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1 **The transcription factor NF-YA10 determines the area explored by**
2 ***Arabidopsis thaliana* roots through direct regulation of LAZY and**
3 **TAC genes**

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16

17 **ABSTRACT**

18 Root developmental plasticity relies on transcriptional reprogramming, which largely
19 depends on the activity of transcription factors (TFs). NF-YA2 and NF-YA10 (Nuclear Factor
20 A2 and A10) are down-regulated by the specific miRNA isoform miR169defg, in contrast to
21 miR169a . Here, we analyzed the role of the *Arabidopsis thaliana* TF NF-YA10 in the
22 regulation of lateral root development. Plants expressing a version of *NF-YA10* resistant to
23 miR169 cleavage showed a perturbation in the lateral root gravitropic response. By
24 extracting novel features of root architecture using the ChronoRoot deep-learning-based
25 phenotyping system, we uncovered a differential emergence angle of lateral roots over time
26 when compared to Col-0. Detailed phenotyping of root growth dynamics revealed that NF-
27 YA10 activity modulates the area explored by *Arabidopsis* roots. Furthermore, we found that
28 NF-YA10 directly regulates *TAC1* and *LAZY* genes by targeting their promoter regions, genes
29 previously linked to gravitropism. Hence, the TF NF-YA10 is a new element in the control of
30 LR gravitropism and root system architecture.

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32 **KEYWORDS:** NF-YA10 transcription factor; root development; gravitropism; *LAZY*; *TAC1*; high
33 throughput phenotyping

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36 INTRODUCTION

37

38 Plant developmental plasticity relies on a plethora of adaptive strategies in response to the
39 environment. The resulting root system architecture needs to ensure efficient anchor and
40 uptake of water and nutrients. The density and length of lateral roots (LRs) expand the plant
41 surface contact with the substrate, thus impacting the general growth of the plant. In the
42 model species *Arabidopsis thaliana*, LR development is tightly regulated by cellular and
43 molecular mechanisms from the very first cell division in the pericycle, through the
44 formation of the new meristem and the emergence of the new organ from the main root.
45 The intricate regulatory network controlling LR development includes key transcription
46 factors (TFs) integrating internal and environmental cues (Lavenus et al., 2015). The
47 regulatory hub formed by specific miR169 isoforms and their target TF *NF-YA2* was
48 previously described as a modulator of root architecture. Plants resistant to the miR169-
49 mediated down-regulation of *NF-YA2* exhibit an enhanced density of LRs explained by
50 altered specific cell type number and greater root meristem size (Sorin et al., 2014).
51 Although the related TF *NF-YA10* (Leyva-Gonzalez et al., 2012, Zhao et al., 2017) is also
52 expressed in roots and regulated by miR169, its potential role in LR development remains
53 unexplored. In contrast, *NF-YA10* was found implicated in leaf development, regulating
54 directly IAA biosynthesis (Zhang et al., 2017). In addition, an enhanced stress-tolerant
55 phenotype was described for plants overexpressing *NF-YA10* and *NF-YA2* (Leyva-Gonzalez et
56 al., 2012). A transcriptomic analysis of both transgenic lines hinted at a functional
57 redundancy between both *NF-YA* TFs with half of common deregulated genes, consistent
58 with the high similarity exhibited by all *NF-YA* TFs at the protein level (Siefers et al., 2009;
59 Petroni et al., 2012; Laloum et al., 2013). Furthermore, single homozygous mutant lines do
60 not show a major phenotype (Zhao et al., 2020) except for embryo-lethality in multiple or
61 specific single *NF-YA* mutants (Fornari et al., 2013; Pegnussat et al., 2008). The activity of the
62 *NF-YA10* promoter revealed by the control of reporter genes indicated that *NF-YA10* is
63 expressed in the shoot apical meristem (SAM) as well as in the main root and LRs, and is
64 induced during phosphate deficiency, oppositely to miR169 (Leyva-Gonzalez et al., 2012;
65 Sorin et al., 2014). Here, we challenged the hypothesis of redundancy between *NF-YA10*
66 and the closely related TF *NF-YA2* by undertaking in-depth characterization of the root
67 system architecture dynamics upon *NF-YA10* deregulation. To this end, we leveraged the

68 potential of ChronoRoot, a high-throughput automatic phenotyping system based on deep
69 learning (Gaggion *et al.*, 2021), for which we expanded here the analysis by introducing two
70 new angle measurements as additional parameters. Plants carrying a *NF-YA10* resistant to
71 miR169 cleavage (*NF-YA10* miRres) exhibit an increased root area, due not only to a greater
72 LR density than the wildtype (WT), but also as a result of an alteration of LR angles,
73 suggesting a link with gravitropic responses. Furthermore, we demonstrated that *NF-YA10*
74 directly regulates *TAC1* and *LAZY* genes, previously linked to the gravitropic response of
75 roots (Kawamoto and Morita, 2022), indicating that *NF-YA10* may act as a coordinator of LR
76 distribution in the rhizosphere, shaping the final surface of the root architecture.

