer containing 50 mM imidazole. In the end, 1-2 mL HIS Elution Buffer (with 50 mM $NaH_2PO_4$, 300 mM NaCl and 50 mM imidazole, pH=8.0) was applied to the column and collected. 20 µL samples in every step were collected and electrophoresed and identified by Coomassie brilliant blue staining. The imidazole in the eluate was removed by ultrafiltration to obtain the purified protein.

## Heterologous expression assays

For promoter-GUS analyses, the *LgHb7* promoter sequence was amplified by PCR and cloned into pENTR and then transferred to pKGWFS7 by the LR reaction; the vector PUB-GFP-HA was cut open with *Kpn* 1 and *Xba* 1, and then the *NLP2* and *NIN* CDS were amplified from cDNA and used to replace the GFP-HA in PUB-GFP-HA, using Gibson cloning (NovoRec plus One step PCR Cloning Kit, Novoprotein, Shanghai, China). For the mutant variants, PCR mutagenesis was used to mutate the RWP-RK domain as follows: *NLP2* WT 1861-1878 bp (AGATGGCCATCGCGCAAG: RWPSRK) to *NLP2m* (AGAGCGGCATCGCGCAAG: RAASRK), *NIN* WT 1966-1984bp (AGATGGCCTTCAAGAAAA: RWPSRK) to *NINm* (AGAGCGGCTTCAAGAAAA: RAASRK). The new constructs pKGWFS7-pLgHb7, PUB-NLP2 and PUB-NLP2m were used for transient transformation of *Nicotiana tabacum* L.. *N.*

*tabacum* leaves co-infiltrated with the constructs were stained with a solution containing 0.5 mM potassium ferricyanide, 0.5 mM potassium ferrocyanide, 0.5 mg/mL 5-bromo-4-chloro-3-indolyl-$\beta$-D-glucuronic acid (X-Gluc), 0.1 % Triton X-100, and 0.1 M sodium phosphate buffer (pH=7.0). The leaves were incubated at 37 °C in the dark for 12-24 h. To stop the reaction and clear the roots, the samples were washed with 75 % ethanol three times. GUS-staining was then photographed. For GUS quantification, *N. tabacum* leaves were infiltrated with the constructs and leaf discs were macerated with 50 mM disodium hydrogen phosphate, 10 mM $Na_2EDTA$, $\beta$-mercaptoethanol, 0.1 % Sarcosyl and 0.1 % TritonX-100) using a JXFSTPRP-48 tissue lyser (Jingxin, Shanghai). The resulting slurry was then centrifuged at 12,000 rpm for 10 min, the supernatant was then mixed with 20 mM 4-MUG and incubated at 37 °C in the dark for 60 min, and then stopped by adding 0.2 M sodium carbonate and then assayed spectrophotometry by microplate reader at 355 nm excitation and 460 nm emission filter. Protein concentrations of the samples were determined using a standard curve based on a concentration gradient made using 4-MUG and BSA.

The design of the dNRE-deleted version of the *LgHb7* promoter is shown below, the bases deleted are indicated by hyphens and the dNRE is indicated in red.

```
pLgHb7     AAATGATTATTGTCTCTTTAATAATGTCAACAGCCATTTCCACAAGCCAATAGATTCTTTAAAAAAAAAATCATAAAAAATC
pLgHb7 mut AAATGATTATTG-----------------------------------------------------------CATAAAAAATC
```

## $^{15}N_2$ fixation assays

The procedure used followed that described by (***30***). Briefly, *M. truncatula* plants 21 dpi with *S. meliloti* Rm2011 were removed from the soil substrate and the intact plants were incubated in 20 % $^{15}N_2$ gas (29 mLof air was removed and replaced with 29 mL $^{15}N_2$), and then incubated for 15 min. The incorporation of $^{15}N_2$ was determined separately by separating roots, shoots, and nodules. Tissue samples were dried overnight at 700 °C, and dry weights were determined. Then, around 100 mg of dried root or shoot was then crushed and sent for combustion and mass spec analysis. Total nitrogen and $^{15}N$ enrichment were measured in a continuous flow isotope ratio mass spectrometer (James Hutton Institute, UK).

## Transcriptomics data

The Affymetrix GeneChip Medicago Transcriptome Array was used in this experiment (***31, 33***). Total RNA was quantified using a NanoDrop ND-2000 (Thermo Scientific) and the RNA integrity was assessed using Agilent Bioanalyzer 2100 (Agilent Technologies). The sample labeling, microarray hybridization and washing were performed based on the manufacturer's standard protocols. Briefly, total RNAs were transcribed to double strand cDNAs and then synthesized cRNAs. Next, 2nd cycle cDNAs were synthesized from cRNAs. Followed fragmentation and biotin labeling, the 2nd cycle cDNAs were hybridized onto the microarray. After washing and staining, the arrays were scanned by the Affymetrix Scanner 3000 (Affymetrix). Affymetrix GeneChip Command Console (version 4.0, Affymetrix) software was used to extract raw data, carry out RMA normalization and to calculate P-values, and FDR corrected P-values. CVs were calculated using Excel.

### Promoter Analysis

The MEME suite was used to analyze 1kb regions upstream of the promoters of the 55 genes most strongly downregulated in *nlp2-1* nodules across conditions. The identified motifs were analyzed with the Tomtom using the Arabidopsis DAP motifs from O'Malley et al. (***34***).

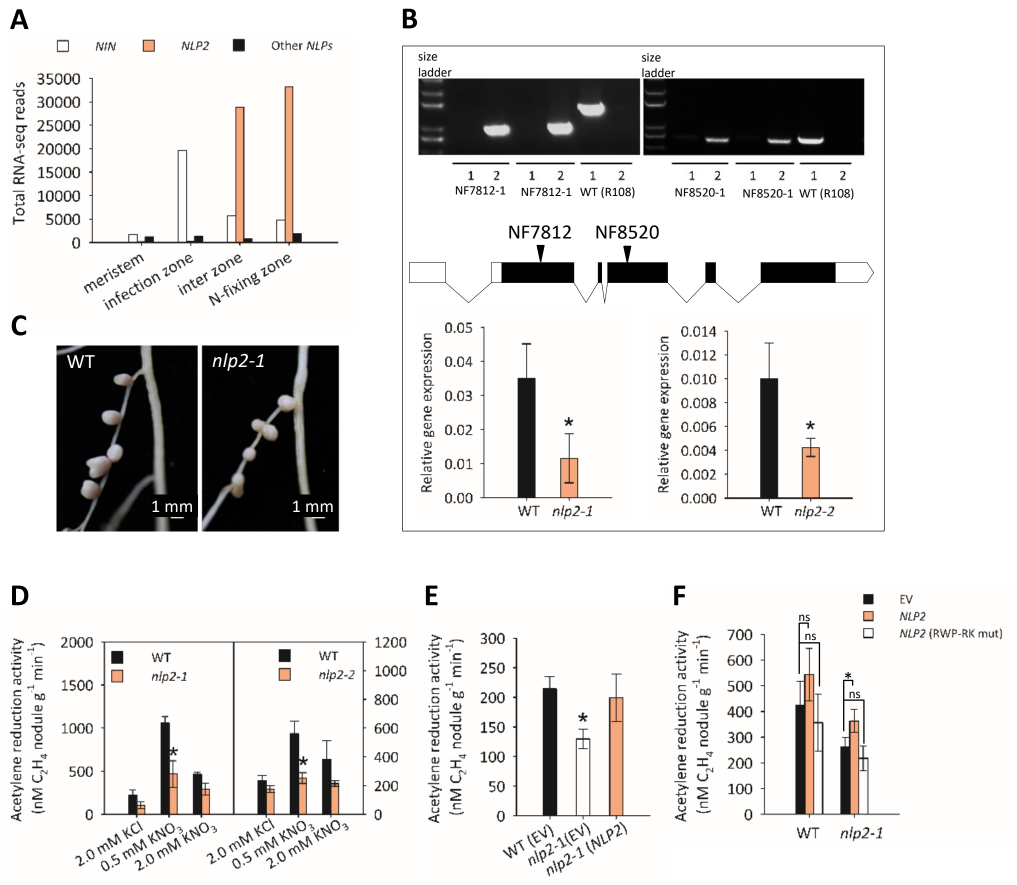


**figure S1. Expression of *NLPs* in *M. truncatula* and isolation of *NLP2 Tnt1* insertion mutants and their nodulation phenotypes.**

