



**HAL**  
open science

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

Andana Barrios, Nicolas Gaggion, Natanael Mansilla, Leandro Lucero, Thomas Blein, Céline Sorin, Enzo Ferrante, Martin Crespi, Federico Ariel

### ► To cite this version:

Andana Barrios, Nicolas Gaggion, Natanael Mansilla, Leandro Lucero, Thomas Blein, et al.. The transcription factor NF-YA10 determines the area explored by *Arabidopsis thaliana* roots through direct regulation of LAZY and TAC genes. 2023. hal-04299899

**HAL Id: hal-04299899**

**<https://hal.science/hal-04299899>**

Preprint submitted on 22 Nov 2023

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

4 Andana Barrios<sup>1,2,3</sup>, Nicolas Gaggion<sup>4</sup>, Natanael Mansilla<sup>3</sup>, Leandro Lucero<sup>3</sup>, Thomas Blein<sup>1,2</sup>, Céline  
5 Sorin<sup>1,2</sup>, Enzo Ferrante<sup>4</sup>, Martin Crespi<sup>1,2</sup> and Federico Ariel<sup>3</sup>

6  
7 <sup>1</sup>Institute of Plant Sciences Paris Saclay IPS2, CNRS, INRA, Université Evry, Université Paris-Saclay,  
8 Bâtiment 630, 91405 Orsay, France.

9 <sup>2</sup>Institute of Plant Sciences Paris-Saclay IPS2, Université de Paris, Bâtiment 630, 91405 Orsay, France.

10 <sup>3</sup>Instituto de Agrobiotecnología del Litoral, CONICET, Universidad Nacional del Litoral, Colectora Ruta  
11 Nacional 168 km 0, 3000, Santa Fe, Argentina.

12 <sup>4</sup>Research institute for signals, systems and computational intelligence sinc(i), CONICET, Universidad  
13 Nacional del Litoral, 3000, Santa Fe, Argentina.

14 <sup>\*</sup>Co-correspondence to: [farriel@santafe-conicet.gov.ar](mailto:farriel@santafe-conicet.gov.ar)

15

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.