77 RESULTS

78 A phylogenetic analysis of plant NF-YA TFs indicated that this family of TFs presents four
79 clades with internal duplications that are characteristic to the plant kingdom (**Supplemental**
80 **Figure 1, Supplemental Table 1**). As previously proposed (Laloum *et al.*, 2013), *NF-YA2* and
81 *NF-YA10* (clade D) arose from a recent duplication which seems to be specific to
82 Brassicaceae, similarly to other NF-YAs such as *NF-YA1/9* (clade C) and *NF-YA4/7* (clade B). In
83 another hand, *NF-YA6* and *NF-YA5*, *NF-YA3* and *NF-YA8* emerged from two duplications
84 inside the clade A (**Figure 1A, Supplemental Table 1**). Expression studies based on
85 transcriptional reporter *pNF-YA10:GUS* assays were used to show *NF-YA10* specific
86 expression in the root vasculature (Leyva-Gonzalez *et al.*, 2012; Sorin *et al.*, 2014). In this
87 study, we used transgenic plants expressing the translational fusion *pNF-YA10:GFP-NF-*
88 *YA10mut* (miR169-resistant *NF-YA10*, called hereafter *NF-YA10* miRres), to localize *NF-YA10*
89 protein expression pattern. By analyzing *NF-YA10* miRres plants, we observed GFP:*NF-YA10*
90 accumulation in the nuclei of root vasculature and cortex cells, and particularly abundant at
91 the base of the LR (**Figure 1B**) suggesting a regulatory role in the development of this organ.

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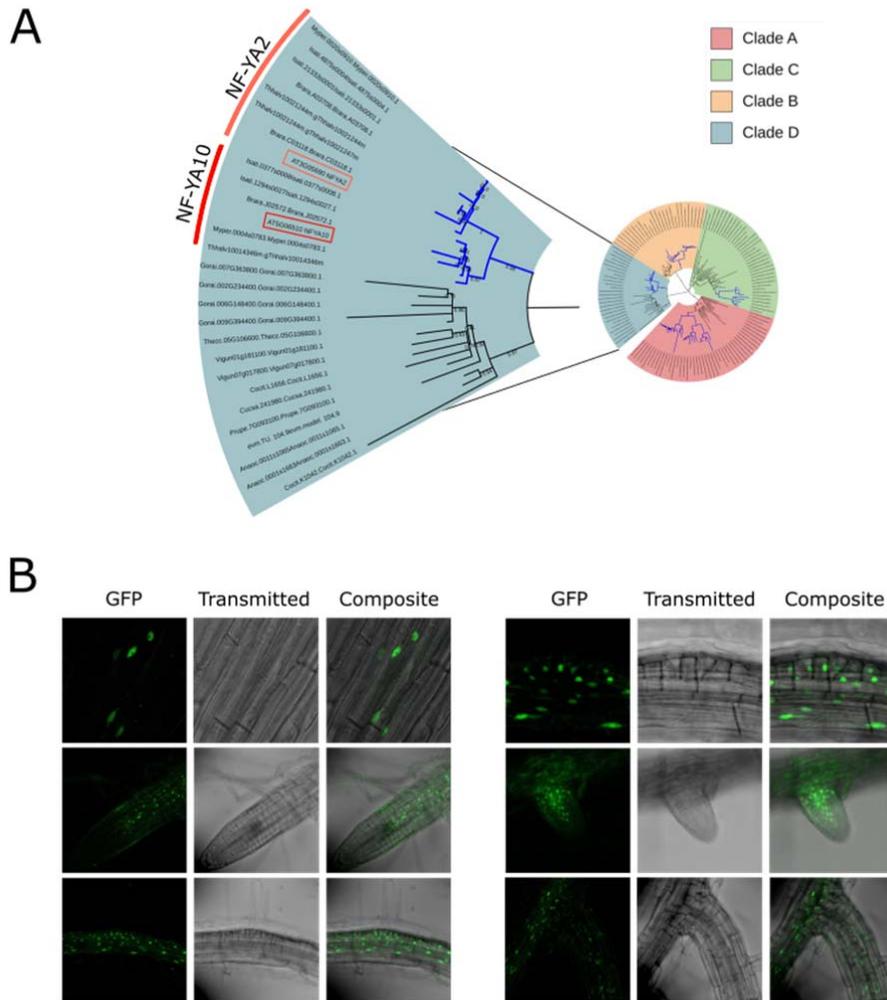
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99 **Figure 1. NF-YA10 diverged from a recent duplication with NF-YA2 within Brassicaceae and is expressed in**
 100 **nuclei of primary and lateral root vasculature cells**

101 (A) Phylogenetic tree of NF-YAs with extended number of Malvidae and Brassicaceae, where AtNF-YA10 is
 102 represented in red and NF-YA2 in orange. The duplications in Brassicaceae are colored in blue. Only branches
 103 with bootstrap values higher than 65% are shown. (B) Localization of NF-YA10 fused to GFP in roots of pNF-
 104 YA10:GFP-NF-YAmiRres.1 8-day-old plants.

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106 A comprehensive characterization of the root architecture dynamics was then undertaken by
 107 using ChronoRoot (Gaggion et al., 2021), i.e. comparing two independent NF-YA10 miRres
 108 lines and the WT. NF-YA10 miRres plants showed a slightly longer main root (MR) than WT, a

109 feature observed since the germination (**Figure 2A**). Interestingly, total LR length in NF-YA10
110 miRres plants increased at a greater speed than the WT, showing a stronger difference than
111 for the MR (**Figure 2B**). Therefore, although NF-YA10 miRres plants exhibit a general faster
112 growth of the whole root system (**Figure 2C**), the relative contribution of the MR to the
113 global root system is less significant (**Figure 2D**). Moreover, the number of LRs was
114 significantly higher in NF-YA10 miRres plants (**Figure 2E**), resulting in an enhanced LR density
115 (**Figure 2F**). The final root architecture of NF-YA10 miRres plants exhibited an enhanced
116 covered surface, which is illustrated by the significantly expanded convex hull area of the full
117 root system (**Figure 2G**). However, the density of the LRs covering the convex hull area
118 (**Figure 2H**) did not emerge as a distinct feature between both independent lines, whereas
119 the aspect ratio (height/width of the root system) of NF-YA10 miRres plants was significantly
120 different from the WT, at least at day 9 (**Figure 2I**), indicating that longer LRs expand away
121 from the MR instead of keeping closer to the MR axis.