(**A**) Expression of *NIN*, *NLP2*, and the cumulative expression of all other *NLPs* (*NLP1*, *3*, *4*, *5*) across nodule zones. Data from laser capture dissection **(*21*)**. (**B**) Identification and characterization of *NLP2* transposon insertion mutants. Detection of two homozygous individuals with a *Tnt1* insertion in *NLP2* at +483 bp (*nlp2-1;* line NF7812) and +1188 bp (*nlp2-2*, NF8520). *EF* was used as a reference gene. (1) *NLP2* gene-specific primers (2) *Tnt1*-specific primer with a *NLP2*-specific primer. The positions of the insertions are indicated by arrowheads, solid black and white indicates exons and UTRs, respectively. Thin lines indicate introns. Relative expression of *NLP2* in *nlp2-1*, *nlp2-2*, and WT using qRT-PCR. n=3. *EF* was used as a reference gene. (**C**) Nodulated roots of WT and *nlp2-1* mutants, 21 dpi with *S. meliloti* Rm2011 (under 0.5 mM $KNO_3$). **(D)** ARA of plants nodulated with *S. meliloti* Rm2011 under different levels of $KNO_3$ or KCl and nodules assayed at 21 dpi. n=3. **(E)** Complementation of ARA in *nlp2-1*. *nlp2-1* seedlings were transformed with *pNLP2-NLP2* or empty vector (EV) controls and evaluated 21 dpi with *S. meliloti* Rm2011 nodulated under 0.5 mM $KNO_3$. n=3, each using nodules from 2-3 composite plants. (**F**) ARA of composite *nlp2* mutant plants transformed with either empty vector (EV) control or with *NLP2* or *NLP2* (RWP-RK mut) with a mutated RWP-RK domain, driven by the native *NLP2* promoter. n=3. For (B, D-F) means (±SD) were compared using Student's one-sided *t*-test, $\alpha$=0.05.

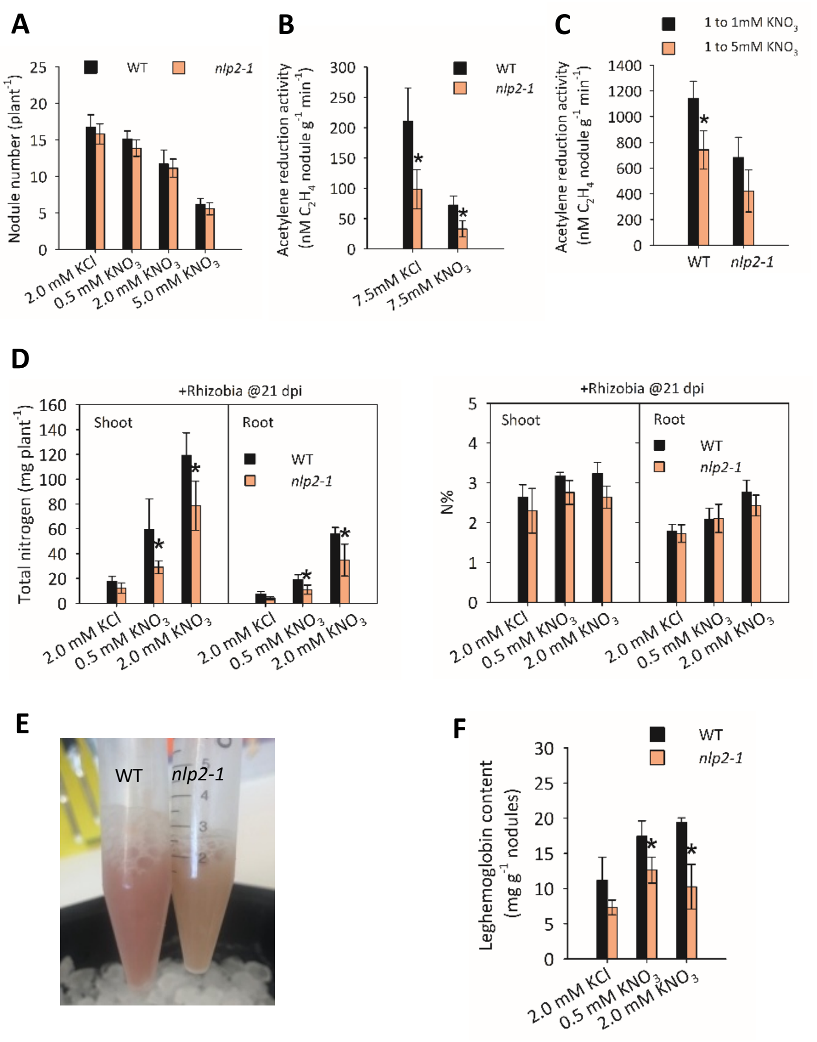
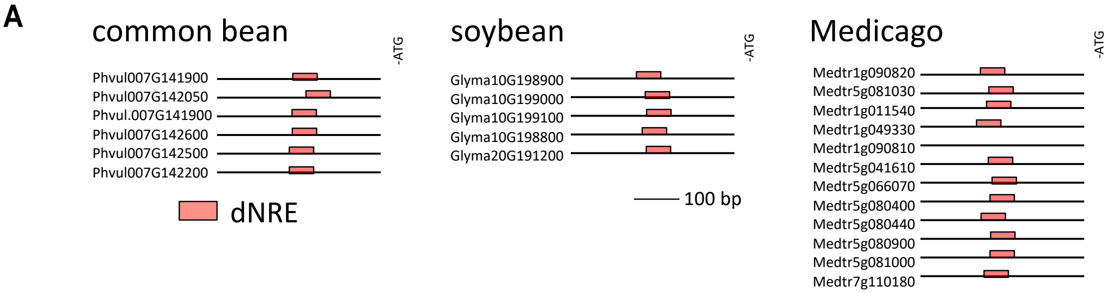


**figure S2**. **$N_2$-fixation and *LgHb* content is reduced in *nlp2-1* nodules.**

**(A)** Nodule numbers of WT and *nlp2-1* mutants under different weekly N-regimes at 21 dpi. **(B)** ARA (nM $C_2H_4$ nodule$^{-1}$ min$^{-1}$) of *nlp2-1* and WT nodules with weekly provision of 7.5 mM KCl or 7.5 mM $KNO_3$. (**C**) ARA of *nlp2-1* and WT nodules two days after addition of $KNO_3$. Plants were nodulated with a weekly provision of 1.0 mM $KNO_3$ and treated with either 1.0 or 5.0 mM $KNO_3$ at 21 dpi. **(D)** Total N (Kjeldahl's) and N% in *nlp2-1* and WT nodules. Plants were nodulated under 0.5 mM $KNO_3$ and evaluated at 21 dpi. (**E**) Ground nodule extracts of *nlp2-1* and WT at the same protein concentration. (**F**) nodule leghemoglobin content. For (A, B and F) , n= 3, for (C) n=4, for (D) n=3-4. Means are shown ±SD is indicated. Means were compared with Student's two-sided *t*-test, α=0.05. All plants were nodulated with *S. meliloti* Rm2011.



**B**

| Gene model | Gene | Promoter sequence | Expression log2(FKPM) | mismatches/ indels |
|---|---|---|---|---|
| Medtr5g066070 | LgHb9 | TTTTGTCTC-TTAATAACTACAATGGTCACCTCCACAAGCCATTATATTCTT | 19.7 | 2 |
| Medtr5g081030 | LgHb2 | TCTGGTCTC-TTCATAATTTCAATGGTCATTTCCACAAGCCAATAGATTCTT | 19.6 | 0 |
| Medtr5g081000 | LgHb8 | TATTGTCTCTATAATATTGTCAATAGCCATTTCCACAAGCCAATAGATTCAT | 19.6 | 0 (1 ins) |
| Medtr5g080440 | LgHb1 | TCTTGTCTC-TTAATAATTTTAATGGTCACCGCCACAAGCCAATAGATTCTT | 18.7 | 0 |
| Medtr1g011540 | LgHb7 | TATTGTCTCTTTAATAATGTCAACAGCCATTTCCACAAGCCAATAGATTCTT | 18.3 | 0 (1 ins) |
| Medtr5g041610 | LgHb6 | TCTTGTCTC-TTAATAATGTCAATAGCCACCTCCACAAGCCAACAAATTCTT | 17.8 | 0 |
| Medtr1g090820 | LgHb10 | AATTGTCTC-TTAATATTGCCAATGGCCACCTCTAAATTAAAGACCAATAGA | 17.7 | 6 |
| Medtr1g049330 | LgHb4 | GATTGTCTC-TTAATAATACCAATAGCCATCTCATAATTAAAGGCCAATAAA | 17.7 | 6 |
| Medtr5g080400 | LgHb3 | TCTTGTCTC-TTAATAATTTCAATGGTCACCCCCAGAAGCCAATAGATTCTT | 15.3 | 0 |
| Medtr1g090810 | LgHb11 | TATTATCTCTT----AATAAAGGTTGCCTCCTCTCAAAGGCCAAGAAATACT | 13.5 | 11 (3 del) |
| Medtr7g110180 | LgHb12 | TCACGACTC-TTTATAATAGTAATGGACGTTTCCACAAGCCAACAAATTTAA | 11.5 | 5 |
| Medtr5g080900 | LgHb5 | TATTGTTTCTTTGATAATGTCAATGACCATTTTCACGATTCTTTTAAATATA | 6.2 | 8 (1 ins) |
| Consensus dNRE | | **KKYYYY-WTMA** **YAAYRGYCAYYBC** **CCAAYARATT** | | /33 |