31

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

34

35

## 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.

92

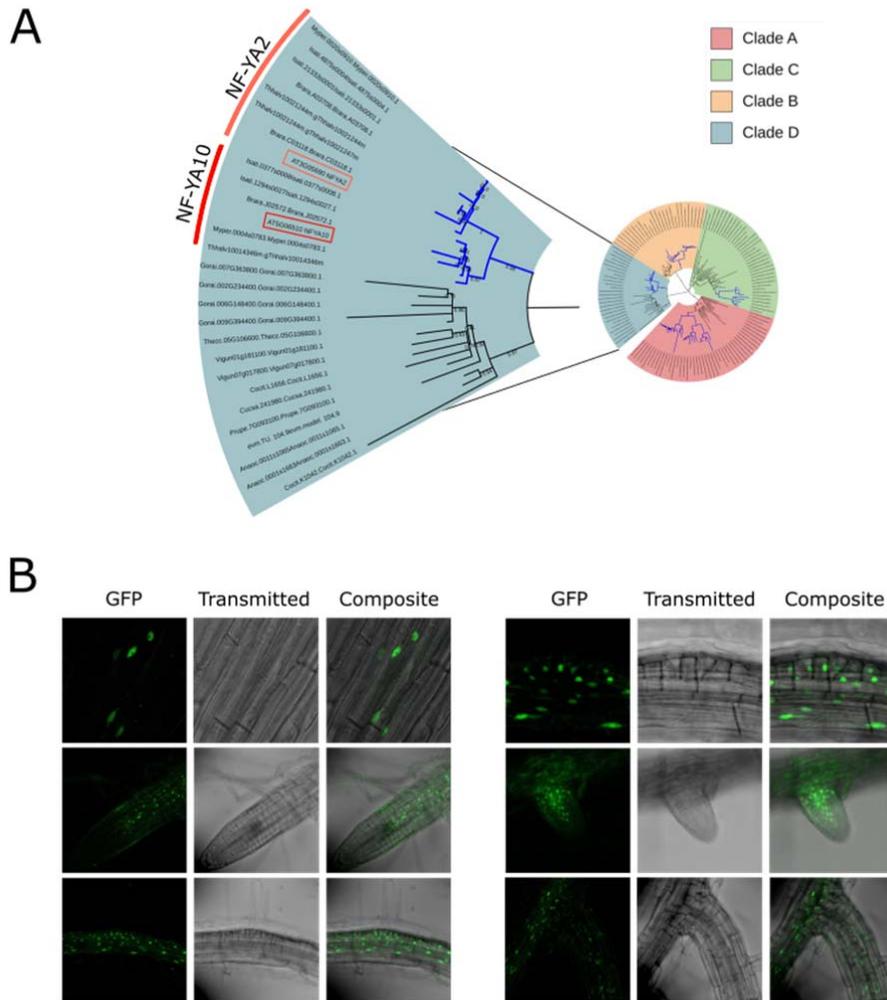
93

94

95

96

97



98

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.

105

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.

