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A Comprehensive Toolkit for Inducible, Cell Type-Specific Gene Expression in Arabidopsis

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One sentence summary: A set of transgenic lines was developed to enable spatio-temporal control of gene expression in Arabidopsis.

Footnotes

Author contributions

A-KS and VL-S generated DNA constructs and transgenic plants; A-KS, VL-S, and ZL analysed transgenic plants; JF, CW, CG, SA, AVB, MF, MG, JEMV, JL contributed GreenGate modules; A-KS, VL-S, TG, and SW designed the project; VL-S, TG, and SW wrote the manuscript with contributions from A-KS and ZL.

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Abstract

Understanding the context-specific role of gene function is a key objective of modern biology. To this end, we generated a resource for inducible cell type-specific trans-activation in *Arabidopsis thaliana* (Arabidopsis) based on the well-established combination of the chimeric GR-LhG4 transcription factor and the synthetic *pOp* promoter. Harnessing the flexibility of the GreenGate cloning system, we produced a comprehensive set of transgenic lines termed GR-LhG4 driver lines targeting most tissues in the Arabidopsis shoot and root with a strong focus on the indeterminate meristems. When we combined these transgenic lines with effectors under the control of the *pOp* promoter, we observed tight temporal and spatial control of gene expression. In particular, inducible expression in F_1 plants obtained from crosses of driver and effector lines allows for rapid assessment of the cell type-specific impact of an effector with high temporal resolution. Thus, our comprehensive and flexible method is suitable for overcoming the limitations of ubiquitous genetic approaches, the outputs of which are often difficult to interpret due to the widespread existence of compensatory mechanisms and the integration of diverging effects in different cell types.

Introduction

The key to the evolutionary success of multicellularity, which arose independently in plants and animals, is the division of labour between highly specialized cell types. This requires the robust specification of cell fate through epigenetic and transcriptional programming, despite the identical genetic makeup of each cell. In plants, cell fate acquisition is largely based on positional information, which depends on cell-to-cell communication and medium to long distance morphogenetic signals that cooperate in organ patterning (Efroni, 2017). Conversely, individual genes, pathways, and metabolites can have diverse or even opposing roles depending on the tissue context. A prominent example for context-dependency of a fundamental patterning process is given by the interplay of the auxin and cytokinin phytohormones (Furuta et al., 2014; Greb and Lohmann, 2016; Truskina and Vernoux, 2017). In the shoot apical meristem, harbouring the stem cell niche ultimately responsible for most above-ground plant organs, cytokinin signalling is associated with maintaining a pluripotent, undifferentiated state, whereas auxin signalling promotes differentiation. In marked contrast, auxin is required for stem cell maintenance in the root apical meristem (RAM) (Pacifici et al., 2015; Weijers and Wagner, 2016). Therefore, the global effects of genetic lesions or of knock-ins can dilute and mask specific functions and are often difficult to interpret.

Routinely, stable genetic gain- and loss-of-function mutants remain the main pillar of the reductionist approach to biology and the phenotypes of such mutants are assessed to deduce a function of the mutated locus in the wild type. However, the function of many gene products is context-specific and thus the phenotypes of mutants or transgenic lines can be complex. In addition, mutant organisms can undergo life-long adaptation, impeding the interpretation of their phenotype. Moreover, transgenic and mutational approaches can interfere with plant vitality, precluding an in-depth analysis.

Many of these problems can be overcome by inducible, cell type-specific expression mediated by two-component transcription activation systems (Moore et al., 2006). An expression cassette is constructed using a heterologous or synthetic promoter and is hence silent unless a cognate transcription factor is present. An efficient approach is to generate transgenic plants called 'driver lines' that express the transcription factor in a spatially and temporally controlled manner, and a 'responder line' carrying the effector construct. After crossing of the two lines, expression can be induced and the phenotypic consequences of the effector can be studied. In the abstract, these expression systems are highly valuable because they ideally enable cell-type specific or stage-specific complementation or knock-down, facilitate time-resolved monitoring of the response to a given cue, can overcome the lethality of constitutive expression, and allow to study cell autonomous and non-cell autonomous effects with high temporal and spatial resolution. However, the considerable effort and time requirements for DNA cloning and the generation of stable transgenic plants are a major bottleneck curtailing their use to date. For the same reason and because distinct tissue-specific promoters were not always available in the past, attention is usually given to one tissue or cell type of interest at a time and unbiased approaches targeting a larger spectrum of individual tissues are rarely followed.

Here, we report on the generation of a comprehensive set of *Arabidopsis thaliana* driver lines suited for tissue-specific trans-activation of an effector cassette in a wide range of cell types and with the possibility to monitor gene activation in space and time by a fluorescent promoter reporter. To ensure rapid, stable induction with minimal adverse effects on plant growth caused by the inducer, our system takes advantage of the widely used LhG4/pOp system (Moore et al., 1998; Craft et al., 2005; Samalova et al., 2005) combined with the ligand binding domain of the rat glucocorticoid receptor (GR) (Picard, 1993) (Craft et al., 2005). LhG4 is a chimeric transcription factor consisting of a mutant version of the *Escherichia coli lac* repressor with high DNA binding affinity (Lehming et al., 1987) and the transcription activation domain of yeast Gal4p (Moore et al., 1998). N-terminal fusion with

the GR ligand binding-domain renders the transcription factor inactive in the cytosol through sequestration by HEAT SHOCK PROTEIN90 (HSP90) in the absence of the inducer. Nuclear import after treatment with the synthetic glucocorticoid dexamethasone (Dex) (Picard, 1993) results in transcriptional activation of expression cassettes that are under the control of the synthetic Op 5' regulatory region consisting of a *Cauliflower mosaic virus* (CaMV) *35S* minimal promoter and two upstream *lac* operators (Moore et al., 1998; Craft et al., 2005). Combining multiple interspersed repeats of the operator elements (*pOp4*; *pOp6*) and localized expression of LhG4 enable strong overexpression of a target gene in a cell type-specific manner (Craft et al., 2005).