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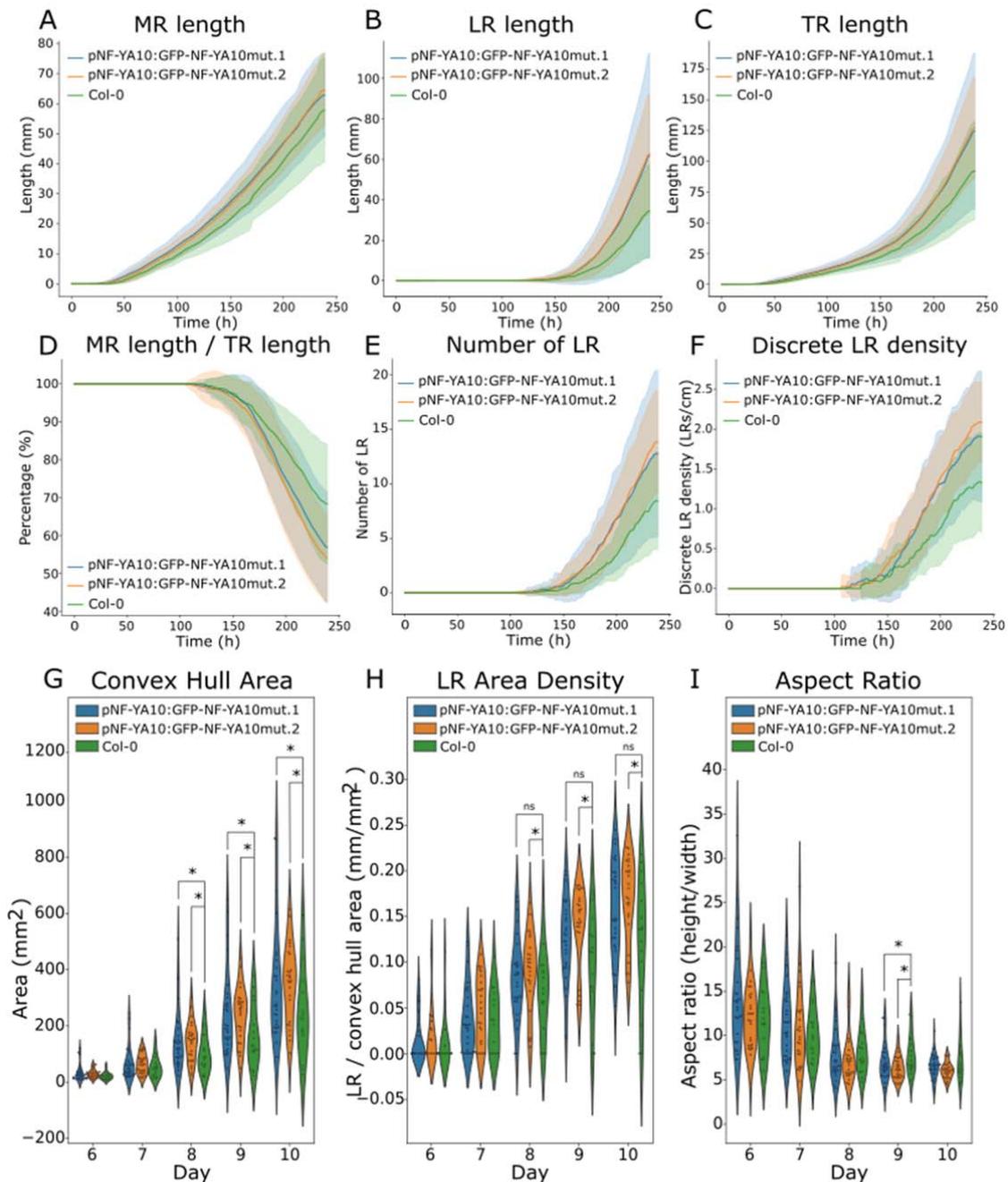
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140 **Figure 2. NF-YA10 up-regulation affects root growth and the resulting root system architecture**

141 ChronoRoot measurements of NF-YA10 miRres and Col-0 WT plants: main root length (A), lateral root length
 142 (B), total root length (C), ratio main root length/total root length (D), number of lateral roots (E), lateral root
 143 density (F). Convex hull area (G), lateral root area density (H) and ratio of root system height and width (I) of
 144 NF-YA10 miRres lines and Col-0 at different ages of the plant. A-F: solid line represent the average value and
 145 the bands represent the standard deviation.

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148 This characteristic feature led us to wonder if the angle of the LRs was affected in NF-YA10
149 miRres plants. To address this issue, two novel parameters were incorporated into
150 ChronoRoot by leveraging information from both the segmentation and graph structures
151 generated by the deep learning-based model. These parameters allowed for tracking the
152 evolution of the base-tip angle (from the base to the tip of each LR) and the emergence
153 angles of LRs over time (**Figure 3A-C, Supplementary Figure 2**), thereby expanding the
154 original ChronoRoot applications. Considering the first LR emerged per plant, NF-YA10
155 miRres seedlings present a higher base-tip angle than the WT during the emergence of LR,
156 reaching a 20°-difference after three days (**Figure 3D**). Accordingly, the emergence angle of
157 LR was also affected, as NF-YA10 miRres plants showed a trend of greater emergence angles
158 than the WT starting from the emergence of the first lateral roots (day 6), which was
159 statistically significant for both independent lines from day 9 on (**Figure 3E**). The potential
160 role of NF-YA10 in gravitropism was also assessed in the MR growth during a bending assay
161 (i.e. plant plates turned 90° and MR growing angles measured afterwards). Interestingly, one
162 of the two NF-YA10 miRres lines showed a significantly delayed response compared to WT
163 suggesting that the role of this TF in LR development may also be relevant in the response of
164 the MR to gravitropic stimuli (**Supplementary Figure 3**).