122

123

124

125

126

127

128

129

130

131

132

133

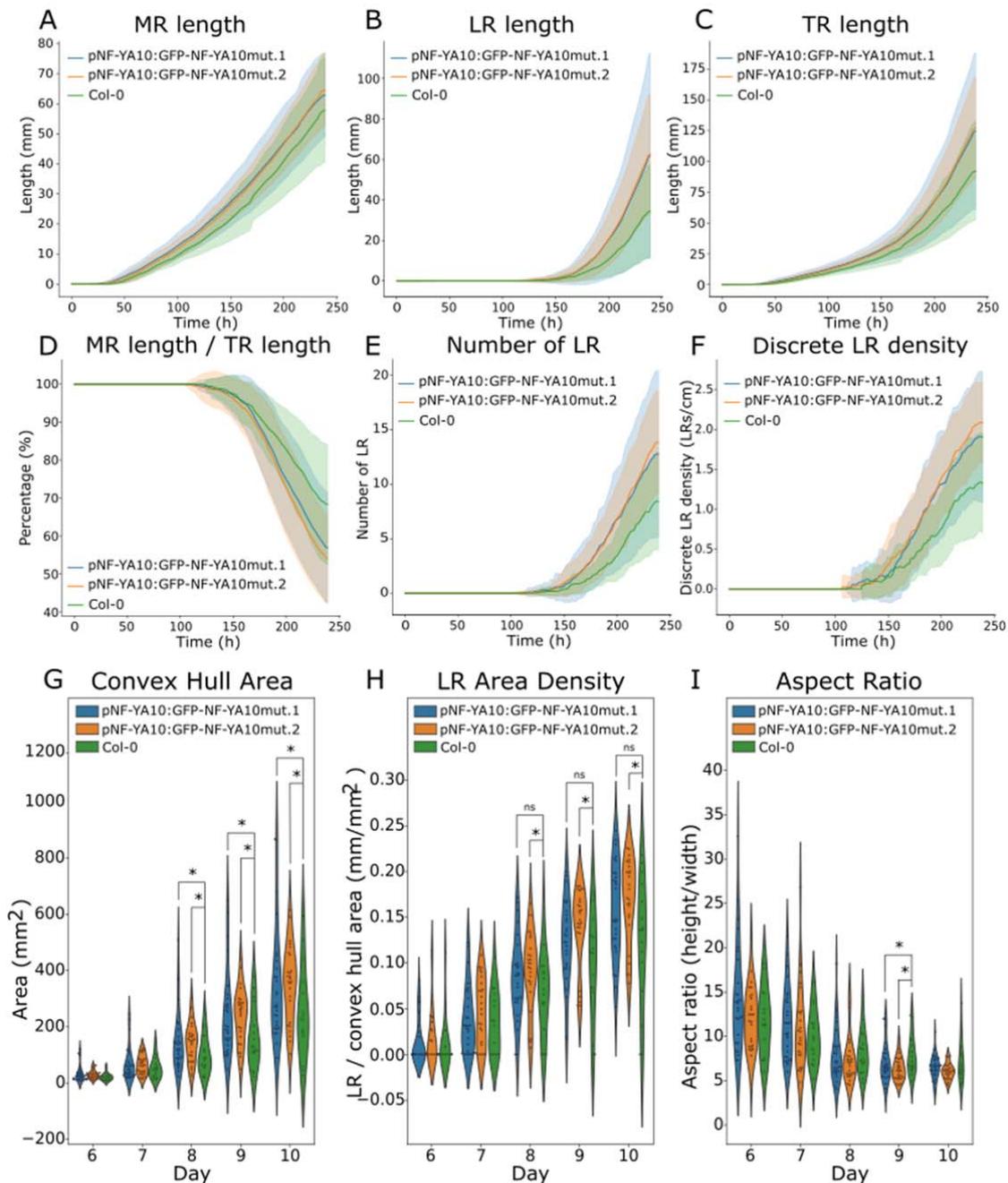
134

135

136

137

138



139

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.

146

147

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**).