Our work builds on these seminal studies by creating 19 well-characterized and stable driver lines targeting most cell types in Arabidopsis with a focus on the three main meristems of the plant, the root apical meristem (RAM), the shoot apical meristem (SAM), and the cambium. Of note, for several cell types such as the pith in the inflorescence stem or the xylem pole pericycle cells in the root, inducible expression systems were not available so far. The driver lines were generated employing the fast and flexible GreenGate cloning system (Lampropoulos et al., 2013), but are compatible with any vector/transgenic line in which the expression of an effector is under the control of derivatives of the *pOp* promoter element (Moore et al., 1998). An important feature of our driver lines is the presence of a fluorescent reporter amenable to live imaging, which allows monitoring the spatio-temporal dynamics of gene induction and may serve as a read-out for any effect on the respective tissue identity. Similarly, it allows us to assess whether the expression of the effector has an impact on the transcriptional circuitries targeting the promoter it is expressed from. The material described here allows testing the effect of genetic perturbations in a broad repertoire of individual tissues on a distinct developmental or physiological process. As trans-activation efficiently occurs in the presence of the inducer in F1 plants derived from a cross between a driver and an effector line, the effect of a given expression cassette can be assessed relatively quickly

144 in a wide range of cell types, demonstrating the usefulness of this resource for the broader
145 research community.

146

147 **Results**

148 **Design of driver lines with cell type-specific expression of GR-LhG4**

149 To generate a comprehensive set of driver lines expressing the chimeric GR-LhG4
150 transcription factor under the control of cell type-specific promoters, we made use of the
151 Golden Gate-type GreenGate cloning system, which enables quick, modular, and scarless
152 assembly of large constructs (Engler et al., 2008; Lampropoulos et al., 2013). Our design
153 included, on the same T-DNA, the coding sequence for an mTurquoise2 fluorescent reporter
154 (Goedhart et al., 2012) targeted to the endoplasmic reticulum (ER) through translational
155 fusion with an N-terminal signal peptide from sweet potato (*Ipomoea batatas*) Sporamin A
156 (SP, (Lampropoulos et al., 2013)) and the ER retention motif His-Asp-Glu-Leu (HDEL) under
157 the control of pOp6 and a minimal CaMV 35S promoter (*pOp6:SP-mTurquoise2-HDEL*) (Fig.
158 1). In our set up, the GR-LhG4 transcription factor is expressed under the control of a tissue-
159 or cell type-specific promoter (pTS). Consequently, GR-LhG4 activates the expression of the
160 mTurquoise2 reporter and any other effector downstream of a *pOp* promoter after Dex
161 treatment specifically in those tissues (Fig. 1). We anticipate that the most utility can be
162 obtained from this system if lines harbouring effector cassettes are crossed with driver lines
163 and analyses are performed with F1 plants. However, other modes such as direct
164 transformation of multiple driver lines or the introgression into different (mutant) backgrounds
165 are also conceivable. Notably, even though the mTurquoise2 reporter is expressed from the
166 same T-DNA as GR-LhG4, there is no mechanistic difference to the activation of an effector
167 *in trans* (Fig. 1).

168 For establishing a rather comprehensive set of driver lines, we first selected respective
169 tissue-specific promoters based on literature reports and our own expression data (Table 1).

Subsequently, we generated stable transgenic driver lines in the Arabidopsis Col-0 background using 19 specific promoters that cover most cell types in the RAM, the SAM, and the cambium. Several of the promoters have been previously shown to work robustly in cell type-specific mis-expression approaches (e.g. Nakajima et al., 2001; Weijers et al., 2006; Mustroph et al., 2009; Miyashima et al., 2011; Roppolo et al., 2011; Vaten et al., 2011; Naseer et al., 2012; Cruz-Ramirez et al., 2013; Ohashi-Ito et al., 2014; Wang et al., 2014; Chaiwanon and Wang, 2015; Serrano-Mislata et al., 2015; Vragovic et al., 2015; Marques-Bueno et al., 2016; Siligato et al., 2016; Doblas et al., 2017). Next, we generated T3 lines in which the resistance to the selective agent sulfadiazine appeared homozygous after segregating as a single locus in the T2 generation based on resistance or standard addition quantitative real-time PCR (SA-qPCR) analyses (Huang et al., 2013).

Validation of the specificity of driver lines.

To confirm the expected expression patterns in the root, driver lines were germinated on medium containing 30 µM Dex or DMSO and analysed with confocal laser scanning microscopy (CLSM) five days after germination (DAG). In each case, we recorded mTurquoise2-derived fluorescence in longitudinal optical sections of the root meristem (Fig. 2 and Supplemental Fig. S1) and, where appropriate, in cross sections through the meristem or the differentiation zone (Supplemental Fig. S2). To visualize expression in the shoot, lines were grown on soil in long day conditions and the aerial part of plants with 15 cm tall inflorescence stems were dipped either in tap water containing 10 µM Dex (Fig. 3) or only the solvent DMSO (Supplemental Fig. S3). After 24 h, freehand sections of the stem were stained with propidium iodide (PI) to highlight xylem elements and analysed by confocal microscopy. To analyse expression in the SAM, inflorescence meristems of 15 cm tall plants were treated with Dex 48 hours before being dissected and imaged with CLSM, again using PI as a cell wall counterstain (Fig. 4). Reporter gene activities were consistent with the expected patterns and strictly dependent on the presence of Dex (Supplemental Fig. S1, Supplemental Fig. S3, and Supplemental Fig. S4). In addition, the complete absence of

reporter activity in tissues adjacent to cells in which activity was expected suggested that the chimeric GR-LhG4 protein does not move between cells. We did not observe any negative effect of Dex treatment on plant growth (Supplemental Fig. S5).