**C**

| Gene model | V2.0 Promoter sequence | Expression log2(FKPM | mismatches/ indels |
|---|---|---|---|
| Glyma10G199100 | TGTTTCTTCTTCATCATGCTGATTGACACCCTCCACAAGCCAAGAGAAACAC | 18.2 | 5 |
| Glyma10G199000 | CATTGGCTCTTCGTCATGCCGATTGACACCCTCCACAAGCCAAGAGAAACTT | 15.9 | 9 |
| Glyma20G191200 | ATTTGGCTCTTCATCATGCCGATTGACACCCTCCACAAGCCAAGAGAAACTT | 15.1 | 8 |
| Glyma10G198800 | GATTGTCTCTTCACCATACCAATTGATCACCCTCCTCCAACAAGCCAAGAGA | 15.0 | 10 |
| Glyma11G121800 | AAAATGGACTACGAAAACTTGAGTAACAAGGTAAGCCACACAAATGGGAATG | 6.2 | 18 |
| Glyma11G121700 | GTTTGTTTCTTGA-AAGCTCAATCAAAGAACGTGGCAACCAAAAGCATGGGA | 0.0 | 11 (1 del) |
| consensus dNRE | **KKYYYYWTMA** **YAAYRGYCAYYBC** **CCAAYARATT** | | /33 |

**figure S3. dNRE elements in promoters of *LgHbs* in different legumes.**
**(A)** dNRE elements (represented by single red boxes) detected in promoters of the *LgHb* homologs from *Phaseolus vulgaris* (common bean), *Glycine max* (soybean) and *M. truncatula* as detected by MEME. **(B)** Comparison of the similarity of dNRE motifs in *M. truncatula LgHb* promoters with the consensus dNRE motif and the expression of the corresponding *LgHb* genes in nodules. Data from (*21*). **(C)** Comparison of the similarity of dNRE motifs in soybean *LgHb* promoters with the consensus dNRE motif and the expression of the corresponding *LgHb* genes in nodules (FPKM: fragments per kilobase of exon model per million RNAseq reads mapped). Data from Soybase. Note a base was inserted (yellow highlighted N) into the consensus sequence to improve the alignment. In (B) and (C), conservation with the consensus motif is indicated in red. Mismatches are underlined. The numbers of mismatches, and insertions/deletions (indels) compared to the 33 bp semi-palindrome motif (indicated by arrows in B) are listed.

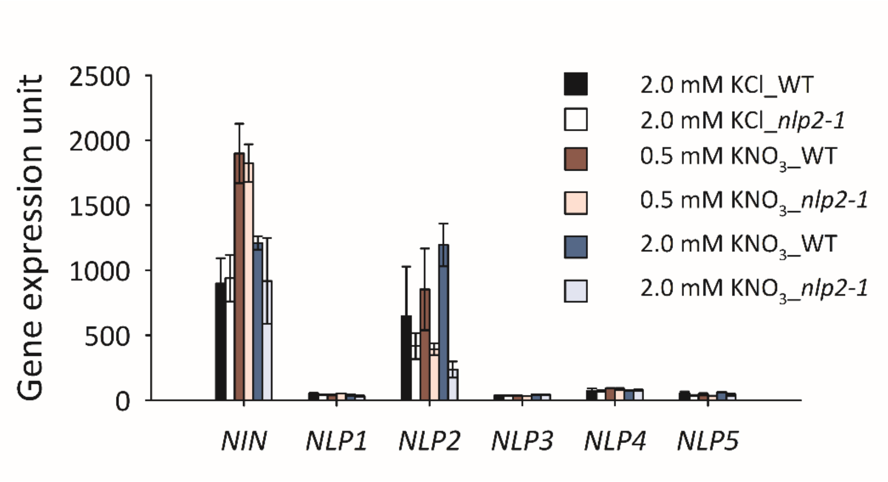


**figure S4**. **Expression of *NLPs* in WT and *nlp2-1* nodules under different N-regimes.**
Affymetrix GeneChip. Nodules from WT and *nlp2-1* were harvested at 21 dpi with *S. meliloti* Rm2011.

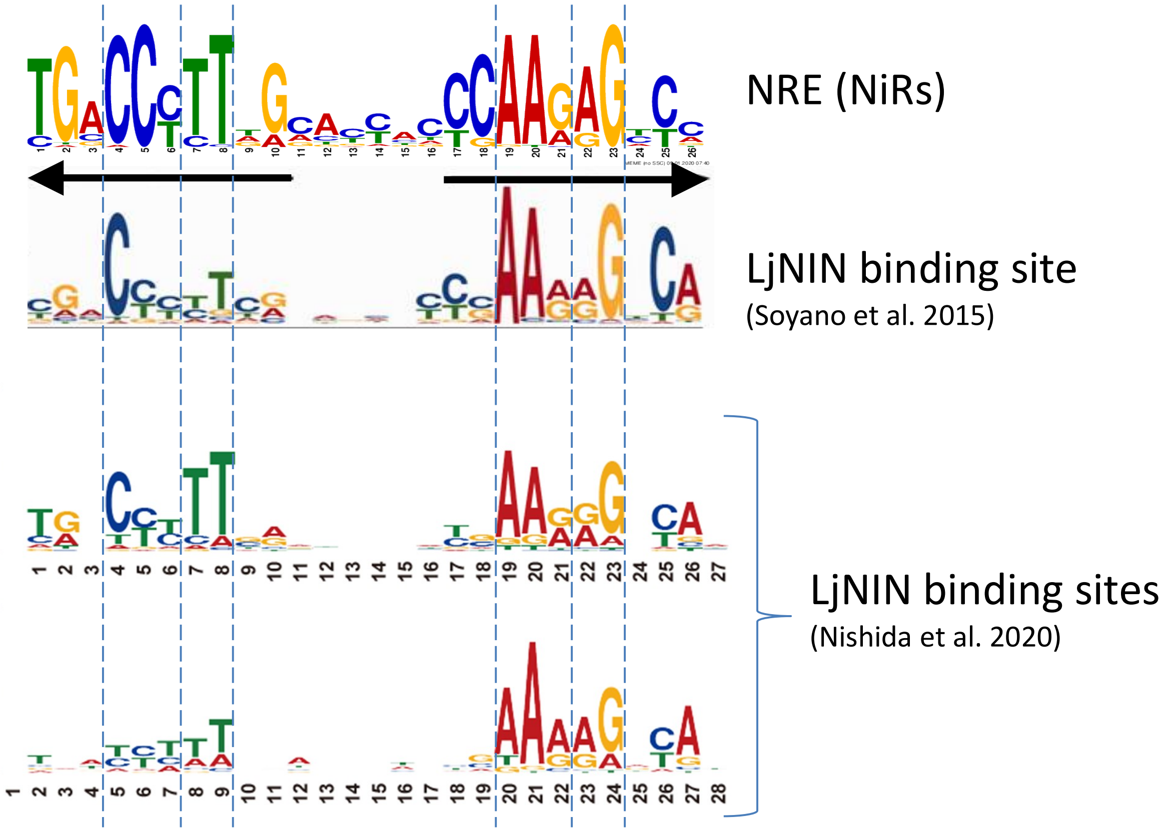


**figure S5. Comparison of NRE and NBS motifs.**
NRE that was determined from 38 *NIR* promoters using MEME is aligned to the reported NIN-binding sites (NBS) (*9, 10*). The semi-palindrome is indicated by arrows. Dotted lines are provided to aid in visual comparison.

RWP-RK (NLP2 WT  1861-1878bp from ATG)
AGATGGCCATCGCGCAAG
 R  W  P  S  R  K

RWP-RK (NLP2 mutation)
AGAGCGGCATCGCGCAAG
 R  A  A  S  R  K

RWP-RK (NIN WT  1966-1984bp from ATG)
AGATGGCCTTCAAGAAAA
 R  W  P  S  R  K
RWP-RK (NIN mutation)
AGAGCGGCTTCAAGAAAA
 R  A  A  S  R  K

**figure S6. Mutated versions of NIN and NLP2 used for EMSA.** The predicted changes in protein sequence are shown below the coding sequence.