165

166

167

168

169

170

171

172

173

174

175

176

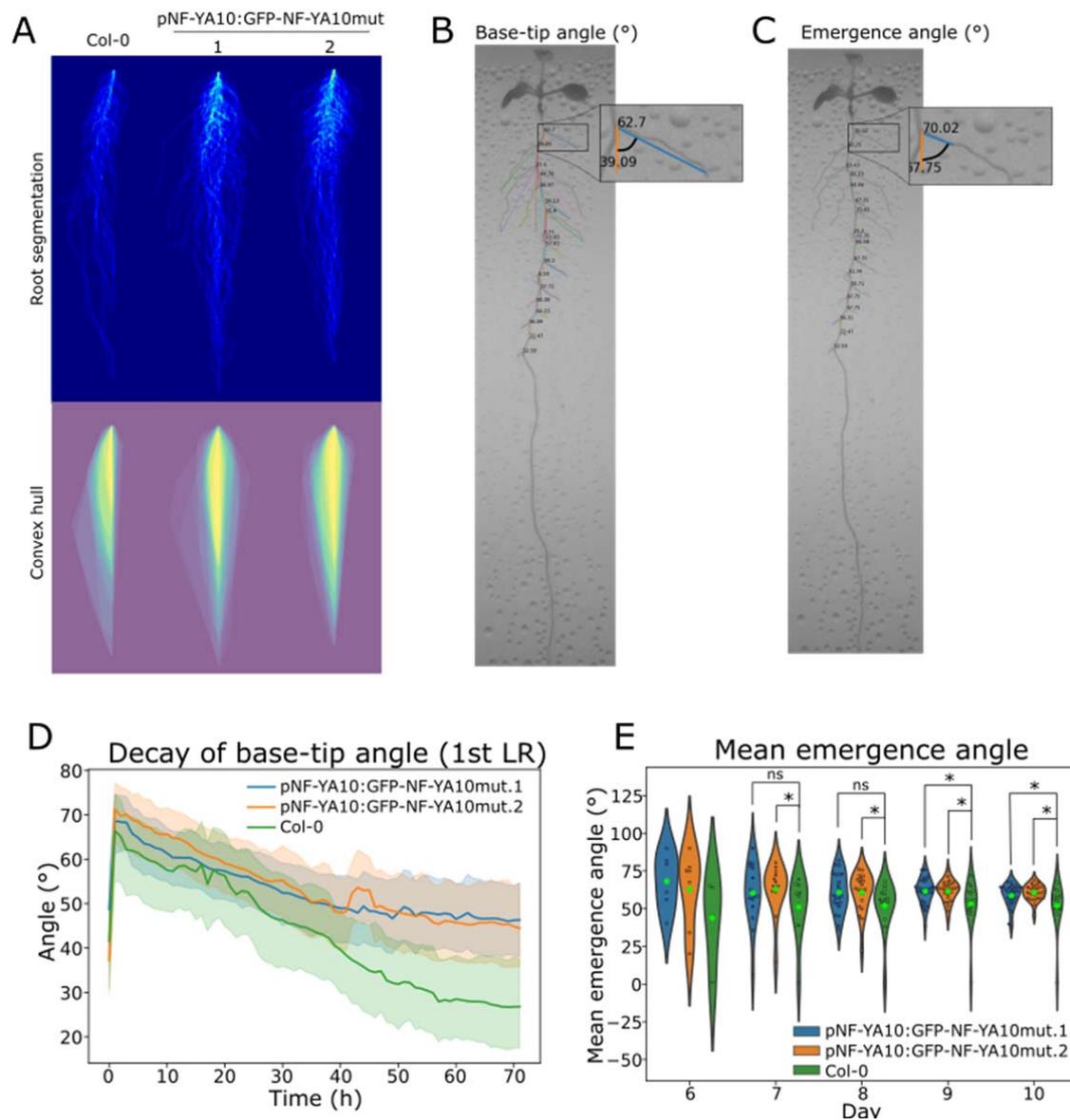
177

178

179

180

181  
182  
183



184  
185  
186  
187  
188  
189  
190  
191  
192

**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.

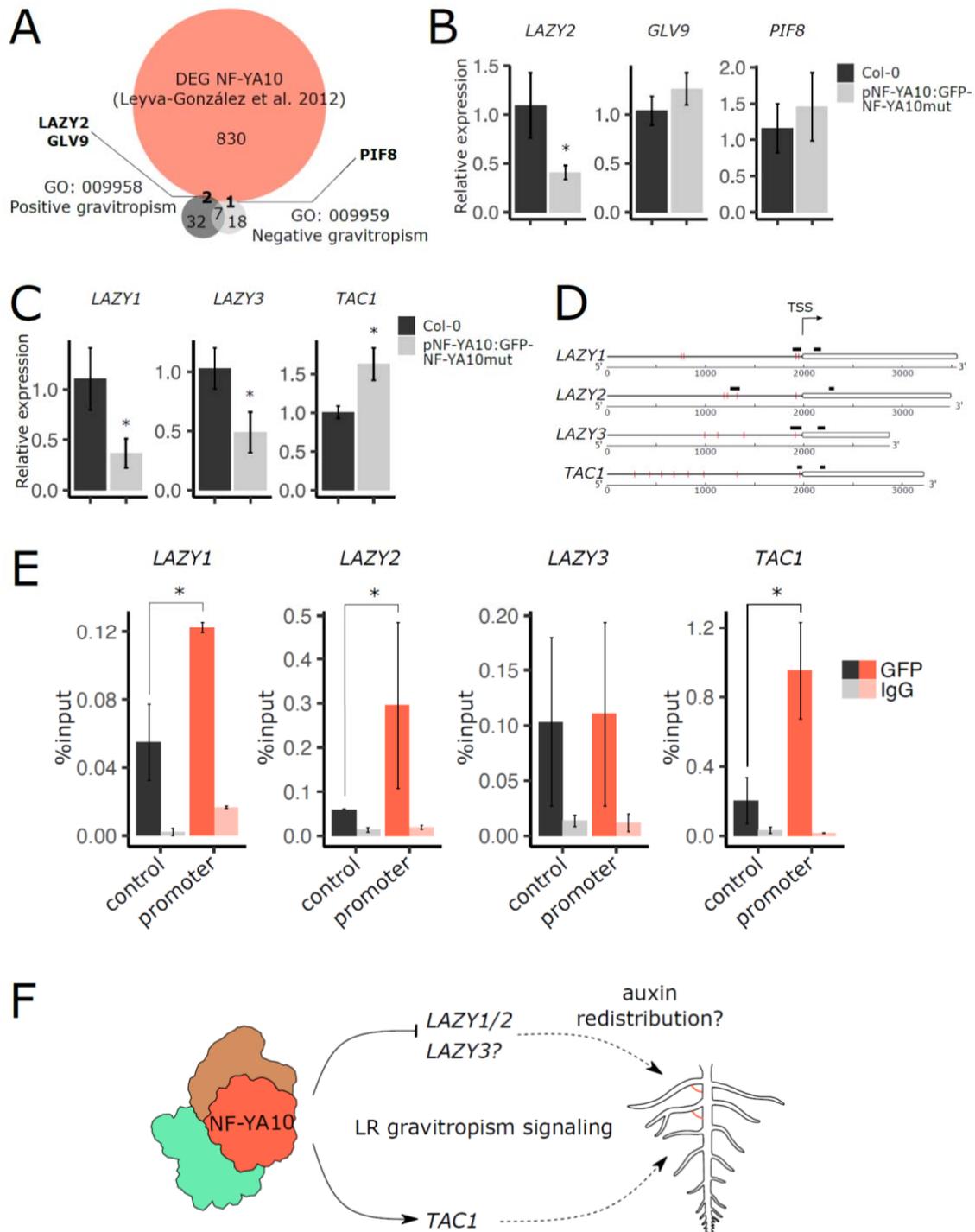
193 To decipher the molecular mechanism behind this phenotype, we looked for potential NF-  
194 YA10 targets involved in lateral organ gravitropism described in the literature, which bear  
195 CCAAT-boxes in their promoter sequences. To this end, we first crossed the list of  
196 differentially expressed 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**).