Characterization of gene activation.

We next tested whether dose-response and induction dynamics previously observed with the GR-LhG4 system (Craft et al., 2005) were recapitulated in our set up. To this end we germinated the *pSCARECROW* (*pSCR*) driver line mediating GR-LhG4 expression in the quiescent centre (QC) and the endodermis (Di Laurenzio et al., 1996; Wysocka-Diller et al., 2000) on plates containing solvent, 0.1 µM, 1 µM, 10 µM, and 100 µM Dex. Visualizing reporter fluorescence 5 DAG indeed revealed increasing reporter activity with increasing Dex concentrations (Fig. 5A), arguing for the possibility to fine tune gene expression by adjusting the levels of the inducer. We noticed that QC cells showed markedly stronger fluorescence compared to the endodermis, putatively reflecting higher promoter GR-LhG4/reporter stability in the QC as this was not observed with previously published lines using the same promoter fragment (Gallagher et al., 2004; Heidstra et al., 2004; Cruz-Ramirez et al., 2013). We therefore quantified fluorescence separately in the QC cells and the endodermal initials (Fig. 5C and Fig. 5D). Whereas the QC did not show a significant difference in fluorescence intensity between any of the treatments (Fig. 5C), the endodermis fluorescence intensity correlated with the concentration of the inducer until saturation appeared to be reached between 10 µM and 100 µM of Dex (Fig. 5D). Consequently, we concluded that, to fine tune gene expression by applying different Dex concentrations, the appropriate concentration range has to be determined for each promoter and cell type individually.

To further assess induction kinetics, the *pSCR* driver line was germinated on plates with control medium and transferred onto plates containing 50 µM Dex after five days. As expected, a time-dependent increase of reporter activity was observed over a period of 24 hours (Fig. 5B). Combined quantification of fluorescence in the QC and the endodermis initials detected reporter activity six hours after induction (Fig. 5E) and the activity values

were close to the values of constitutive Dex treatment after 24 hours (Fig. 5D and Fig. 5E). These observations suggested that six hours are sufficient to allow nuclear import of GR-LhG4, the induction of gene transcription, and initial protein translation, and that within 24 hours, protein levels reached a steady-state level. In addition, 5 day old roots that were either induced at 2 DAG, 3DAG, or 4 DAG showed similar reporter activities, demonstrating that responsiveness to the inducer is sustainable (Supplemental Fig. S6). To assess the kinetics of reporter expression after removal of the inducer, we germinated the *pSCR*>GR>*mTurquoise2* line on Dex-containing medium and transferred the seedlings to Dex-free medium 2 DAG. Quantifying reporter fluorescence revealed that one day after transfer, fluorescence intensity was indistinguishable from control plants transferred to inducer-containing plates, but declined over the course of the next two days to hardly detectable levels (Supplemental Fig. S7).

To estimate the level of transcription mediated by the GR-LhG4/pOp system we employed a line expressing *PECTIN METHYLESTERASE INHIBITOR5* (*PMEI5*) (Wolf et al., 2012) under control of the strong and nearly-ubiquitous *35S* promoter (*p35S:PMEI5*). When comparing roots from the *p35S:PMEI5* line with roots from a Dex-treated GR-LhG4/pOp line conferring expression of the same *PMEI5* coding sequence in xylem pole pericycle (XPP) cells (designated as *pXPP*>GR>*PMEI5* (Craft et al., 2005)), we observed *PMEI5* transcript levels similar to or slightly exceeding those in the *p35S:PMEI5* line (Supplemental Fig. S8). This was despite the fact that the *XPP* expression domain contains only approximately six cell files in the young root (Supplemental Fig. S2). Thus, we concluded that, although activating transcription in a very local manner, the GR-LhG4/pOp system can lead to strong expression in the respective cell types.

The ER-localized mTurquoise2 reporter present in our driver lines is transcribed from the same T-DNA that harbours the GR-LhG4 module (Fig. 1). To analyse the response of an independent T-DNA insertion carrying the *pOp6* element *in trans*, we generated a transgenic line carrying an ER-targeted mVenus reporter under the control of the *pOp6* promoter

(*pOp6:SP-mVenus-HDEL*) and crossed it with the *pSCR* driver line. The resulting F1 plants did not show any reporter activity when grown on plates without Dex (Fig. 6), again confirming that the GR-LhG4/pOp system is fully Dex-dependent. After Dex induction, we visualized both mTurquoise2 and mVenus fluorescence in the root and the stem and observed a complete congruence of both reporter activities (Fig. 6). Likewise, transgenic lines expressing a nucleus-targeted triple green fluorescent protein (GFP) fusion protein under the control of the *pOp6* promoter were generated and crossed with the *pCLAVATA3* (*CLV3*) driver line mediating expression in stem cells of the SAM (Fletcher et al., 1999). As expected, upon Dex induction, the 3xGFP-NLS signal was observed in a narrow domain at the tip of the SAM which also expressed the mTurquoise2 marker (Fig. 6). Together, these observations confirmed robust and specific trans-activation of transgenes in F1 plants.