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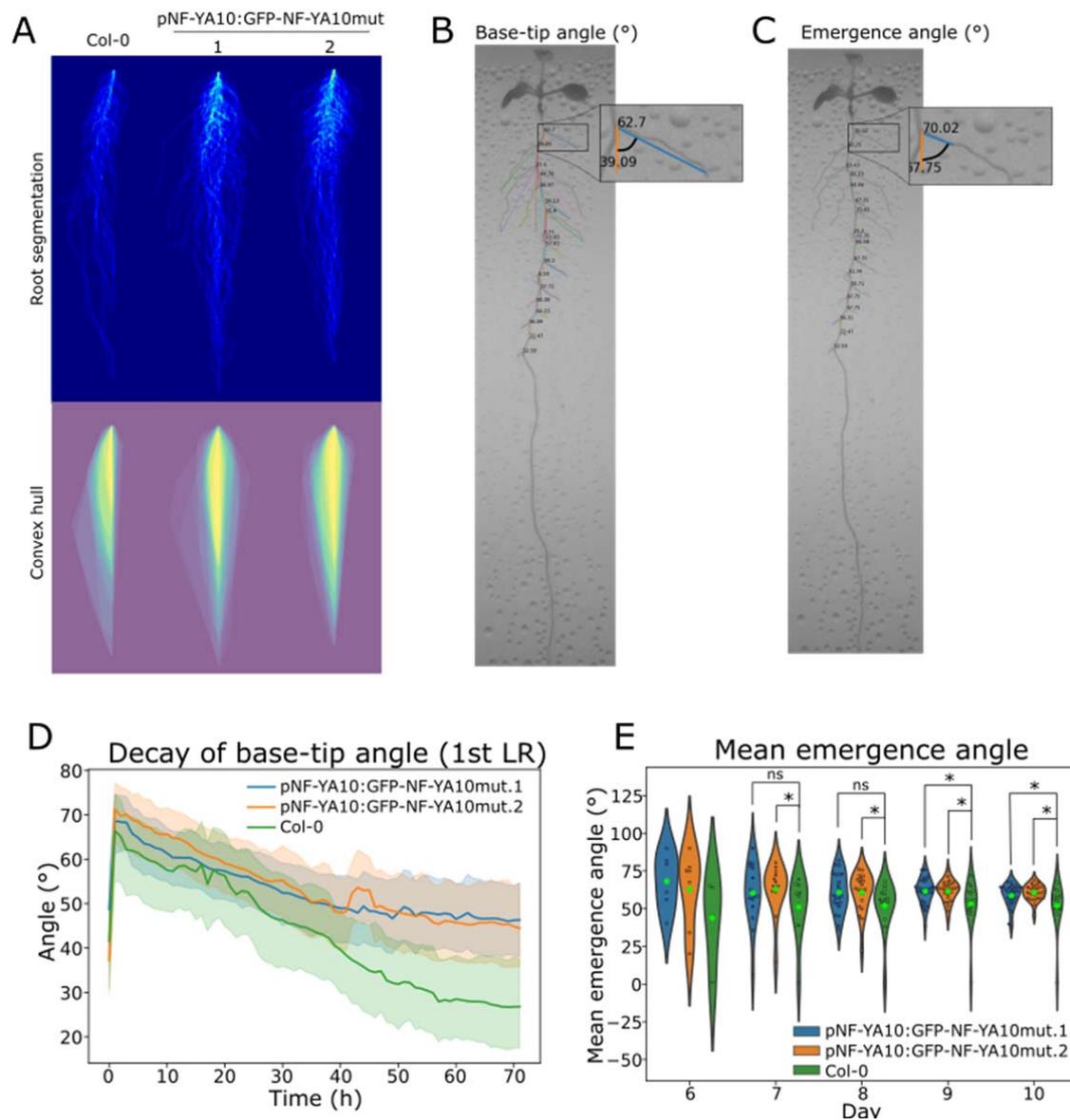
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Figure 3. Two new features of ChronoRoot allowed us to uncover NF-YA10 as a regulator of lateral root gravitropism by leveraging information from both the segmentation and graph structures generated by the system
(A) Superposition of all NF-YA10 miRes and Col-0 root profiles in mock conditions. Representative plant of NF-YA10 miRes and zoom on two novel ChronoRoot measurements: (B) base-tip angle and (C) emergence angle respectively. (D) Dynamics of tip decay of the first lateral root to emerge along the time of NF-YA10 miRes plants and Col-0. (E) Mean emergence angle of NF-YA10 miRes and Col-0 roots at different ages of the plant.