223

224

225

226



227

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.

293  
294  
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](http://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).

384

385

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

#### 428 **FUNDING**

429 This project was financially supported by grants from Agencia I+D+i (PICT), Universidad  
430 Nacional del Litoral (CAI+D), International Research Project LOCOSYM (CNRS-CONICET). LL,  
431 EF and FA are members of CONICET and NG is a fellow of the same institution. AB is a fellow  
432 of Paris-Saclay and CONICET. NM was a fellow of Agencia I+D+i.

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

459 **REFERENCES**

460 **Bai, H., Murali, B., Barber, K., and Wolverson, C.** (2013). Low phosphate alters lateral root  
461 setpoint angle and gravitropism. *Am J Bot* **100**:175–182.

462 **Boratyn, G. M., Camacho, C., Cooper, P. S., Coulouris, G., Fong, A., Ma, N., Madden, T. L.,**  
463 **Matten, W. T., McGinnis, S. D., Merezuk, Y., et al.** (2013). BLAST: a more efficient report  
464 with usability improvements. *Nucleic Acids Research* **41**:W29–W33.

465 **ChronoRoot: High-throughput phenotyping by deep segmentation networks reveals novel**  
466 **temporal parameters of plant root system architecture** (2021). *Gigascience* Advance Access  
467 published July 1, 2021, doi:10.1093/gigascience/giab052.

468 **Clough, S. J., and Bent, A. F.** (1998). Floral dip: a simplified method for *Agrobacterium*-  
469 mediated transformation of *Arabidopsis thaliana*: Floral dip transformation of *Arabidopsis*.  
470 *The Plant Journal* **16**:735–743.