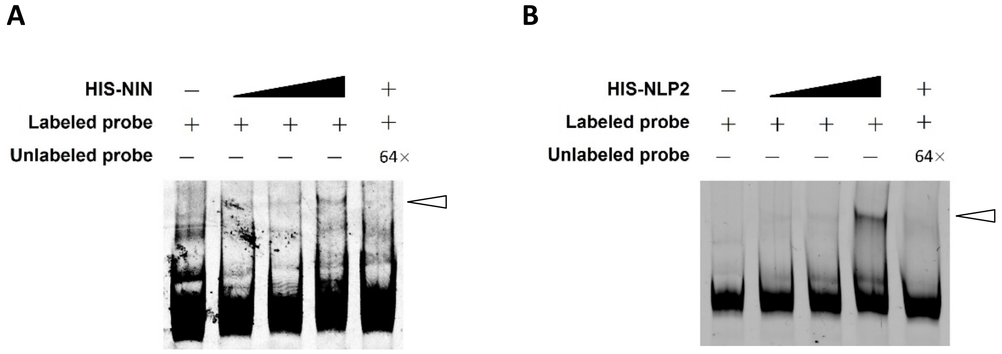


**figure S7. EMSA to test for interaction between a *LgHb1* promoter fragment with NLP2 and NIN.** (**A**) CY5-labeled *LgHb1* promoter fragment containing the dNRE with HIS-tagged NIN fragment containing the RWP-RK domain. (**B**) EMSA using CY5-labeled *LgHb1* promoter fragment containing the dNRE and a HIS-tagged NLP2 fragment containing the RWP-RK domain. Arrows indicate a band that was abolished by addition of excess unlabeled probe.

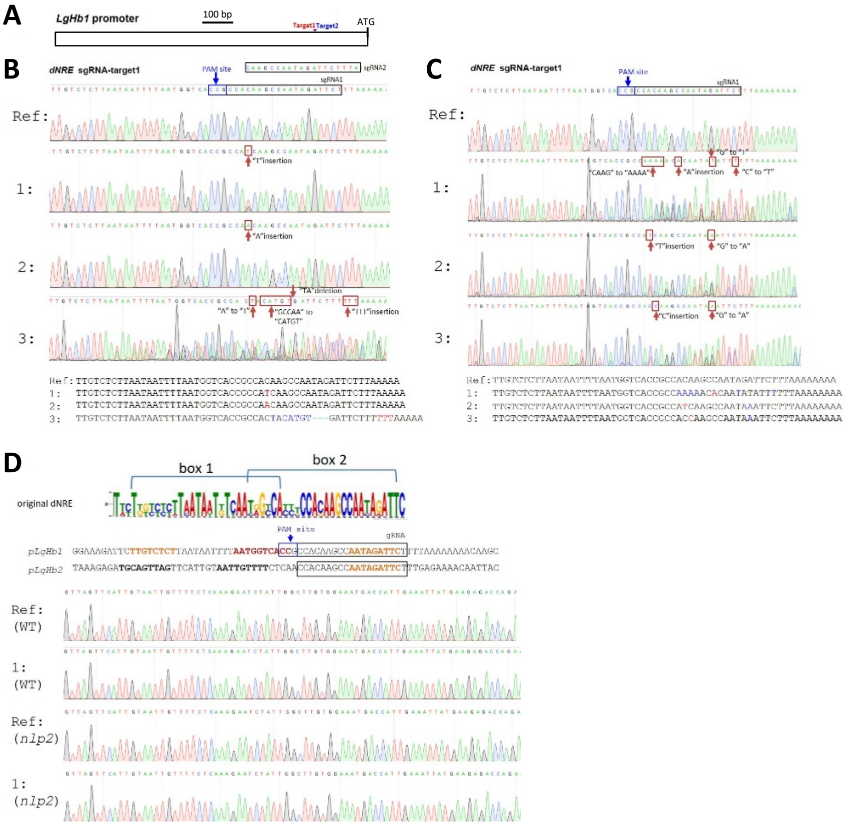


**figure S8. Targeted mutation of the dNRE element in the promoter of *LgHb1*.**
**(A)** Location of the dNRE target in the *LgHb1* promoter **(B, C)** Editing events in WT (A) and *nlp2-1* (C) nodules of composite plants transformed with *p35S:Cas9* and two gRNAs targeting the dNRE of *LgHb1* (dNRE-KO) using *A. rhizogenes* hairy-root transformation. DNA was harvested from nodules harvested 21 dpi with *S. meliloti* Rm2011 and the target region was PCR amplified and sequenced. In (B) and (C) Ref indicates sequence of target region of nodules from WT or *nlp2-1* roots transformed with empty vector (EV), and 1-3 represent sequences of the target region from individual nodules of dNRE-KO plants. Mutations are indicated in the chromatogram with red arrows and boxes, and are shown below in red (insertions), blue (substitutions) or green (deletion) text. **(D)** The *M. truncatula* R108 genome was searched for other potential binding sites for the gRNAs. Only one other perfectly matching site was found in the promoter sequence of *LgHb2* corresponding to the dNRE; gRNA1 was found to be perfectly complementary to the *LgHb2* dNRE but lacked a PAM site, so this site was used as a negative control. The original dNRE motif is shown for reference. The *LgHb2* promoter was not edited in either WT or *nlp2-1* nodules of the dNRE-KO plants.

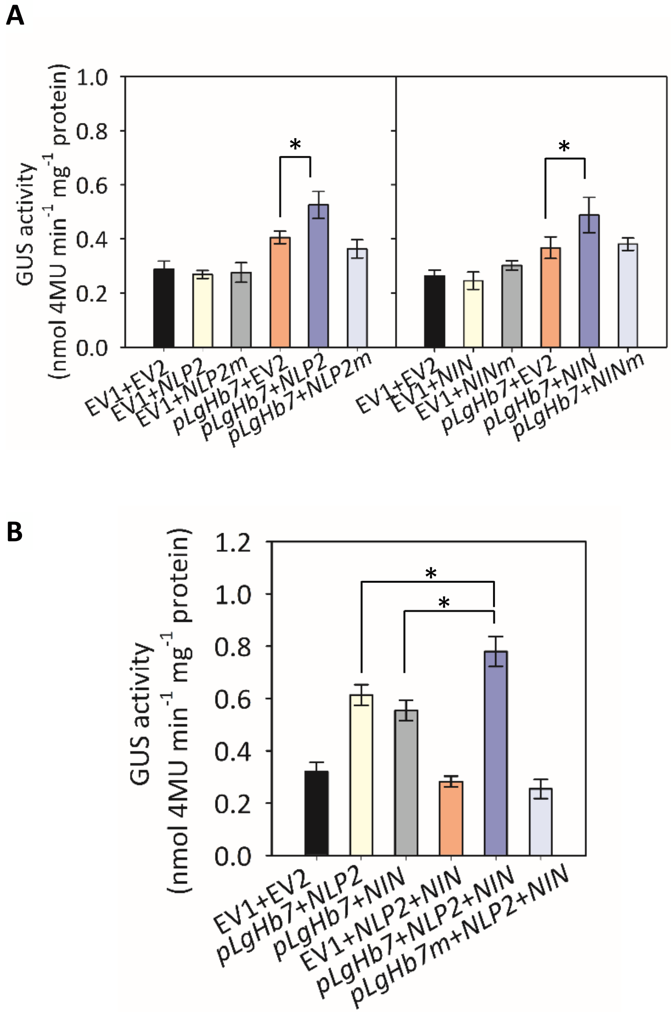


**figure S9. Trans-activation of the *LgHb7* promoter by NLP2 and NIN.**
(**A**) The *pLgHb7:GUS* reporter was co-infiltrated into *N. benthamiana* leaves with either vectors for expression of *NLP2*, *NIN,* or versions of these vectors in which the RWP-RK sequence has been mutated (*NLP2m* and *NINm*). (**B**) *A. tumefaciens* carrying vectors for expression of *NIN* and/or *NLP2* were co-infiltrated into *N. benthamiana* with a vector in which the *GUS* gene is driven by a -342 to -1 bp fragment of the *LgHb7* promoter (*pLgHb7*) containing the dNRE or a mutated form (*LgHb7m)* with the dNRE deleted (see supplemental methods for details). EV1: empty vector no-promoter control, EV2: empty vector no-*NLP2* control. *NLP2* and *NIN* expression were driven by the 35S promoter. n=3, ±SD. Each replicate consisted of six leaves. α=0.05, means were compared using a Student's *t*-test.