Cell type-specific induction of VND7 demonstrates efficacy of trans-activation

To explore the potential of our lines to mediate the expression of a biologically active effector, we crossed the *pSCR* driver line with a line harbouring the *VASCULAR RELATED NAC-DOMAIN PROTEIN 7* (*VND7*) effector fused to the VP16 activation domain able to induce the formation of xylem vessels in a broad range of cell types (Kubo et al., 2005; Yamaguchi et al., 2010). F1 plants were grown on control medium for five days and then transferred to medium containing either 10 µM Dex or solvent. Five days later, fully differentiated vessel-like elements could be observed in the endodermis of the root and hypocotyl (Fig. 7), whereas in DMSO-treated controls xylem elements were clearly restricted to the stele. These results demonstrate that this resource for cell type-specific and inducible trans-activation can be used to study gene function with high spatio-temporal resolution.

Discussion

In this study, we combined the proven efficacy of the well-established GR-LhG4/pOp expression system (Craft et al., 2005; Rutherford et al., 2005; Samalova et al., 2005) with

277 the ease of cloning enabled by the GreenGate system (Lampropoulos et al., 2013) to
278 provide a comprehensive toolbox for inducible, cell type-specific expression in Arabidopsis.
279 The driver lines described here cover a large proportion of the known cell types in the three
280 main meristems of the plant, the RAM, the SAM, and the cambium. Our analysis
281 demonstrates that this system achieves non-leaky, adjustable, and robust trans-activation of
282 effectors in the F1 generation after crossing with effector-carrying plants. Therefore,
283 generating a line harbouring an effector cassette under the control of the *pOp6* promoter
284 should enable users to rapidly assess a battery of different expression regimes for a wide
285 range of applications. In most cases, the effector might be the coding region of a gene one
286 may want to miss-express in a spatially and temporally controlled manner, but other uses
287 are conceivable, such as adjustable (pulsed) expression of reporters, domain specific knock-
288 down through artificial microRNAs, cell type-specific complementation studies, the
289 acquisition of cell type-specific transcriptomes/translatomes/proteomes/epigenomes, or the
290 local induction of genome editing, for example through expression of Cre recombinase or
291 clustered regularly interspaced short palindromic repeats (CRISPR)/CRISPR-associated
292 protein 9 (Cas9) (CRISPR/Cas9) modules (e.g. Birnbaum et al., 2003; Brady et al., 2007;
293 Dinneny et al., 2008; Gifford et al., 2008; Mustroph et al., 2009; Deal and Henikoff, 2011;
294 Hacham et al., 2011; Iyer-Pascuzzi et al., 2011; Petricka et al., 2012; Fridman et al., 2014;
295 Adrian et al., 2015; Vragovic et al., 2015; Efroni et al., 2016; Kang et al., 2017). Thus, this
296 system should be a valuable tool for the generation of inducible genetic perturbations to
297 overcome the limitations of “endpoint” genetics and study genetic activities in specific tissue
298 contexts.

299 **Design of the trans-activation system**

300 Two-component trans-activation and chemically-induced gene expression systems have
301 been widely used by plant biologist in the past. For example, a large collection of enhancer
302 trapping lines based on the yeast Gal4 transcription factor (Haseloff, 1999; Engineer et al.,
303 2005) are an invaluable tool for constitutive, tissue-specific trans activation in Arabidopsis

(Aoyama and Chua, 1997; Sabatini et al., 2003; Weijers et al., 2003; Swarup et al., 2005; Weijers et al., 2005). In addition, an inducible system based on Gal and cognate upstream activation sequence (UAS) has been devised (Aoyama and Chua, 1997) but appears to induce unspecific growth defects (Kang et al., 1999). Trans-activation based on LhG4 (Moore et al., 1998) shows only minimal detrimental effects on plant development, is thoroughly characterized and optimized (Moore et al., 1998; Baroux et al., 2005; Craft et al., 2005; Rutherford et al., 2005; Samalova et al., 2005; Moore et al., 2006) and has been used by the plant community in a number of studies (e.g. Schoof et al., 2000; Baroux et al., 2001; Eshed et al., 2001; Hay and Tsiantis, 2006; Nodine and Bartel, 2012; Sauret-Gueto et al., 2013; Hazak et al., 2014; Serrano-Mislata et al., 2015; Jiang and Berger, 2017). Parallel to the development of these tools for cell type-specific expression, a number of inducible systems have been conceived to enable temporal control of gene expression (Gatz et al., 1992; Weinmann et al., 1994; Caddick et al., 1998; Zuo et al., 2000). Subsequently, combining and optimizing the available technology has succeeded in generating tools to mediate inducible expression in a cell type-specific manner (Deveaux et al., 2003; Laufs et al., 2003; Maizel and Weigel, 2004; Craft et al., 2005).

For the generation of this resource, we build on ground-breaking previous work establishing the LhG4 system in combination with the GR ligand binding domain (Craft et al., 2005), which has since been proven to be a valuable resource (e.g. Reddy and Meyerowitz, 2005; Ongaro et al., 2008; Ongaro and Leyser, 2008; Heisler et al., 2010; Jiang et al., 2011; Dello Ioio et al., 2012; Merelo et al., 2016; Caggiano et al., 2017; Tao et al., 2017). For the generation of our driver lines, we exploited the power of the GreenGate cloning system (Lampropoulos et al., 2013). We were able to rapidly assemble a large number of constructs efficiently, circumventing the bottleneck previously imposed by the challenging generation of large DNA constructs with varying promoter elements, coding regions, and terminators. The limiting factor in generating this resource was thus plant transformation, and obtaining single insertion, homozygous transgenic lines. As a general workflow, we aimed to generate at

least 40 T1 transformants, then scored segregation rations of antibiotic/herbicide resistance in the T2 generation and maintained lines in which the resistance segregated as a single locus. These lines usually showed similar characteristics concerning the response to the inducer and the expression levels achieved through trans-activation (based on fluorescence intensity). Nevertheless, reporter expression in any set of newly generated driver lines should be carefully assessed and compared with the literature and within lines, as genome integration in the vicinity of endogenous promoter and/or enhancer elements might influence the expression pattern. As expected, we occasionally observed widespread silencing in the T2 generation of the driver lines, which did not correlate with any particular DNA element present in multiple constructs