- 471 **Czechowski, T., Stitt, M., Altmann, T., Udvardi, M. K., and Scheible, W.-R.** (2005). Genome-  
472 Wide Identification and Testing of Superior Reference Genes for Transcript Normalization in  
473 *Arabidopsis*. *Plant Physiology* **139**:5–17.
- 474 **Delport, W., Poon, A. F. Y., Frost, S. D. W., and Kosakovsky Pond, S. L.** (2010). Datamonkey  
475 2010: a suite of phylogenetic analysis tools for evolutionary biology. *Bioinformatics* **26**:2455–  
476 2457.
- 477 **Dolfini D, Zambelli F, Pedrazzoli M, Mantovani R, Pavese G.** (2016) A high definition look at  
478 the NF-Y regulome reveals genome-wide associations with selected transcription factors.  
479 *Nucleic Acids Res.* **2**; 4684-702.
- 480 **Dong, Z., Jiang, C., Chen, X., Zhang, T., Ding, L., Song, W., Luo, H., Lai, J., Chen, H., Liu, R., et**  
481 **al.** (2013). Maize LAZY1 Mediates Shoot Gravitropism and Inflorescence Development  
482 through Regulating Auxin Transport, Auxin Signaling, and Light Response1[C][W]. *Plant*  
483 *Physiol* **163**:1306–1322.
- 484 **Edgar, R. C.** (2004). MUSCLE: multiple sequence alignment with high accuracy and high  
485 throughput. *Nucleic Acids Research* **32**:1792–1797.
- 486 **Fornari, M., Calvenzani, V., Masiero, S., Tonelli, C., and Petroni, K.** (2013). The Arabidopsis  
487 NF-YA3 and NF-YA8 Genes Are Functionally Redundant and Are Required in Early  
488 Embryogenesis. *PLoS ONE* **8**:e82043.
- 489 **Ge, L., and Chen, R.** (2019). Negative gravitropic response of roots directs auxin flow to  
490 control root gravitropism. *Plant Cell Environ* **42**:2372–2383.
- 491 **Goodstein, D. M., Shu, S., Howson, R., Neupane, R., Hayes, R. D., Fazo, J., Mitros, T., Dirks,**  
492 **W., Hellsten, U., Putnam, N., et al.** (2012). Phytozome: a comparative platform for green  
493 plant genomics. *Nucleic Acids Research* **40**:D1178–D1186.
- 494 **Gouy, M., Guindon, S., and Gascuel, O.** (2010). SeaView Version 4: A Multiplatform  
495 Graphical User Interface for Sequence Alignment and Phylogenetic Tree Building. *Molecular*  
496 *Biology and Evolution* **27**:221–224.
- 497 **Kawamoto, N., and Morita, M. T.** (2022). Gravity sensing and responses in the coordination  
498 of the shoot gravitropic setpoint angle. *New Phytologist* **236**:1637–1654.
- 499 **Laloum, T., De Mita, S., Gamas, P., Baudin, M., and Niebel, A.** (2013). CCAAT-box binding  
500 transcription factors in plants: Y so many? *Trends in Plant Science* **18**:157–166.

- 501 **Lampropoulos, A., Sutikovic, Z., Wenzl, C., Maegele, I., Lohmann, J. U., and Forner, J.**  
502 (2013). GreenGate - A Novel, Versatile, and Efficient Cloning System for Plant Transgenesis.  
503 *PLoS ONE* **8**:e83043.
- 504 **Lavenus, J., Goh, T., Guyomarc'h, S., Hill, K., Lucas, M., Voß, U., Kenobi, K., Wilson, M. H.,**  
505 **Farcot, E., Hagen, G., Guilfoyle T. J., Fukaki H., Laplaze L., and Bennett M. J.** (2015).  
506 Inference of the Arabidopsis Lateral Root Gene Regulatory Network Suggests a Bifurcation  
507 Mechanism That Defines Primordia Flanking and Central Zones. *Plant Cell* **27**:1368–1388.
- 508 **Letunic, I., and Bork, P.** (2016). Interactive tree of life (iTOL) v3: an online tool for the display  
509 and annotation of phylogenetic and other trees. *Nucleic Acids Res* **44**:W242–W245.
- 510 **Leyva-González, M. A., Ibarra-Laclette, E., Cruz-Ramírez, A., and Herrera-Estrella, L.** (2012).  
511 Functional and Transcriptome Analysis Reveals an Acclimatization Strategy for Abiotic Stress  
512 Tolerance Mediated by Arabidopsis NF-YA Family Members. *PLoS ONE* **7**:e48138.
- 513 **Pagnussat, G. C., Yu, H.-J., Ngo, Q. A., Rajani, S., Mayalagu, S., Johnson, C. S., Capron, A.,**  
514 **Xie, L.-F., Ye, D., and Sundaresan, V.** (2005). Genetic and molecular identification of genes  
515 required for female gametophyte development and function in *Arabidopsis*. *Development*  
516 **132**:603–614.
- 517 **Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., Preibisch,**  
518 **S., Rueden, C., Saalfeld, S., Schmid, B., et al.** (2012). Fiji: an open-source platform for  
519 biological-image analysis. *Nat Methods* **9**:676–682.
- 520 **Sorin, C., Declerck, M., Christ, A., Blein, T., Ma, L., Lelandais-Brière, C., Njo, M. F.,**  
521 **Beeckman, T., Crespi, M., and Hartmann, C.** (2014). A mi R 169 isoform regulates specific NF  
522 -YA targets and root architecture in Arabidopsis. *New Phytol* **202**:1197–1211.
- 523 **Yang, M., Wang, C., Hassan, M. A., Li, F., Xia, X., Shi, S., Xiao, Y., and He, Z.** (2021). QTL  
524 mapping of root traits in wheat under different phosphorus levels using hydroponic culture.  
525 *BMC Genomics* **22**:174.
- 526 **Yoshihara, T., and Spalding, E. P.** (2017). LAZY Genes Mediate the Effects of Gravity on Auxin  
527 Gradients and Plant Architecture. *Plant Physiol.* **175**:959–969.
- 528 **Zhang, M., Hu, X., Zhu, M., Xu, M., and Wang, L.** (2017). Transcription factors NF-YA2 and  
529 NF-YA10 regulate leaf growth via auxin signaling in Arabidopsis. *Sci Rep* **7**:1395.