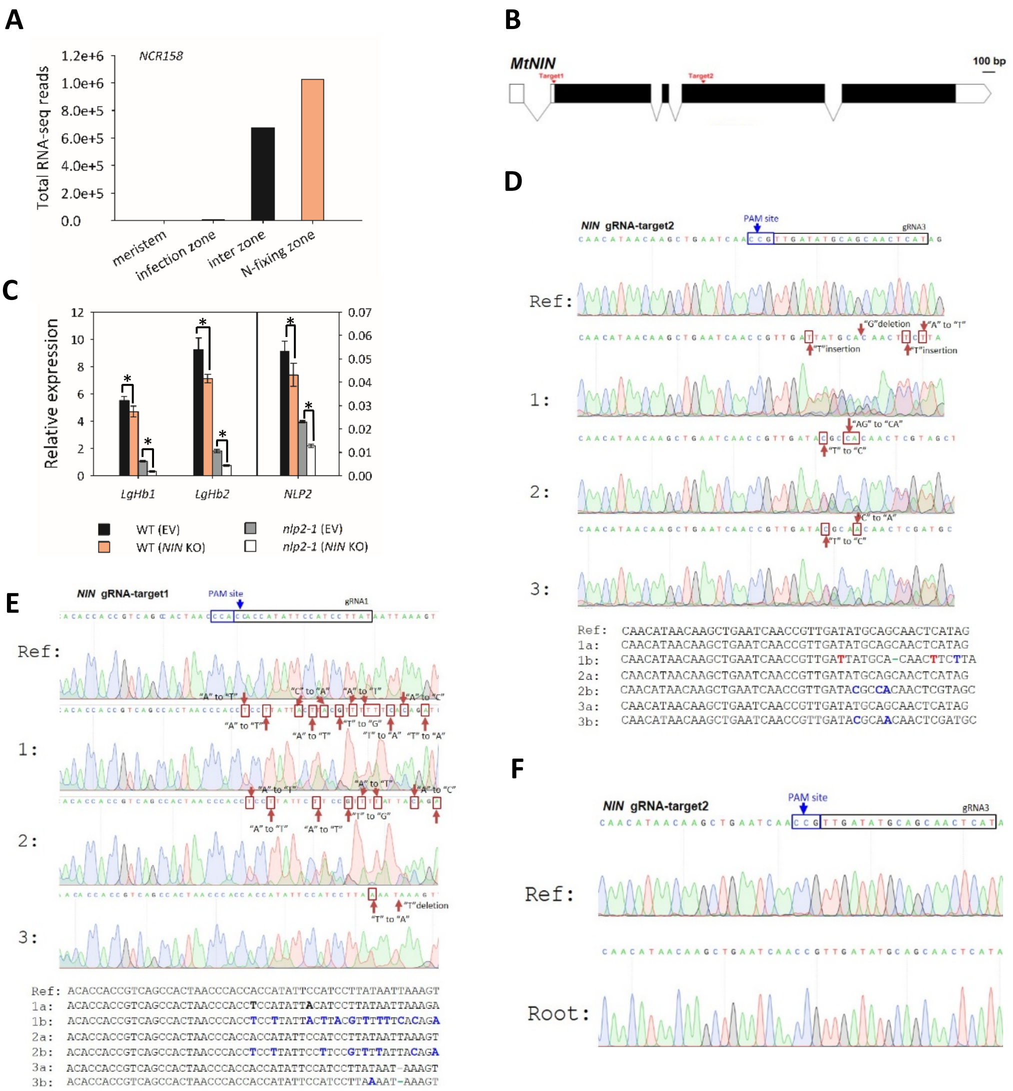
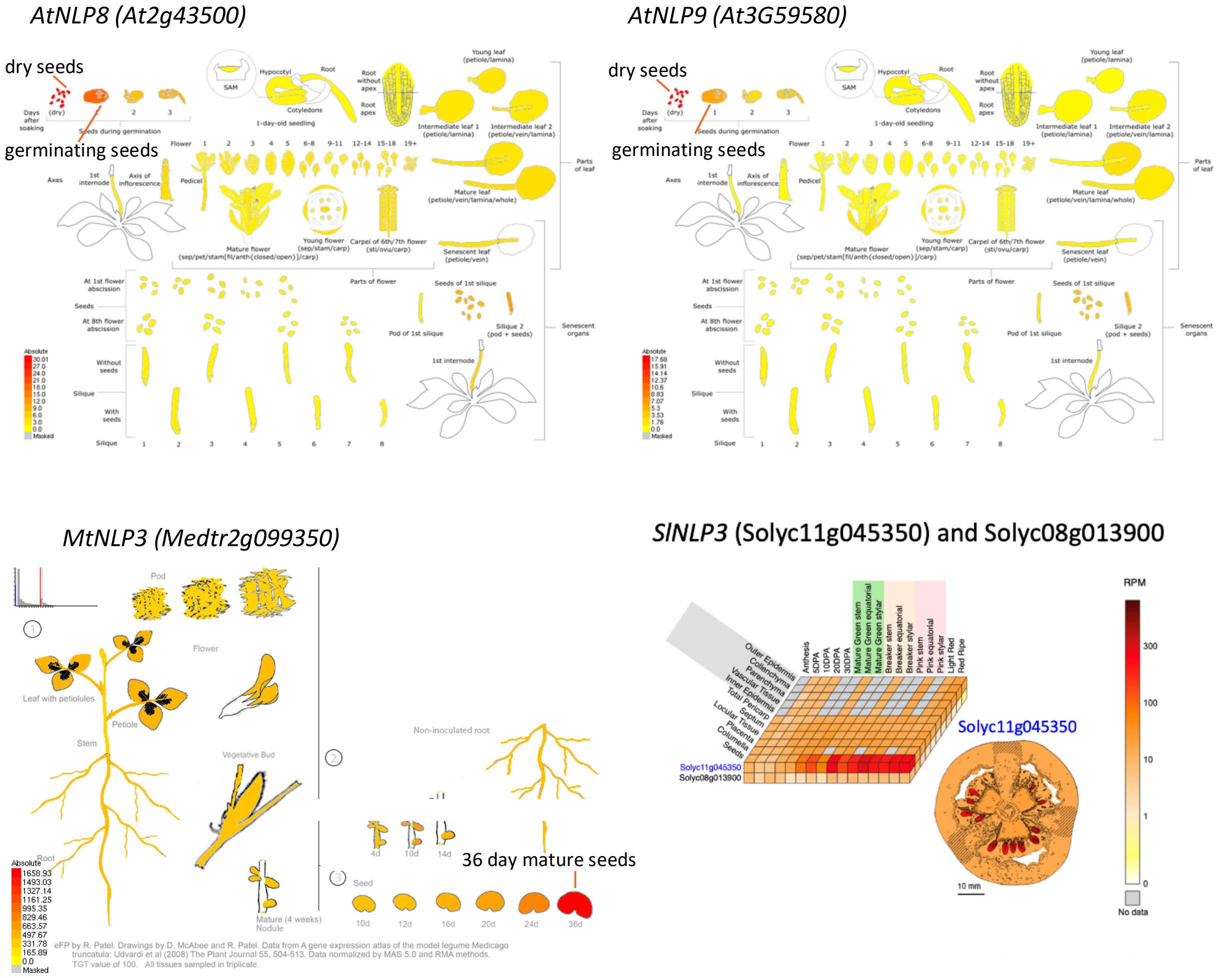


**figure S10. CRISPR-induced editing of *NIN* in WT and *nlp2-1* nodules using tissue-specific knockout.** *NIN*-KO constructs containing *Cas9* driven by the *NCR158* promoter which is expressed specifically in the nodule $N_2$-fixation zone, were introduced into *M. truncatula* roots using *A. rhizogenes* hairy-root transformation. **(A)** Expression of *NCR158* (Medtr7g027180) across nodule zones. Data from (*29*). **(B)** The position of the gRNAs targets used to edit *NIN* in WT (target 2) and *nlp2-1* (target 1). (**C**) Relative expression (qRT-PCR) of *LgHb1*, *LgHb2* and *NLP2* in nodules of *NIN*-KO and empty vector (EV) transformed roots of *nlp2-1* and WT. **(D)** One nodule was harvested from roots of seven separate *NIN*-KO composite plants. In five of the seven plants target 2 was edited and no editing was seen in nodules of the other two plants. Three examples of editing are shown for gRNA2. **(E)** A construct with a gRNA targeting *NIN* (target 1) was introduced into *nlp2-1* by hairy-root transformation. Three examples of editing are shown (1-3). For (B and C) nodules of EV-transformed roots were used as a reference and mutations are indicated in the chromatogram with red arrows and boxes and are shown below in red (insertions), blue (substitutions) or green (deletion) text. **(F)** Roots from nodulated WT plants transformed with *NIN*-KO were not edited at target site 2.