An important feature of our driver lines is the incorporation of a reporter amenable to live imaging, which can be used to monitor the induction and visualize the spatial expression domain. In addition, it allows us to assess whether the expression of the effector has an impact on the transcriptional circuitries of the cell type it is expressed from. For some applications, the internal reporter of the driver lines might also serve as an inducible marker even in the absence of any further effector expression. We chose mTurquoise2 as a fluorescent reporter, since its spectral characteristics make it compatible with more widely used green and red fluorophores, and it displays high photostability, fast maturation, and high quantum yield (Goedhart et al., 2012). The fluorescent protein was N-terminally fused with a signal peptide and modified with a C-terminal HDEL motif to mediate retention in the ER, which in our experience is the preferable subcellular localization for a fluorescent reporter when cross sections through the highly differentiated cells of the stem are required.

Trans-activation characteristics

Our system allows stringent temporal control of gene expression, as indicated by the lack of reporter expression in the absence of the inducer Dex. Moreover, the trans-activated reporter faithfully reproduced previously described expression patterns associated with the respective 5’ regulatory regions, suggesting that the chimeric GR-LhG4 transcription factor is

not cell-to-cell mobile. However, we noticed that in some cases trans-activation led to slightly different expression patterns as compared to fusions of the same 5' regulatory region with a reporter gene *in cis*. For example, expression driven from the *CLV3* promoter seemed broader than what was described in *pCLV3:XFP* lines, but consistent with a similarly designed *pCLV3*-driven trans-activation (Serrano-Mislata et al., 2015), possibly because the multiple binding sites of the *pOp6* promoter increase expression in cells where the *CLV3* promoter is only weakly active. Alternatively, high protein stability of the chimeric transcription factor, the reporter, or both, might cause prolonged activity of these proteins in cells that are already displaced from the stem cell region. This potential issue is less relevant for organs such as the root, where cells of one cell type also largely have the same clonal identity (Kidner et al., 2000; Costa, 2016).

Our experiments, in agreement with previous results, suggested that GR-LhG4/pOp-mediated trans-activation can achieve tissue-specific overexpression of the target gene, dependent on the concentration of the inducer. However, the possibility of "squelching", the sequestration of general transcription factors required for other processes by the LhG4 activation domain, must be taken into account at very high expression levels. Consistent with previous reports (Craft et al., 2005), our analysis of the *pSCR* driver line revealed a linear dose-response over at least two orders of magnitude, but the induction kinetics might be affected by the genomic location of the transgene and thus should be empirically determined for each line. It should be noted that expression of effectors using LhG4/pOp systems can be quenched by adding Isopropyl β-D-1-thiogalactopyranoside (IPTG) (Craft et al., 2005), which would allow pulsing experiments. However, we did not test the effect of IPTG in our lines.

Distribution of driver lines and DNA constructs

The lines described here, as well as DNA constructs, are available to the community upon request. While GR-LhG4 and the sulfadiazine resistance gene are constitutively expressed, care should be taken to amplify seeds only from non-induced plants to minimize the chance

384 of inducing post transcriptional gene silencing through high expression levels of the reporter
385 (Schubert et al., 2004; Abranches et al., 2005).

386

Material and methods.

Cloning

All constructs were produced by GreenGate cloning (Lampropoulos et al., 2013) using the modules described in Supplemental Table S1. The *Eco*31I (*Bsa*I) sites of the *SCR*, *PXY* and *WOX4* promoters were removed by the QuickChange XL Site-Directed Mutagenesis Kit (Agilent Technologies, USA) using the primers in Supplementary Table S1 following the manufacturer's instructions. The *Eco*31I site of the *ATHB-8* promoter was removed by amplifying the 5' part of the promoter up to the endogenous *Eco*31I restriction site, which was mutated by a single base exchange in the primer. This primer contained an *Eco*31I restriction site in the 5' overhang. The 3' fragment of the promoter was amplified with a forward primer directed against the region immediately 3' of the endogenous *Eco*31I site (containing a Eco31I site in the 5' overhang) and the reverse primer binding to the region immediately upstream of the ATG. The two fragments were amplified separately, digested with *Eco*31I, and ligated afterwards. As *Eco*31I is a Type IIs restriction enzyme, the recognition site in the primer overhangs were removed by digestion.

The repetitive sequences of the *pOp* promoter increase the likelihood of recombination events while amplifying the plasmids. To discriminate against clones with shorter *pOp* sequences, we designed primers that bind in the short flanking sequences at the beginning and end of *pOp6* (*pOp6*_F TGCATATGTCGAGCTCAAGAA; *pOp6*_R CTTATATAGAGGAAGGGTCTT) for PCR amplification and size assessment through gel electrophoresis. Final constructs were always confirmed by sequencing in *E. coli* and *Agrobacterium tumefaciens*. The occasional recombination events were only detected in *E. coli*.

Plant material and growth conditions.