530 **Zhao, H., Lin, K., Ma, L., Chen, Q., Gan, S., and Li, G.** (2020). Arabidopsis NUCLEAR FACTOR Y  
531 A8 inhibits the juvenile-to-adult transition by activating transcription of MIR156s. *Journal of*  
532 *Experimental Botany* **71**:4890–4902.

533

## Parsed Citations

- Bai, H., Murali, B., Barber, K., and Wolverton, C. (2013). Low phosphate alters lateral root setpoint angle and gravitropism. *Am J Bot* 100:175–182.  
Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)
- Boratyn, G. M., Camacho, C., Cooper, P. S., Coulouris, G., Fong, A., Ma, N., Madden, T. L., Matten, W. T., McGinnis, S. D., Merezuk, Y., et al. (2013). BLAST: a more efficient report with usability improvements. *Nucleic Acids Research* 41:W29–W33.  
Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)
- ChronoRoot: High-throughput phenotyping by deep segmentation networks reveals novel temporal parameters of plant root system architecture (2021). *Gigascience Advance Access* published July 1, 2021, doi:10.1093/gigascience/giab052.  
Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)
- Clough, S. J., and Bent, A. F. (1998). Floral dip: a simplified method for *Agrobacterium*-mediated transformation of *Arabidopsis thaliana*: Floral dip transformation of *Arabidopsis*. *The Plant Journal* 16:735–743.  
Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)
- Czechowski, T., Stitt, M., Altmann, T., Udvardi, M. K., and Scheible, W.-R. (2005). Genome-Wide Identification and Testing of Superior Reference Genes for Transcript Normalization in *Arabidopsis*. *Plant Physiology* 139:5–17.  
Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)
- Delport, W., Poon, A. F. Y., Frost, S. D. W., and Kosakovsky Pond, S. L. (2010). Datamonkey 2010: a suite of phylogenetic analysis tools for evolutionary biology. *Bioinformatics* 26:2455–2457.  
Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)
- Dolfini D, Zambelli F, Pedrazzoli M, Mantovani R, Pavesi G. (2016) A high definition look at the NF-Y regulome reveals genome-wide associations with selected transcription factors. *Nucleic Acids Res.* 2; 4684-702.  
Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)
- Dong, Z., Jiang, C., Chen, X., Zhang, T., Ding, L., Song, W., Luo, H., Lai, J., Chen, H., Liu, R., et al. (2013). Maize LAZY1 Mediates Shoot Gravitropism and Inflorescence Development through Regulating Auxin Transport, Auxin Signaling, and Light Response1[C][W]. *Plant Physiol* 163:1306–1322.  
Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)
- Edgar, R. C. (2004). MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32:1792–1797.  
Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)
- Fornari, M., Calvenzani, V., Masiero, S., Tonelli, C., and Petroni, K. (2013). The *Arabidopsis* NF-YA3 and NF-YA8 Genes Are Functionally Redundant and Are Required in Early Embryogenesis. *PLoS ONE* 8:e82043.  
Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)
- Ge, L., and Chen, R. (2019). Negative gravitropic response of roots directs auxin flow to control root gravitropism. *Plant Cell Environ* 42:2372–2383.  
Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)
- Goodstein, D. M., Shu, S., Howson, R., Neupane, R., Hayes, R. D., Fazo, J., Mitros, T., Dirks, W., Hellsten, U., Putnam, N., et al. (2012). Phytozome: a comparative platform for green plant genomics. *Nucleic Acids Research* 40:D1178–D1186.  
Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)
- Gouy, M., Guindon, S., and Gascuel, O. (2010). SeaView Version 4: A Multiplatform Graphical User Interface for Sequence Alignment and Phylogenetic Tree Building. *Molecular Biology and Evolution* 27:221–224.  
Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)
- Kawamoto, N., and Morita, M. T. (2022). Gravity sensing and responses in the coordination of the shoot gravitropic setpoint angle. *New Phytologist* 236:1637–1654.  
Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)
- Laloum, T., De Mita, S., Gamas, P., Baudin, M., and Niebel, A. (2013). CCAAT-box binding transcription factors in plants: Y so many? *Trends in Plant Science* 18:157–166.  
Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)
- Lampropoulos, A., Sutikovic, Z., Wenzl, C., Maegele, I., Lohmann, J. U., and Forner, J. (2013). GreenGate - A Novel, Versatile, and Efficient Cloning System for Plant Transgenesis. *PLoS ONE* 8:e83043.  
Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)
- Lavenus, J., Goh, T., Guyomarc'h, S., Hill, K., Lucas, M., Voß, U., Kenobi, K., Wilson, M. H., Farcot, E., Hagen, G., Guilfoyle T. J., Fukaki H., Laplaze L., and Bennett M. J. (2015). Inference of the *Arabidopsis* Lateral Root Gene Regulatory Network Suggests a Bifurcation Mechanism That Defines Primordia Flanking and Central Zones. *Plant Cell* 27:1368–1388.

Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)

**Letunic, I., and Bork, P. (2016). Interactive tree of life (iTOL) v3: an online tool for the display and annotation of phylogenetic and other trees. *Nucleic Acids Res* 44:W242–W245.**

Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)

**Leyva-González, M. A., Ibarra-Laclette, E., Cruz-Ramírez, A., and Herrera-Estrella, L. (2012). Functional and Transcriptome Analysis Reveals an Acclimatization Strategy for Abiotic Stress Tolerance Mediated by Arabidopsis NF-YA Family Members. *PLoS ONE* 7:e48138.**

Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)

**Pagnussat, G. C., Yu, H.-J., Ngo, Q. A., Rajani, S., Mayalagu, S., Johnson, C. S., Capron, A., Xie, L.-F., Ye, D., and Sundaresan, V. (2005). Genetic and molecular identification of genes required for female gametophyte development and function in Arabidopsis. *Development* 132:603–614.**

Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)

**Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., Preibisch, S., Rueden, C., Saalfeld, S., Schmid, B., et al. (2012). Fiji: an open-source platform for biological-image analysis. *Nat Methods* 9:676–682.**

Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)

**Sorin, C., Declerck, M., Christ, A., Blein, T., Ma, L., Lelandais-Brière, C., Njo, M. F., Beeckman, T., Crespi, M., and Hartmann, C. (2014). A mi R 169 isoform regulates specific NF - YA targets and root architecture in Arabidopsis. *New Phytol* 202:1197–1211.**

Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)

**Yang, M., Wang, C., Hassan, M. A., Li, F., Xia, X., Shi, S., Xiao, Y., and He, Z. (2021). QTL mapping of root traits in wheat under different phosphorus levels using hydroponic culture. *BMC Genomics* 22:174.**

Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)

**Yoshihara, T., and Spalding, E. P. (2017). LAZY Genes Mediate the Effects of Gravity on Auxin Gradients and Plant Architecture. *Plant Physiol.* 175:959–969.**

Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)

**Zhang, M., Hu, X., Zhu, M., Xu, M., and Wang, L. (2017). Transcription factors NF-YA2 and NF-YA10 regulate leaf growth via auxin signaling in Arabidopsis. *Sci Rep* 7:1395.**

Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)

**Zhao, H., Lin, K., Ma, L., Chen, Q., Gan, S., and Li, G. (2020). Arabidopsis NUCLEAR FACTOR Y A8 inhibits the juvenile-to-adult transition by activating transcription of MIR156s. *Journal of Experimental Botany* 71:4890–4902.**

Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)