*AtNLP8 (At2g43500)*

*AtNLP9 (At3G59580)*

*MtNLP3 (Medtr2g099350)*

*SlNLP3* (Solyc11g045350) and Solyc08g013900

**fig S11. Some orthologs of nodule expressed NLPs are expressed in seeds.** Expression profiles of *AtNLP8/9* in *A. thaliana*, Solyc11g045350 and Solyc08g013900 in *Solanum lycopersicum* (tomato), and *MtNLP3*. Data from the Medicago Gene Atlas v3.0 (presented with the eGFP browser (presented with the eGFP browser (*32, 34, 35*) and from the "Tomato Expression Atlas": tea.solgenomics.net".

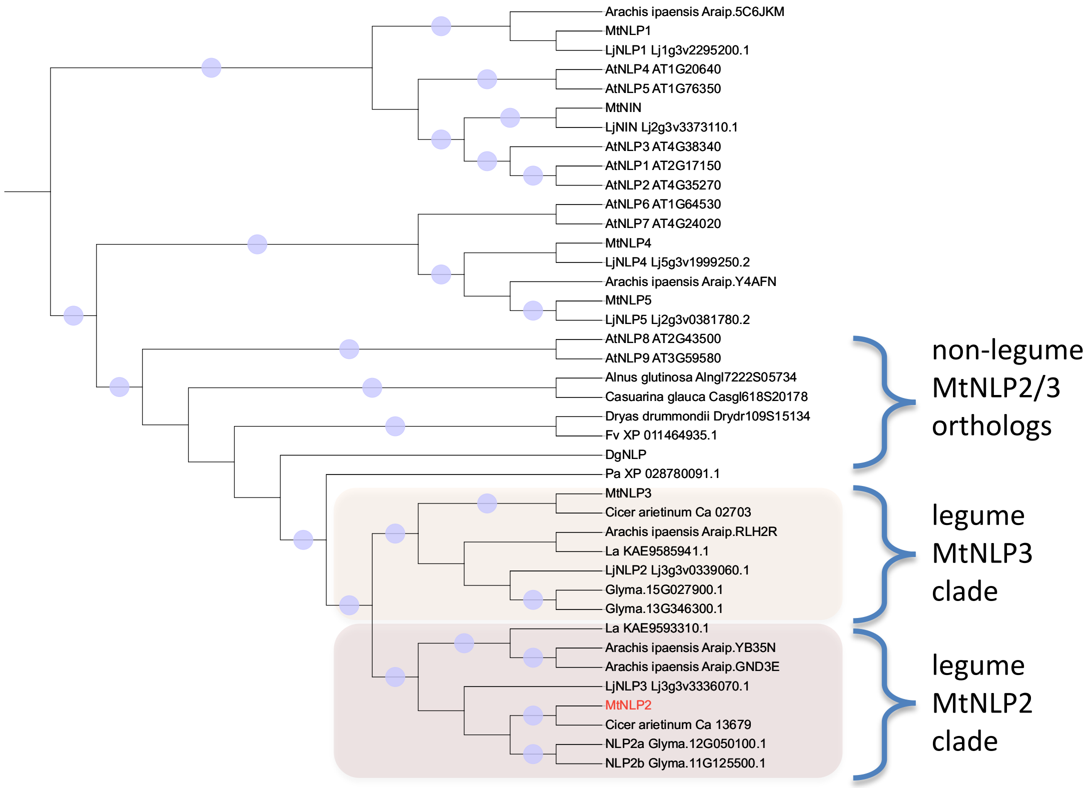


**figure S12. Phylogenetic distribution of NLPs.** MtNLP2 belongs to a legume-specific clade and has orthologs in papilionoid legumes but none in the early diverged legume *Prosopis alba* (Pa) (*Caesalpiniodeae*), and the nodulating non-legumes *Datisca glomerata* (Dg)*, Casuarina glauca,* and *Alnus glutinosa.* MtNLP2 is indicated in red, the MtNLP3 and MtNLP2 clades are indicated by shading. Glyma: *Glycine max*, La: *Lupinus angustifolius,* Fv: *Fragaria vesca.* At: *Arabodopsis thaliana,* Lj: *Lotus japonicus,* Mt: *Medicago truncatula.* The circles indicate >85% bootstrap branch support.

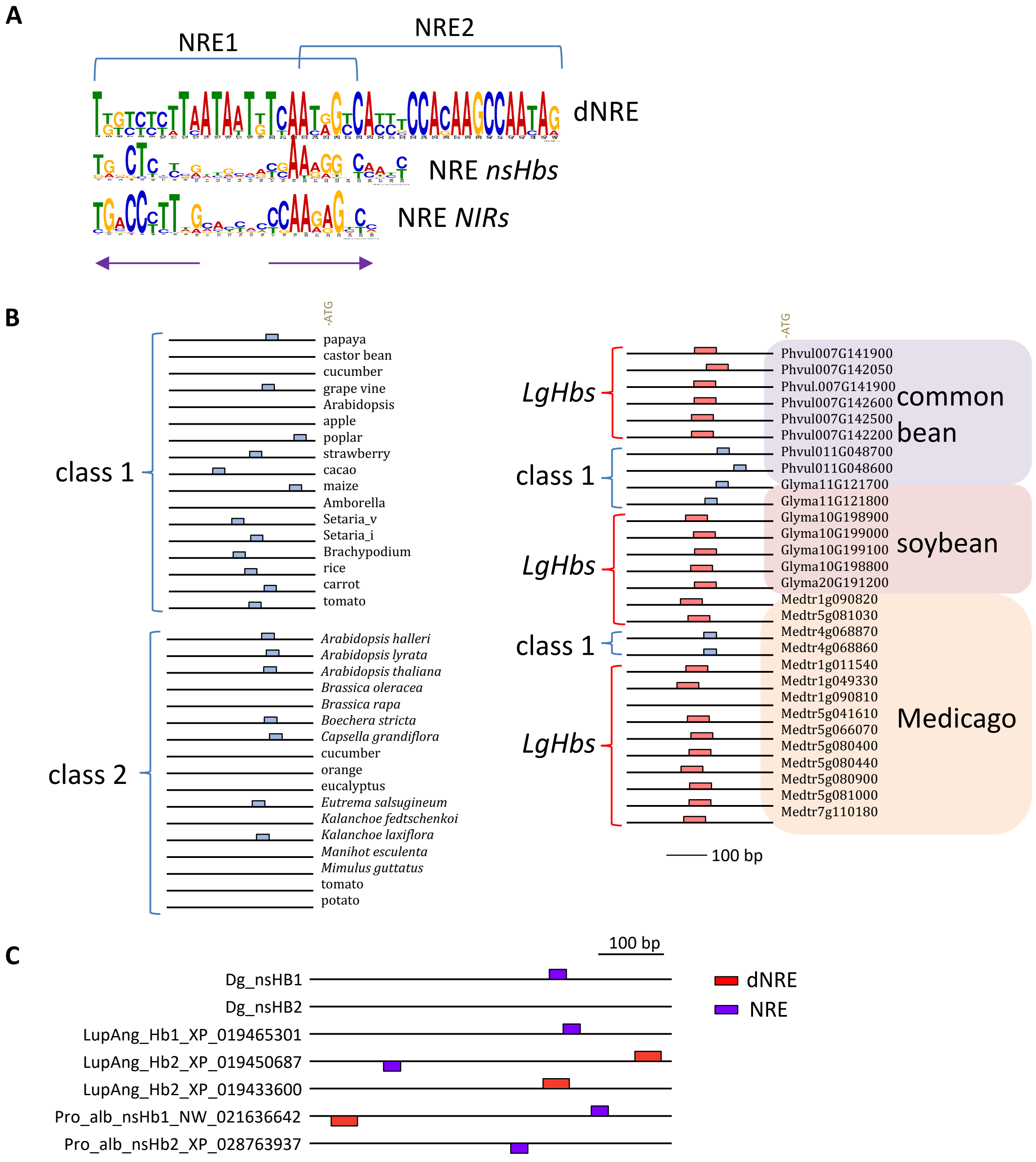


**figure S13. NRE and dNRE elements in promoters of *nsHbs* and *LgHbs*.**
**(A)** Motifs of NRE elements detected in promoters of 18 of 23 class I *nsHbs*, and 8 of 17 class II *nsHbs*. The dNRE and the NRE detected in promoters of 38 *NIR* genes from different species are aligned for comparison. **(B)** Positions of NREs and dNREs in promoters of class I and class II *nsHbs* and *LgHbs*. The motifs were detected using MEME. (**C**) dNRE and NRE elements in *Hb* promoters of *Datisca glomerata* (Dg), *Prosopis alba* (Pro_alb) and *Lupinus angustifolius* (LupAng). Motifs were detected by meme using an an extended dataset of NRE/dNRE containing promoters.