All constructs were transformed by the floral dip method (Clough and Bent, 1998) as modified by (Zhang et al., 2006) into Arabidopsis Col-0. Transformed seeds were selected

413 on ½ MS plates containing 1.875-3.75 µg/ml sulfadiazine or 7.5 µ/ml glufosinate ammonium.
414 Only single integration lines based on T2 segregation ratios were propagated to T3, in which
415 plants homozygous for the resistance were selected. All plants were grown in long day
416 conditions (L16:D8) at 22ºC. For root analysis, plants were grown vertically in ½ MS plates
417 containing 1% sucrose and 0.9% plant agar (Duchefa P1001, Haarlem, The Netherlands).
418 For the induction treatments in plates, the seeds were sown on plates containing Dex
419 (Sigma_D4903, Missouri, United States) in the indicated concentration while the same
420 volume of DMSO (D139-1, Fisher Scientific, UK) was added for the mock control. For the
421 trans-activation experiment, seeds were sown on plates without Dex and seedlings were
422 transferred to Dex-containing plates at 1, 6 and 24 hours before imaging five DAG. For
423 analysis of the stem, the aerial parts of 15 cm tall plants were dipped for 30 s in either tap
424 water containing 10 µM Dex with 0.02% Silwet L-77 (Kurt Obermeier GmbH & Co. KG, Bad
425 Berleburg, Germany) or water with the same volume of DMSO with 0.02% Silwet. After 24
426 hours, free-hand sections of the stem were performed with a razor blade. Sections were
427 transferred to a small petri dish (35/10 mm, Greiner Bio-One GmbH, Germany) with 0.25
428 mg/ml of propidium iodide for 5 min and mounted on microscope slides to be visualized by
429 CSLM. For SAM imaging, the inflorescence meristems of 25-30 DAG plants were sprayed
430 with 10 µM Dex, whereas an equal volume of DMSO was added to water sprayed onto the
431 mock controls. 48 h after the treatment, the inflorescence meristems were dissected by
432 cutting of the stem, flowers and buds. The SAM was stained in 0.25 mg/ml propidium iodide
433 (Sigma-Aldrich, P4170) for 5 min and mounted in a 3% agarose small petri dish (35/10mm,
434 Greiner Bio-One GmbH, Germany) and visualized by CLSM.

435 **Microscopy**

436 Root samples were imaged using a Leica TCS SP5 laser scanning confocal microscope with
437 a HCX PL APO lambda blue 63x water immersion objective. The mTurquoise2 fluorophore
438 was excited by an argon laser at 458 nm and emission was collected between 460 and 516
439 nm. The mVenus fluorophore was excited by 514 nm and emission was collected between

520 and 580 nm. Cells were counter-stained by PI (Sigma-Aldrich, P4170) and imaged with 488 nm for excitation and emission was collected between 590 and 660 nm.

For stem and SAM samples we used a Nikon (Minato, Tokyo, Japan) A1 Confocal with a CFI Apo LWD 25x water immersion objective. The PI counter-stained cells were imaged with 561 nm for excitation and 570-620 nm for emission. The mTurquoise2 fluorescence was acquired using excitation at 405 nm and emission was collected between 425-475 nm. For the trans-activation experiments, the 3xGFP-NLS signal in the SAM was imaged with 488 nm for excitation and 500-550 nm for emission. In the root, mVenus was excited with 514 nm and the emission was collected between 500-550 nm.

For visualization of the xylem, plants were germinated in ½ MS plates and 5 DAG were transferred to either 10 µM Dex or mock containing ½ MS plates. To visualise the ectopic xylem formation, plants were collected five days after induction and fixed overnight in a 1:3 acetic acid:ethanol solution. Then, they were cleared in a 8:1:2 chloral hydrate:glycerol:water solution for at least 3 hours. Samples were mounted on microscope slides containing 50% glycerol solution and brightfield images were obtained using an Axioimager M1 microscope equipped with an AxioCamHRc (Carl Zeiss, Jena, Germany).

qPCR and SA-qPCR analysis

Analysis of *PMEI5* expression by qPCR was performed as described (Wolf et al., 2012). For standard addition quantitative real-time PCR (SA-qPCR), plant DNA extraction was performed as in (Allen et al., 2006) and SA-qPCR was performed as in (Huang et al., 2013). Quadruplicate qPCR reactions were performed in a final volume of 12.50 µl, including 6.25 µl of ABsolute qPCR SYBR Green Mix (Thermo Scientific), 0.25 µl of each primer (10 µM), 2 µl of genomic DNA (1.6 ng /µl) with different amounts (0, 1 or 3 µl) of plasmid (0.1 pg/µl) as a reference. The *SulfR* resistance gene was amplified with primers SulfR_Fwd GCATGATCTAACCCTCTGTCTC and SulfR_Rvs GAAGTCACTCGTTCCCACTAG, plasmid

target sequence was amplified with PL_Fwd GCCGTACTAAACCTCTCATCG and PL_Rvs CTGACCGGAAAGTTTGTTATTCG.

Accession Numbers

The Arabidopsis Genome Initiative numbers of genes used in this study are: *SCR* (AT3G54220), *ATHB-8* (AT4G32880), *XPP* (At4g30450), *AHP6* (AT1G80100), *PXY* (AT5G61480), *TMO5* (AT3G25710), *SMXL5* (AT5G57130), *CASP1* (AT2G36100), *VND7* (AT1G71930), *APL* (AT1G79430), *NST3* (AT1G32770), *WOX4* (AT1G46480), *PMEI5* (AT2G31430), *LTP1* (AT2G38540), AT2G3830, *ML1* (AT4G21750), *CLV3* (AT2G27250), *REV* (AT5G60690), *UFO* (AT1G30950), *CUC2* (AT5G53950).

Supplemental Data

Supplemental Figure S1. Analysis of DMSO-treated mock controls for driver line seedling root induction 5 DAG.

Supplemental Figure S2. Analysis of induced driver lines in 5 DAG seedling root.

Supplemental Figure S3. Analysis of DMSO-treated driver lines in the stem.

Supplemental Figure S4. Analysis of DMSO-treated driver lines in the SAM.

Supplemental Figure S5. Growth on 50 µM Dex does not impair root growth of Col-0.