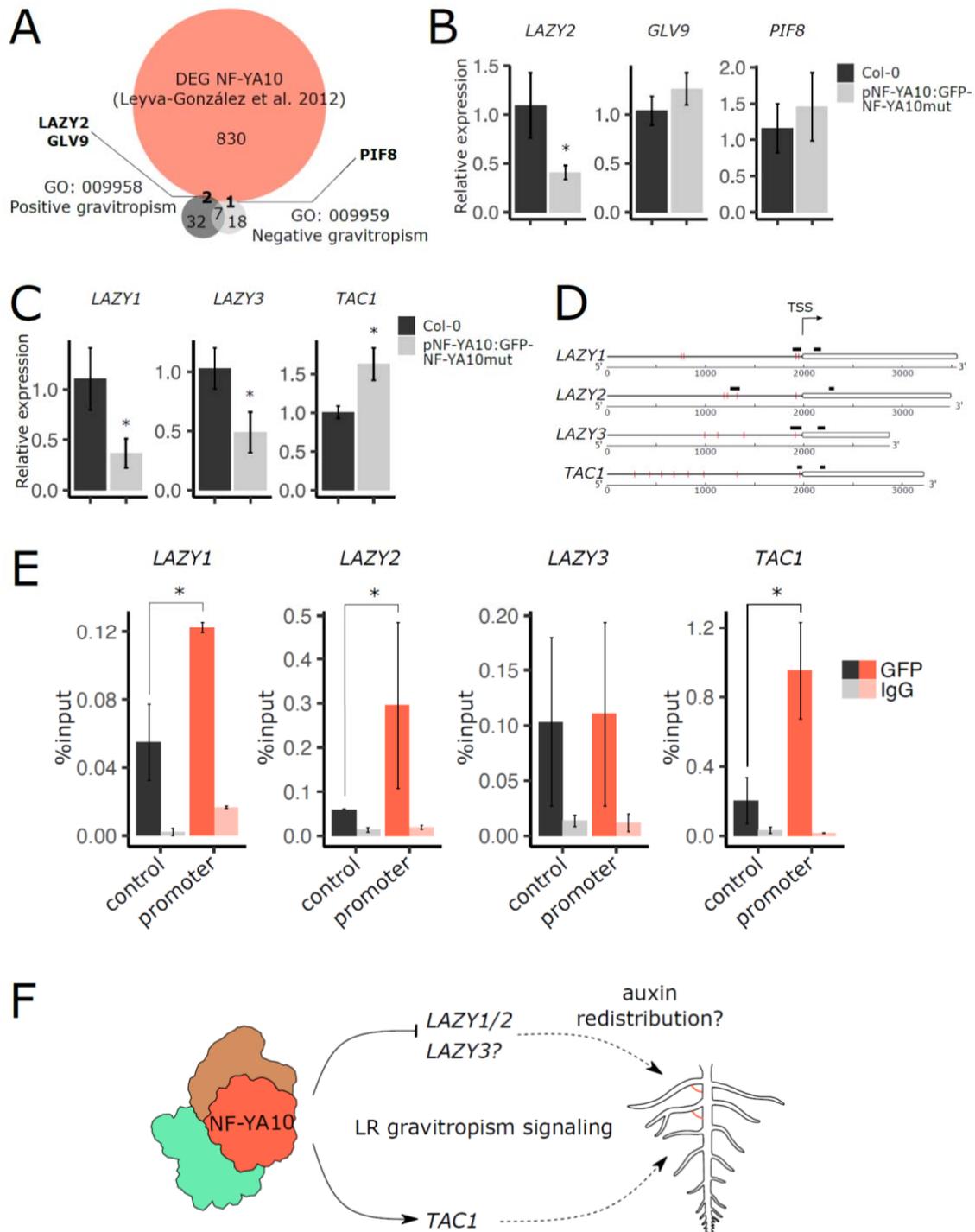
193 To decipher the molecular mechanism behind this phenotype, we looked for potential NF-
194 YA10 targets involved in lateral organ gravitropism described in the literature, which bear
195 CCAAT-boxes in their promoter sequences. To this end, we first crossed the list of
196 differentially expressed genes (DEGs) in NF-YA10-inducible overexpressor (Leyva-González et
197 al., 2012) with TAIR Gene Ontology lists for genes related positively or negatively to
198 gravitropism (**Supplementary Table 2**). Among them, we identified the genes *LAZY2* and
199 *GLV9*, and *PIF8* respectively (**Figure 4A**). In contrast to *GLV9* and *PIF8*, *LAZY2* was
200 transcriptionally deregulated in roots of NF-YA10 miRres plants (**Figure 4B**). Considering the
201 behavior of *LAZY2* in NF-YA10-deregulated plants, we further investigated the transcriptional
202 levels of members of the LAZY protein-encoding gene family, which have been linked to
203 redundant activity (Hollander *et al.*, 2020). Particularly, *TAC1* (*TILLER ANGLE CONTROL 1*) and
204 *LAZY1/2/3* are known to be essential for accurate gravitropic auxin-driven sensing of roots
205 and shoots. Interestingly, it was shown that LRs in the *lazy1/lazy2/lazy3* triple mutant
206 display a disturbed gravitropic response whereas *tac1* simple mutant has an increased
207 gravitropic phenotype (Hollander *et al.*, 2020). Thus, we assessed their level of expression in
208 NF-YA10 miRres roots. *LAZY1*, *LAZY2* and *LAZY3* were all repressed compared to WT while
209 *TAC1* was induced (**Figure 4C**), in agreement with the mutant gravitropic phenotypes
210 observed. In order to determine if NF-YA10 directly regulates these genes, we performed
211 ChIP-qPCR targeting TSS-proximal CCAAT boxes present in their promoter regions, compared
212 to ChIP enrichment in their respective gene bodies taken as the negative control (probes
213 distribution indicated in **Figure 4D**). In basal conditions, *LAZY1*, *LAZY2* and *TAC1* emerged as
214 direct targets of NF-YA10 (**Figure 4E**). *LAZY3* appears only as a potential direct target,
215 considering that the negative control within the gene body is close to the CCAAT box
216 assessed. Altogether, our results suggest that regulation of NF-YA10 expression is critical for
217 the control of the root system architecture, notably determining the final volumetric root
218 distribution by modulating root growth, LR development and their gravitropic response. NF-
219 YA10 recognizes the promoters and regulates a subset of root developmental genes,
220 including the antagonistic *TAC1* and *LAZY* genes, known to be involved in LR gravitropic
221 signaling suggesting it maybe a new regulatory circuit controlling the long-term surface of
222 the root system (**Figure 4F**).