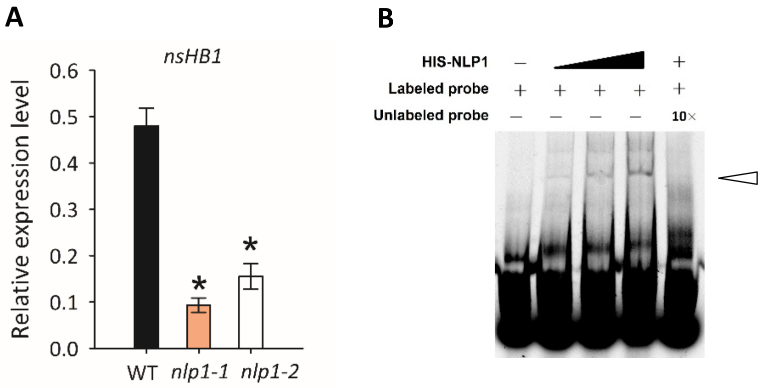


**figure S14. NLP1 regulates the expression of *M. truncatula nsHB1* and binds to its NRE motif.**
**(A)** Relative expression of the *M. truncatula nsHB1* under nitrate replete conditions. n=4. The means are shown ±SD and were compared using Student's *t*-test, n=3, α=0.05. *EF* was used as a reference gene. **(B)** EMSA showing binding of NLP1 to a probe with 2×NRE from the *nsHB1* (Medtr4g068860) promoter. Details on the probe design are provided in the Supplementary Material. Arrow indicates band that was abolished by addition of excess unlabeled probe.

**Table S1. Expression of heme biosynthesis genes and nitrate transporters in nodules of *nlp2-1* and WT of plants nodulated under different $NO_3^-$ regimes.** Affymetrix GeneChip. P value, *P<0.05, **P <0.01.

| | | ***nlp2*/WT (gene expression units)** | | | | | |
|---|---|---|---|---|---|---|---|
| **Gene model** | **Encoded protein** | **2.0 mM KCl** | | **0.5 mM $KNO_3$** | | **2.0 mM $KNO_3$** | |
| | | **Fold change** | **P value** | **Fold change** | **P value** | **Fold change** | **P value** |
| Medtr5g098800 | coproporphyrinogen III oxidase | -1.39* | 0.04 | -1.3 | 0.33 | -1.56* | 0.02 |
| Medtr2g076340 | uroporphyrinogen decarboxylase | 1.07 | 0.57 | 1.1 | 0.53 | -1.32 | 0.06 |
| Medtr3g072330 | uroporphyrinogen decarboxylase | -1.14 | 0.17 | 1.31* | 0.01 | -1.24 | 0.11 |
| Medtr1g052525 | uroporphyrinogen III synthase | -1.43 | 0.40 | -1.38 | 0.17 | -1.16 | 0.26 |
| Medtr3g101350 | uroporphyrinogen III synthase | -1.03 | 0.86 | 1.1 | 0.57 | -1.14 | 0.36 |
| Medtr7g034345 | uroporphyrinogen-III C-methyltransferase | -1.07 | 0.70 | -2.19** | 8.4E-05 | -2.67** | 8.2E-05 |
| Medtr3g026780 | uroporphyrinogen-III C-methyltransferase | -1.04 | 0.81 | -3.37** | 4.8E-07 | -2.61** | 6.2E-06 |
| Medtr3g075110 | oxygen-independent coproporphyrinogen III oxidase, putative | 1.52* | 0.04 | -1.01 | 0.95 | 1.44 | 0.21 |
| Medtr3g118070 | glutamate-1-semialdehyde 2,1-aminomutase | -1.02 | 0.16 | -1.31** | 0.01 | -1.57** | 3.6E-05 |
| Medtr1g085730 | protoporphyrinogen IX oxidase | -1.16 | 0.15 | -1.39 | 0.06 | -1.89* | 0.001 |
| Medtr3g088610 | delta-aminolevulinic acid dehydratase | -1 | 0.95 | 1.29* | 0.04 | -1.53* | 0.01 |
| Medtr4g057890 | *NRT2.2* | -2.56 | 0.12 | -5.55* | 0.004 | -6.28* | 0.05 |
| Medtr4g057865 | *NRT2.1* | -3.27 | 0.07 | -6.87* | 0.003 | -5.40* | 0.05 |
| Medtr4g104730 | *NAR2.1b* | -2.42** | 0.003 | -2.38** | 0.0001 | -2.13* | 0.02 |
| Medtr4g104700 | *NAR2.1a* | -1.92** | 0.01 | -2.03** | 0.001 | -1.92** | 0.01 |

**Table S2. Expression of JA biosynthesis genes in nodules of *nlp2-1* and WT of plants nodulated under 2.0 mM KCl or 2.0 mM $KNO_3$.** Affymetrix GeneChip. P value, *P<0.05, **P <0.01.

| **Gene model** | **Gene name** | ***nlp2-1*/WT (gene expression unit)** | | | |
|---|---|---|---|---|---|
| | | **2.0 mM KCl** | | **2.0 mM $KNO_3$** | |
| | | **Fold change** | **P value** | **Fold change** | **P value** |
| Medtr5g013530 | *Jasmonate ZIM-domain Protein 1A (JAZ1A)* | 1.07 | 0.29 | 6.43* | 0.03 |
| Medtr2g042900 | *Jasmonate ZIM-domain Protein 2 (JAZ2)* | -1.25 | 0.26 | 2.09** | 0.01 |
| Medtr4g054920 | *CYP94C1* | -1.1 | 0.07 | 2.23 | 0.06 |
| Medtr5g053950 | *Allene Oxide Cyclase 4 (AOC 4)* | -1.01 | 0.42 | 2.07* | 0.05 |
| Medtr7g068780 | *Fatty Acid Desaturase 8 (FAD8)* | -1.02 | 0.43 | 2.28** | 0.002 |
| Medtr8g067280 | *MYC2* | 1.08 | 0.44 | 1.51 | 0.10 |

## Table S3. NRE and dNRE elements detected in promoters of the 55 most strongly downregulated genes in *nlp2* nodules.

| Gene Model (Mtv4.0) | Mtv4.0 annotation | NRE/dNRE |
|---|---|---|
| **Medtr2g100710.1** | 6-phosphofructokinase | |
| **Medtr1g026070.1** | anaphase-promoting complex subunit 11 RING-H2 | |
| **Medtr3g089005.1** | basic blue-like protein | NRE |
| **Medtr3g089125.1** | bidirectional sugar transporter | NRE |
| **Medtr2g099790.1** | calmodulin-binding family protein | NRE |
| **Medtr1g093850.1** | CHUP | NRE |
| **Medtr3g079850.1** | *SymCRK* | NRE |
| **Medtr4g130780.1** | early nodulin-like protein | |
| **Medtr4g099400.1** | expansin-B1-like protein | |
| **Medtr4g086020.1** | ferredoxin-nitrite reductase (NiR) | NRE |
| **Medtr1g069825.1** | G1-like protein | |
| **Medtr5g067410.1** | glutamyl-tRNA reductase | |
| **Medtr5g081555.1** | hypothetical protein | |
| **Medtr8g044120.1** | hypothetical protein | |
| **Medtr4g107630.1** | integral membrane HPP family protein | |
| **Medtr7g099870.1** | ion channel regulatory protein UNC-93 | |
| **Medtr7g114870.1** | IQ calmodulin-binding motif protein | NRE |
| **Medtr3g030420.1** | late nodulin | NRE |
| **Medtr6g091605.1** | late nodulin | NRE |
| **Medtr1g011540.1** | *LgHb7* | dNRE |
| **Medtr1g049330.1** | *LgHb4* | NRE |
| **Medtr1g090810.1** | *LgHb11* | NRE |
| **Medtr5g041610.1** | *LgHb6* | dNRE |
| **Medtr5g080400.1** | *LgHb3* | dNRE |
| **Medtr5g080440.1** | *LgHb1* | dNRE |
| **Medtr5g081000.1** | *LgHb8* | dNRE |
| **Medtr5g081030.1** | *LgHb2* | dNRE |
| **Medtr0693s0050.1** | Myb/SANT-like DNA-binding domain protein | |
| **Medtr4g128540.1** | Myb/SANT-like DNA-binding domain protein | NRE |
| **Medtr7g103390.1** | Myb/SANT-like DNA-binding domain protein | |
| **Medtr0003s0210.1** | Nodule Cysteine-Rich (NCR) secreted peptide | NRE |
| **Medtr0111s0050.1** | Nodule Cysteine-Rich (NCR) secreted peptide | NRE |
| **Medtr0115s0030.1** | Nodule Cysteine-Rich (NCR) secreted peptide | NRE |
| **Medtr1g041915.1** | Nodule Cysteine-Rich (NCR) secreted peptide | NRE |
| **Medtr2g048203.1** | Nodule Cysteine-Rich (NCR) secreted peptide | NRE |
| **Medtr2g450630.1** | Nodule Cysteine-Rich (NCR) secreted peptide | |
| **Medtr3g006650.1** | Nodule Cysteine-Rich (NCR) secreted peptide | |
| **Medtr3g031320.1** | Nodule Cysteine-Rich (NCR) secreted peptide | NRE |
| **Medtr3g436500.1** | Nodule Cysteine-Rich (NCR) secreted peptide | NRE |
| **Medtr4g059900.1** | Nodule Cysteine-Rich (NCR) secreted peptide | NRE |
| **Medtr6g090485.1** | Nodule Cysteine-Rich (NCR) secreted peptide | NRE |
| **Medtr7g071310.1** | Nodule Cysteine-Rich (NCR) secreted peptide | NRE |
| **Medtr8g039130.1** | Nodule Cysteine-Rich (NCR) secreted peptide | NRE |
| **Medtr8g064070.1** | Nodule Cysteine-Rich (NCR) secreted peptide | NRE |
| **Medtr8g069310.1** | Nodule Cysteine-Rich (NCR) secreted peptide | |
| **Medtr2g041100.1** | Nodule-specific Glycine Rich Peptide | NRE |
| **Medtr5g069890.1** | Nodule-specific Glycine Rich Peptide | NRE |
| **Medtr7g098180.1** | peptide transporter | |