Supplemental Figure S6. Reporter activation in the *pSCR*>GR>*mTurquoise2* line is sustainable.

Supplemental Figure S7. Kinetics of *pSCR*>GR>*mTurquoise2* reporter activity after removal of inducer.

Supplemental Figure S8. Quantification of GR-LhG4-mediated trans-activation.

Supplemental Table S1. List of primers used and DNA constructs generated in this study.

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Tables

Promoter		Expression	Reference
pSCR	*SCARECROW*	Endodermis, quiescent centre in RAM, starch sheath in stem	(Di Laurenzio et al., 1996; Wysocka-Diller et al., 2000)
pATHB-8	*HOMEOBOX GENE 8*	Procambium, xylem precursors and columella in RAM	(Baima et al., 1995)
pXPP	*XYLEM POLE PERICYCLE*	Xylem pole pericycle cells	(Andersen et al., 2018)
pAHP6	*HISTIDINE PHOSPHOTRANSFER PROTEIN 6*	Protoxylem precursors, pericycle, organ primordia in the SAM	(Mahonen et al., 2006; Besnard et al., 2014)
pPXY	*PHLOEM INTERCALATED WITH XYLEM*	(Pro-)cambium	(Fisher and Turner, 2007)
pTMO5	*TARGET OF MONOPTEROS 5*	Xylem precursors	(Schlereth et al., 2010; De Rybel et al., 2013)
pSMXL5	*SMAX1-LIKE 5*	Phloem (precursors)	(Wallner et al., 2017)
pCASP1	*CASPARIAN STRIP MEMBRANE DOMAIN PROTEIN 1*	Endodermis	(Roppolo et al., 2011)
pVND7	*VASCULAR RELATED NAC-DOMAIN PROTEIN 7*	Protoxylem (differentiating) in root, vessels in stem	(Kubo et al., 2005)
pAPL	*ALTERED PHLOEM DEVELOPMENT*	Phloem (differentiating)	(Bonke et al., 2003)
pNST3	*NAC SECONDARY WALL THICKENING PROMOTING 3*	Fibres	(Mitsuda et al., 2007)
pWOX4	*WUSCHEL RELATED HOMEOBOX 4*	(Pro-)cambium	(Hirakawa et al., 2010)
pLTP1	*LIPID TRANSFER PROTEIN 1*	Epidermis in stem	(Thoma et al., 1994)
pAT2G3830		Pith	(Valerio et al., 2004)
pML1	*MERISTEM LAYER 1*	L1 layer, epidermis	(Lu et al., 1996)
pCLV3	*CLAVATA3*	SAM stem cells	(Fletcher et al., 1999)
pREV	*REVOLUTA*	SAM central zone	(Otsuga et al., 2001)
pUFO	*UBUSUAL FLOWER ORGANS*	SAM peripheral zone	(Levin and Meyerowitz, 1995)
pCUC2	*CUP-SHAPED COTYLEDON 2*	Boundaries in SAM and leaf	(Aida et al., 1997)

502 **Table 1**: Overview of promoters utilized in this study.

Figure Legends

Figure 1. Overview of the Dex-inducible GR-LhG4/pOp system. In driver lines, expression of the synthetic transcription factor LhG4 is controlled by a tissue-specific promoter (*pTS*), whereas translational fusion with the ligand binding domain of rat glucocorticoid receptor (GR) prevents nuclear translocation in the absence of the inducer (Dex). After crossing with an effector line harbouring a transcriptional cassette under the control of a *pOp* element and a TATA box-containing minimal 35S promoter and addition of Dex, GR-LhG4 drives the expression of the effector as well as the mTurquoise2 reporter encoded by the driver line.

Figure 2. Analysis of induced driver lines in seedling roots. A, Schematic representation of root tissue layers. B-I, Induced driver line roots displaying fluorescence from propidium iodide (PI)-stained cell walls and the mTurquoise2 reporter (see Fig. 1 and Table 1). The indicated promoters mediate expression in the differentiating endodermis (B, *pCASPARIAN STRIP MEMBRANE DOMAIN PROTEIN 1* (p*CASP1)*), phloem precursor cells and adjacent pericycle cells (C, *pHISTIDINE PHOSPHOTRANSFER PROTEIN 6* (p*AHP6)*), xylem precursor cells (D, *pTARGET OF MONOPTEROS* 5 (p*TMO5)*), xylem pole pericycle cells (E, pXYLEM POLE PERICYCLE (p*XPP)*), stele initials, cortex/endodermis initial (CEI) and columella initials (F, *pHOMEOBOX GENE 8* (p*ATHB-8)*), endodermis, CEI and quiescent centre (G, *pSCARECROW* (p*SCR)*), stele initials, phloem and procambial cells (H, *pSMAX1-LIKE 5*, (p*SMXL5)*), and procambial cells (I, *pPHLOEM INTERCALATED WITH XYLEM* (p*PXY)*). PI fluorescence is false-coloured in magenta and mTurquoise2 fluorescence in green. Bars = 50 µm.

Figure 3. Analysis of induced driver lines in the stem. A, Schematic representation of inflorescence stem tissue layers. B-I, Induced driver line stems displaying fluorescence from propidium iodide (PI)-stained cell walls and the mTurquoise2 reporter (see Fig. 1 and Table 1). The promoters mediate expression in differentiated phloem (B, *pALTERED PHLOEM DEVELOPMENT*, (p*APL)*), xylem fibres and interfascicular fibres (C, *pNAC SECONDARY WALL THICKENING PROMOTING 3* (p*NST3)*), starch sheath (D, p*SCR*), cambium (E,

530 *pWUSCHEL RELATED HOMEOBOX 4* (p*WOX4*), xylem vessels (F, pVASCULAR
531 RELATED NAC DOMAIN PROTEIN 7 (*pVND7*), epidermal cells (G, *pLIPID TRANSFER*
532 *PROTEIN 1* (p*LTP1)*), the incipient phloem (H, p*SMXL5*), and pith (I, p*AT2G38380*). PI
533 fluorescence is false-coloured in magenta and mTurquoise2 fluorescence in green. Bars =
534 50 µm.