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228 **Figure 4. NF-YA10 binds to *TAC1* and *LAZYs* promoters, resulting in antagonistic regulation of these genes**

229 (A) Venn diagram of DEGs from Leyva-González et al., 2012 and genes comprised in Gene Ontology terms of

230 positive and negative gravitropism. (B) Location of CCAAT boxes are indicated in red lines and the respective

231 DNA regions assessed in ChIP-qPCR in black for each of the genes *TAC1*, *LAZY1*, *LAZY2* and *LAZY3*. (C) Relative

232 expression of *TAC1* and *LAZYs* in NF-YA10 miRres and Col-0 roots of 8-day-old seedlings. (D) Chromatin
233 immunoprecipitation (ChIP)-qPCR analysis of NF-YA10 binding at *TAC1* and *LAZYs* gene and promoter regions in
234 8-day-old NF-YA10 miRres and Col-0 seedlings. (E) Proposed model for the NF-YA10-dependent lateral root
235 gravitropic response. In (B), (C) and (E), values correspond to the mean and error bars to the standard deviation
236 of three biological replicates. The asterisks indicate a p-value < 0.05 (Mann-Whitney test).

237

238 **DISCUSSION**

239 In animals, the NF-Y complex is described as a pioneer TF (Dolfini et al., 2016), able to recruit
240 chromatin remodelers and downstream TFs to modulate the activity of target genes. In
241 Arabidopsis, NF-YA, NF-B and NF-YC are encoded by respectively 10, 13 and 13 genes
242 boosting the diversification of molecular and physiological roles of this TF family, based on
243 the wide range of combinations likely occurring in different cell types from the organism
244 (Laloum et al., 2013). Among them, NF-YA2 and NF-YA10 emerged from a recent
245 Brassicaceae-specific duplication inside a clade with low divergence degree, thus exhibiting
246 few changes in the protein sequence. Both NF-YA genes are targets of the specific isoform of
247 miR169-defg, and plants resistant to the downregulation driven by this miRNA showed
248 similar LR phenotype (Sorin *et al.* 2014; and **Figure 2**). For a better characterization of NF-
249 YA10 miRres plants, two novel root parameters were determined by ChronoRoot through
250 the development of ad hoc deep segmentation networks: base-tip angle and emergence
251 angle of LRs. These measures were respectively 20° and 8° higher in NF-YA10 miRres lateral
252 roots than in the WT, causing, together with higher LR density, a significant increase of the
253 area occupied by the root system in two dimensions over the agar plate. Strikingly,
254 Arabidopsis WT roots exhibit a similar phenotype in response to phosphate starvation (Bai *et*
255 *al.*, 2013) and it was previously shown that the promoter of *NF-YA10* is induced under these
256 conditions, whereas miR169 was repressed (Leyva-González *et al.*, 2012). Our observations
257 suggest that NF-YA10 may participate in the control of LR gravitropism in response to low
258 phosphate concentrations. Considering that root-specific targets of NF-YA10 are yet
259 unknown, we searched for potential targets that could be linked to the regulation of LR
260 gravitropism, among which we identified *TAC1* and *LAZYs* genes, described as components of
261 the signaling pathway controlling gravitropism in shoots and roots (Kawamoto and Morita,
262 2022).

263 All four genes assessed turned out to be up- or down-regulated by NF-YA10 in NF-YA10
264 miRres plants. In contrast to *LAZY1*, *LAZY2* and *TAC1* determined by ChIP-qPCR, *LAZY3* was

265 not significantly enriched by NF-YA10 compared to the nearby negative control. Further
266 research will be required to determine how this regulation may take place under phosphate
267 starvation. Notably, lugol-staining of LRs revealed no observable changes in amyloplast
268 distribution in NF-YA10 miRres roots, suggesting that NF-YA10 may operate downstream the
269 known gravity sensing organelle (**Supplementary Figure 4**). Lower levels of auxin were
270 detected in NF-YA10 OE leaves, and a microarray transcriptomic approach of the same
271 plants served to determine that the expression of a significant subset of auxin-related genes
272 depends on NF-YA10 (Zhao *et al.*, 2017), further suggesting that this TF may play an
273 important role in auxin homeostasis, likely explaining the phenotypes observed in root
274 growth, development and LR gravitropism. Furthermore, the use of the synthetic reporter
275 DR5 allowed demonstrating that auxin signaling was increased in triple *lazy2/lazy3/lazy4*
276 mutant roots (Yoshihara & Spalding, 2017; Ge & Chen, 2019), further linking the impact of
277 the NF-YA10-LAZYs hub on auxin-driven root development. In addition, the ortholog of
278 Arabidopsis *LAZY1* in maize, *ZmLAZY1*, directly interacts with the early auxin response factor
279 *ZmIAA17* in the nucleus of maize cells (Dong *et al.*, 2013). In Arabidopsis, the dwarf late-
280 senescent phenotype of NF-YA10 overexpressing plants under the control of a 35S
281 promoter, was previously proposed to be caused by a reduction of plant growth directed by
282 transcriptional regulation of cell wall and sucrose pathways actors (Leyva-González *et al.*,
283 2012). In contrast to 35S-mediated overexpression, a miR-resistant version induces a slight
284 up-regulation and in the same cells expressing the NF-YA10 TF. Therefore, we propose that
285 NF-YA10 contributes to orchestrate LR development in addition to auxin and cell expansion
286 related genes, by fine-tuning gravitropism signaling through regulation of *LAZY* genes
287 expression. Indeed, NF-YA10 deregulation results in a larger root area. It was shown that
288 enhanced root surface area positively correlated with plant weight, opening new
289 perspectives about the potential of NF-Y TFs for the improvement of relevant traits for
290 hydroponics culture and more globally for agriculture (Yang *et al.*, 2021). Therefore, further
291 research about how LRs explore the substrate under the control of transcriptional regulators
292 could help to improve crop growth based on nutrients uptake, including phosphates.