| | | |
|---|---|---|
| **Medtr8g090375.1** | peroxisomal acyl-CoA oxidase | |
| **Medtr1g080020.1** | phosphoenolpyruvate carboxylase-related kinase | |
| **Medtr6g060570.1** | phosphopyruvate hydratase | NRE |
| **Medtr2g085065.1** | Serine/Threonine kinase family protein | |
| **Medtr5g027460.1** | transmembrane protein, putative | |
| **Medtr4g088350.1** | triose phosphate/phosphate translocator | |
| **Medtr4g094335.1** | *SEN1* | NRE |

**Table S4. Accession numbers of genes mentioned in this manuscript.** Heme and JA related genes are provided in Tables S1 and S2, respectively.

| Abbreviation | Gene name | Gene ID |
|---|---|---|
| *NIN* | *Nodule Inception* | Medtr5g099060 |
| *NLP1* | *NIN-LIKE PROTEIN 1* | Medtr3g115400 |
| *NLP2* | *NIN-LIKE PROTEIN 2* | Medtr4g068000 |
| *NLP3* | *NIN-LIKE PROTEIN 3* | Medtr2g099350 |
| *NLP4* | *NIN-LIKE PROTEIN 4* | Medtr1g100970 |
| *NLP5* | *NIN-LIKE PROTEIN 5* | Medtr0022s0430 |
| *LgHb1* | *Leghemoglobin 1* | Medtr5g080440 |
| *LgHb2* | *Leghemoglobin 2* | Medtr5g081030 |
| *LgHb3* | *Leghemoglobin 3* | Medtr5g080400 |
| *LgHb4* | *Leghemoglobin 4* | Medtr1g049330 |
| *LgHb5* | *Leghemoglobin 5* | Medtr5g080900 |
| *LgHb6* | *Leghemoglobin 6* | Medtr5g041610 |
| *LgHb7* | *Leghemoglobin 7* | Medtr1g011540 |
| *LgHb8* | *Leghemoglobin 8* | Medtr5g081000 |
| *LgHb9* | *Leghemoglobin 9* | Medtr5g066070 |
| *LgHb10* | *Leghemoglobin 10* | Medtr1g090820 |
| *LgHb11* | *Leghemoglobin 11* | Medtr1g090810 |
| *LgHb12* | *Leghemoglobin 12* | Medtr7g110180 |
| *NCR158* | *Nodule-specific, cysteine-rich 158* | Medtr7g027180 |
| *NIR* | *Nitrite Reductase* | Medtr4g086020 |
| *nsHB1* | *Non-symbiotic Hemoglobin 1* | Medtr4g068860 |

## Table S5. Oligo DNA sequence for PCR primers used in this study

| Primer name | Purpose | Sequence (5'-3') |
|---|---|---|
| NF7812-F | *nlp2-1* mutant screening | GTTTAGTTGTTTGTCTTGTTTG3 |
| NF7812-R | | CAAAGTATATGGTGGAAGTAGC |
| Tnt1-F | | TCCTTGTTGGATTGGTAGCCAACTTTGTTG |
| NF8520-F | *nlp2-2* mutant screening | GAGCTGCATTAACAGAGATA |
| NF8520-R | | CTGACTGTAAGCAGCTTGAT |
| qMtEF-F | qPCR | CTTTGCTTGGTGCTGTTTAGATGG |
| qMtEF-R | | ATTCCAAAGGCGGCTGCATA |
| nsHB-qF | qPCR | TAGCACGTAACCCTTACCCTTCAG |
| nsHB-qR | | GTTTTTGAGCTGATGGAGCAATCTC |
| qMtNIN_F | qPCR | GCAAAGAGCATCGGTGTGTG |
| qMtNIN_R | | GCCAATCTGTATGGCACCCT |
| qLgHb1-F | qPCR | CTGAGGGGATTTATGCCAAA |
| qLgHb1-R | | TTCTCCAGTTGCTCGGAGTT |
| qLgHb2-F | qPCR | TTCAACTTCGAGCAACAGGA |
| qLgHb2-R | | TGCCAATCCATCATAAGCAA |
| qLgHb7-F | qPCR | TGTTCAACTCCGAGCAACAG |
| qLgHb7-R | | TCCCAAATTTAACCCATTGC |
| qLgHb8-F | qPCR | GAGAAAGCACCTGCAGCAAA |
| qLgHb8-R | | TGTGCAGCTGAATCGCGTA |
| qNLP2-F | qPCR | GCACAAGTTTGGGCACCTAT |
| qNLP2-R | | AGGTCCATTCAGGAACATGC |
| qNiR-F | qPCR | GGACGATGGAGTTGAGAAAG |
| qNiR-R | | ATGTTTTTGGACGAGTGATG |
| pNLP2-F | Construct pL0V-PU-41295 | GAAGACTTGGAGAGAGTTGGGTCGTGAAATAT |
| pNLP2-R | | GAAGACTTCATTGTTCAGGTTGGTGAGAAAATTAG |
| NLP2-F | Construct pL0V-SC-41308 | GAAGACTTAATGATGGAAGGCCAATATTCGTC |
| NLP2-R | | GAAGACTTACCTTCAACTGTCACTGCCGCCATGTATA |
| PUB-NLP2-F | Heterologous expression | TTGTTGATGTGATTACAGTCTAGAATGGAAGGCCAATATTCGTCAAAGG |
| PUB-NLP2-R | | TGGAACATCGTATGGGTAGGTACCACTGTCACTGCCGCCATGTATATTG |
| PUB-NIN–F | | TTGTTGATGTGATTACAGTCTAGAATGGAATATGGTGGTGGGTTAGTG |
| PUB-NIN-R | | TGGAACATCGTATGGGTAGGTACCGGAGGATGGACTGCTGCTGCTG |
| NLP2-attB-F | Truncated NLP2 for EMSA | GGGGACAAGTTTGTACAAAAAAGCAGGCTTCTACAGTCAGGCAACAAGTGG |
| NLP2-attB-R | | GGGGACCACTTTGTACAAGAAAGCTGGGTTCAACTGTCACTGCCGCCATGTA |
| pNCR158-F | Amplify *NCR* promoter for CRISPR construct | gcatgcctgcaggtcaacGTGGTGTTTACCATTCTCTG |
| pNCR158-R | | ggtccttgtaatccatctagaAATTTTTTCTCTTTTGCATGTG |
| NRE-gRNA-DT1 | CRISPR dNRE Knock out | GAGAATCTATTGGCTTGTGG |
| NRE-gRNA-DT2 | | CAAGCCAATAGATTCTTTAC |
| NIN-gRNA-G-DT1-F | CRISPR NIN Knock out | TAAGGATGGAATATGGTGG |
| NIN-gRNA-G-DT2-R | | TTGATATGCAGCAACTCAT |

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## Appendix

**1. The promoters of the 55 most downregulated genes in nlp2 nodules that were used to identify the dNRE motifs shown in Fig 3A and S13A.**

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## 2. 38 Nitrite Reductase (NiR) promoters used to identify the NRE shown in Fig 3A, S5, and S13A

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### 3. Class I (C1) and Class 2 (C2) non-symbiotic hemoglobin promoters analysed in Fig S13B

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### 5. Hemoglobin promoters of early diverged legumes and nodulating non-legumes presented in Fig S13C.

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CATTATAAGTCTACTTCAATCCCAAATACCCAAAACCAGGTTCGCTTTGCCGCAAACAGCCCCTTGTTTA
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>Dg_nsHB2 isolate NF-2018-6 scaffold27403_cov80
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