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295

296 MATERIAL AND METHODS

297

298 Plant lines generated and used for this study

299 All plants used in this study are in Columbia-0 background. pNF-YA10:GFP-NF-YA10miRres
300 lines were obtained using the GreenGate vectors (Lampropoulos *et al.*, 2013), using 2000-pb
301 region upstream of the start codon of *NF-YA10* amplified from genomic DNA and CDS of NF-
302 YA10 without miR cleavage site amplified from cDNA. Arabidopsis plants were transformed
303 by floral dip (Clough and Bent 1998) using *Agrobacterium tumefaciens* C58. Homozygous
304 mutants of miR169 resistant line of NF-YA10 were identified by PCR (see primers in
305 **Supplementary Table 3**).

306

307 Growth conditions and phenotypic analyses

308 For phenotype analyses, plants were grown vertically on plates placed in a growing chamber
309 in long day conditions (16 h in light 130uE; 8 h in dark; 23°C). Plants were grown on solid
310 half-strength MS medium (MS/2) supplemented with 0.8g/L agar (Sigma-Aldrich, A1296
311 #BCBL6182V) and 1% sucrose, buffered at pH 5,6. Temporal phenotyping was performed
312 using ChronoRoot (Gaggion *et al.*, 2021). In the case of gravitropic assays, plates were
313 rotated at 90° when reaching 7 DAS and photographed after 24 hours. Images were then
314 analyzed with ImageJ to measure the root tip angle of each plant (n=15) formed after
315 reorientation. For the observation of amyloplasts, 8-day-old plants (n=15) were dipped for 8
316 minutes in Lugol staining solution (0.1% I, 1%KI, Sigma-Aldrich) and observed in an Eclipse
317 E200 Microscope (Nikon) equipped with a Nikon D5300 camera.

318

319 Confocal laser scanning and Fluorescence microscopy (CLSM)

320 For CLSM, roots of stable two independent lines of NF-YA10 miRres plants were imaged with
321 a Leica TCS SP8 confocal laser scanning microscope. For GFP signal imaging, samples were
322 excited at 488 nm and the detection was set at 493–530nm, and the transmitted light was
323 also imaged. All the images were captured using a 20x or 63x lens. Image processing was
324 performed using Fiji software (Schindelin *et al.* 2012).

325

326

327 **Sequence alignment and phylogenetic tree analysis**

328 Protein sequences corresponding to plant NF-YA family members were identified using the
329 BLASTP tool (Boratyn et al., 2013) and downloaded from Phytozome 13 ([https://phytozome-
330 next.jgi.doe.gov/](https://phytozome-next.jgi.doe.gov/)) (Goodstein et al., 2012). Proteins from other organisms were obtained
331 from the NCBI database. For the tree in **Supplementary Figure 1**, protein sequences of plant
332 species were selected by choosing members from the main phylogenetic clades, giving a
333 total of 81 protein sequences (**Supplementary Table 1**). Three no-plant species sequences
334 were using for tree rooting. For the tree in **Figure 1A**, several protein sequences from
335 Brassicaceae and Brassicales-Malvales species were added to improve resolution in this
336 group of organisms, resulting in a total of 137 protein sequences (**Supplementary Table 1**).
337 The alignments were made using MUSCLE default parameters (Edgar, 2004). The
338 phylogenetic trees were built using the Seaview 4.5.0 software and the PhyML-aLRT-SH-LIKE
339 algorithm (Gouy et al., 2010) with maximum likelihood tree reconstruction. A model of the
340 amino acid substitution matrix was chosen through the Datamonkey bioinformatic server
341 (www.datamonkey.org; Delpor *et al.*, 2010), which selected the VT model. The resulting
342 trees were represented using iTOL (<http://itol.embl.de/itol.cgi>; (Letunic & Bork, 2016))
343 showing branches with bootstrap values higher than 65%.

344

345 **Quantification of transcript levels by RT-qPCR**

346 Total RNA was extracted from roots using TRI Reagent (Sigma-Aldrich) and treated with
347 DNaseI (NEB) as indicated by the manufacturers. Reverse transcription was performed using
348 1µg total RNA and the M-MLV Reverse Transcriptase (Promega). qPCR was performed on a
349 StepOne™ Real-Time PCR System (Thermo Fisher) with Sso Advanced Universal mix (BioRad)
350 in standard protocol (40 cycles, 60°C annealing). Primers used in this study are listed in
351 **Supplementary Table 3**. Data were analyzed using the $\Delta\Delta C_t$ method using ACTIN
352 (AT3G18780) for gene normalization (Czechowski et al., 2005).

353

354 **Chromatin immunoprecipitation**

355 Three biological replicates of 8 DAS whole seedlings grown in control condition were
356 collected. CHIP was performed using anti-GFP (Abcam ab290) and anti-immunoglobulin G
357 (IgG) anti-IgG (Abcam ab6702), as described in Ariel et al. 2020, starting from 5 g of seedlings
358 crosslinked in 1% (v/v) formaldehyde. Chromatin was sonicated in a water bath Bioruptor

359 Plus (Diagenode; 10 cycles of 30 s ON and 30 s OFF pulses at high intensity). Antibody-coated
360 Protein A Dynabeads (Invitrogen) were incubated 12 h at 4°C with the samples.
361 Immunoprecipitated chromatin was reverse crosslinked with 20 mg of Proteinase K (Thermo
362 Fisher, #EO0491) overnight at 65°C. Finally, DNA was recovered using
363 phenol/chloroform/isoamyl alcohol (25:24:1, Sigma) followed by ethanol precipitation. For
364 input samples, 10% of sonicated chromatin were collected for each sample before the
365 immunoprecipitation and reverse crosslinked and extracted as the immunoprecipitated
366 samples. Results are expressed as enrichments, corresponding to GFP or IgG percent of
367 input, measured by qPCR (primers used are listed in **Supplementary Table 3**).

368

369 **Construction of Angle Parameters based on ChronoRoot**

370 To construct the new angle parameters, specifically the base-tip angle (**Figure 3B**) and the
371 emergence angle of LR (**Figure 3C**), we first proceeded on extracting the LRs from the labeled
372 skeleton of each plant. Then, to preserve the labels and information pertaining to the order
373 in which the LRs began to grow, we matched the extracted LRs across time-steps. We
374 performed the matching from one time-step to the previous one by using the pixel position
375 where the root initiated. With the position, skeleton, and label of each plant root
376 established, we proceeded to measure the LR base-tip angle. This angle was calculated for
377 each LR by examining the right triangle formed by the base position, the tip, and the Y-axis.
378 For the second angle parameter, i.e. the emergence angle, instead of measuring it from the
379 base to the tip, we established a fixed distance in millimeters (2 mm in our study, though
380 adjustable as a parameter) to construct the right triangle (see **Figure 3C**). We traversed 2
381 mm along the skeleton from the base and measured the angle between the Y-axis and this
382 point to calculate it. Source code for ChronoRoot is publicly available on GitHub
383 (<https://github.com/ngaggion/ChronoRoot>, Gaggion et al., 2021).

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386

387 **FIGURE LEGENDS**

388 **Figure 1. NF-YA10 diverged from a recent duplication with NF-YA2 within Brassicaceae**
389 **and is expressed in nuclei of primary and lateral root vasculature cells**

390 (A) Phylogenetic tree of NF-YAs with extended number of Malvidae and Brassicaceae, where
391 AtNF-YA10 is represented in red. (B) Localization of NF-YA10 fused to GFP in roots of pNF-
392 YA10:GFP-NF-YAmiRres.1 8-day-old plants.

393

394 **Figure 2. NF-YA10 up-regulation affects root growth and the resulting root system**
395 **architecture**

396 ChronoRoot measurements of NF-YA10 miRres and Col-0 WT plants: main root length (A),
397 lateral root length (B), total root length (C), ratio main root length/total root length (D),
398 number of lateral roots (E), lateral root density (F). Convex hull area (G), lateral root area
399 density (H) and ratio of root system height and width (I) of NF-YA10 miRres lines and Col-0 at
400 different ages of the plant. A-F: solid lines and corresponding bands represent the average
401 value and the standard deviation respectively. G-I: The asterisks indicate a p-value < 0.05
402 (Mann-Whitney test).

403

404 **Figure 3. Two new features of ChronoRoot allowed us to uncover NF-YA10 as a regulator**
405 **of lateral root gravitropism by leveraging information from both the segmentation and**
406 **graph structures generated by the system**

407 (A) Superposition of all NF-YA10 miRres and Col-0 root profiles in mock conditions.
408 Representative plant of NF-YA10 miRres and zoom on two novel ChronoRoot
409 measurements: (B) base-tip angle and (C) emergence angle respectively. (D) Dynamics of tip
410 decay of the first lateral root to emerge along the time of NF-YA10 miRres plants and Col-0.
411 Solid lines and corresponding bands represent the average value and the standard deviation
412 respectively. (E) Mean emergence angle of NF-YA10 miRres and Col-0 roots at different ages
413 of the plant. The asterisks indicate a p-value < 0.05 (Mann-Whitney test).

414

415 **Figure 4. NF-YA10 binds to *TAC1* and *LAZYs* promoters, resulting in antagonistic regulation**
416 **of these genes**

417 (A) Venn diagram of DEGs from Leyva-González et al., 2012 and genes comprised in Gene
418 Ontology terms of positive and negative gravitropism. (B) Location of CCAAT boxes and the

419 respective DNA probes used in ChIP-qPCR for the study of the genes *TAC1*, *LAZ1*, *LAZY2* and
420 *LAZY3*. (C) Relative expression of *TAC1* and *LAZYs* in NF-YA10 miRres and Col-0 roots of 8-
421 day-old seedlings. (D) Chromatin immunoprecipitation (ChIP)-qPCR analysis of NF-YA10
422 binding at *TAC1* and *LAZYs* gene and promoter regions in 8-day-old NF-YA10 miRres and Col-
423 0 seedlings. (E) Proposed model for the NF-YA10-dependent lateral root gravitropic
424 response. In (B), (C) and (E), values correspond to the mean and error bars to the standard
425 deviation of three biological replicates. The asterisks indicate a p-value < 0.05 (Mann-
426 Whitney test).

427

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433

434 **DISCLOSURES**

435

436 **Ethics approval and consent to participate**

437 Not applicable for this study.

438

439 **Competing interests**

440 The authors declare that they have no competing interests.

441

442 **SUPPLEMENTARY FIGURES**

443 **Figure S1.** Phylogenetic tree of NF-YAs in plant and non-plant organisms, where AtNF-YA10 is
444 represented in red.

445 **Figure S2.** Representative plants of NF-YA10 miRres (line 2) and WT with corresponding
446 measures of base-tip and emergence angles.

447 **Figure S3.** (A) Representative photography of 8-day-old NF-YA10 miRres and Col-0 seedlings
448 and (B) mean angle of corresponding primary roots 48 hours after gravistimulation.

449 **Figure S4.** Representative photography of (A) primary and (B) lateral root apices of 8-day-
450 old NF-YA10 miRres and Col-0 seedlings showing amyloplasts stained with lugol.

451

452 **SUPPLEMENTARY TABLES**

453 **Table S1.** Table of species and sequences used for phylogenetic analyses.

454 **Table S2.** Lists of differentially expressed genes (DEGs) in *NF-YA10*-inducible overexpressor
455 (Leyva-González et al., 2012) and genes assigned to TAIR Gene Ontology terms related
456 positive and negative gravitropism.

457 **Table S3.** Table of primers used in this study.

458

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