535

536 **Figure 4**. Analysis of induced driver lines in the shoot apical meristem (SAM). A, Schematic
537 representation of cell identity domains in the SAM. B-G, Induced driver line stems displaying
538 fluorescence from propidium iodide (PI)-stained cell walls and the mTurquoise2 reporter (see
539 Fig. 1 and Table 1). The left and middle panels are maximum projections of confocal stack,
540 the right panels consist of a single median confocal xy section and xz and yz view of the
541 stack. The indicated promoters mediate expression in the L1 layer/epidermis (B,
542 *pMERISTEM LAYER 1* (*pML1)*), the stem cell domain (C, *pCLV3*), the central zone (D,
543 *pREVOLUTA* (*pREV)*), the peripheral zone (E, *pUNUSUAL FLOWER ORGANS* (*pUFO)*),
544 the boundary domain (F, *pCUP-SHAPED COTYLEDON* (*pCUC2)*), and organ primordia (G,
545 *pAHP6*). PI fluorescence is false-coloured in magenta and mTurquoise2 fluorescence in
546 green. Bars = 20 µm.

547 **Figure 5.** Dose-response and time course analysis of driver line seedling roots. A, The
548 *pSCR* driver line was grown on 0, 0.1, 1, 10 and 100 µM Dex and imaged five DAG. B,
549 Time-course of pSCR driver line induction for 1, 6 and 24 hours with 10 µM Dex. C,
550 Quantification of the mTurquoise2 fluorescence intensity dose-response in quiescent centre
551 cells and CEI (cells outlined in white in panel A). D, Quantification of mTurquoise2
552 fluorescence intensity of the first 3 endodermal cells after the CEI (cells outlined in blue in
553 panel A). E, quantification of the induction time-course (B) in quiescent centre cells, CEI and
554 the first 3 endodermal cells. Significant differences in (C, D, and E) are based on the results
555 of a two-tailed t test with $p < 0.05$, $p < 0.01$, $p < 0.001$, n=3-6 roots each. Bars = 50 µm.

Figure 6. Induction of mTurquoise2 and mVenus/3xGFP fluorescence in the root, stem and SAM of F1 plants from a driver line-effector line cross. Cells are counter-stained with PI (which, in the stem, highlights lignified vessel elements and fibres). Fluorescence channels are false-coloured. Bars = 50 µm for the root and the stem, 40 µm for the SAM.

Figure 7. Cell-type specific induction demonstrates the efficacy of trans-activation. Plants expressing VND7-VP16 as an effector in the endodermal cells (*pSCR*>GR>*VND7-VP16*) show ectopic vessel formation (white arrows) after 5 days of Dex induction in both root and hypocotyl endodermis, in contrast to DMSO-treated plants. The spiral secondary cell wall thickening was observed after fixing and clearing the samples and visualized by DIC (differential interference contrast microscope). E = endodermis, P = pericycle, X = xylem. Bars = 20 µm.

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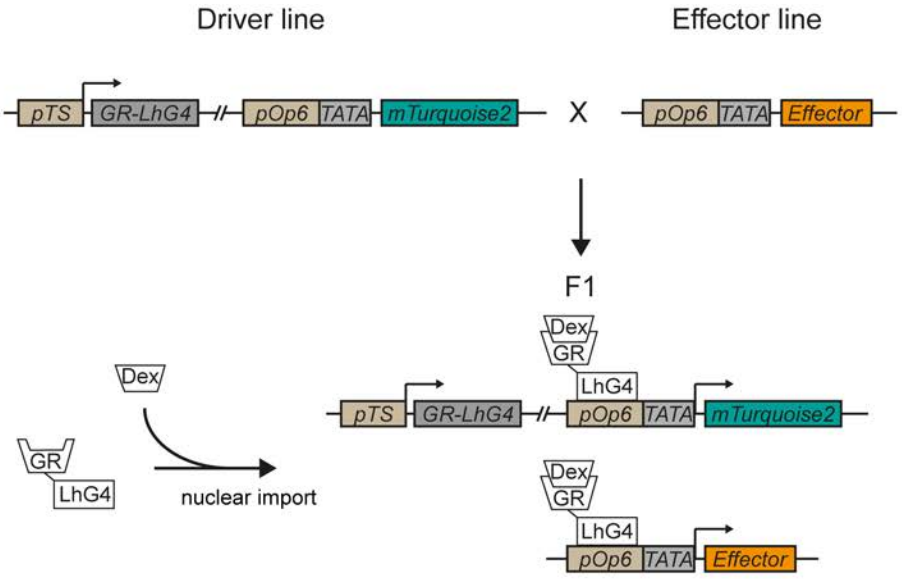

Figure 1. Overview of the Dex-inducible GR-LhG4/pOp system. In driver lines, expression of the synthetic transcription factor LhG4 is controlled by a tissue-specific promoter (pTS), whereas translational fusion with the ligand binding domain of rat glucocorticoid receptor (GR) prevents nuclear translocation in the absence of the inducer (Dex). After crossing with an effector line harbouring a transcriptional cassette under the control of a pOp element and a TATA box-containing minimal 35S promoter and addition of Dex, GR-LhG4 drives the expression of the effector as well as the mTurquoise2 reporter encoded by the driver line.

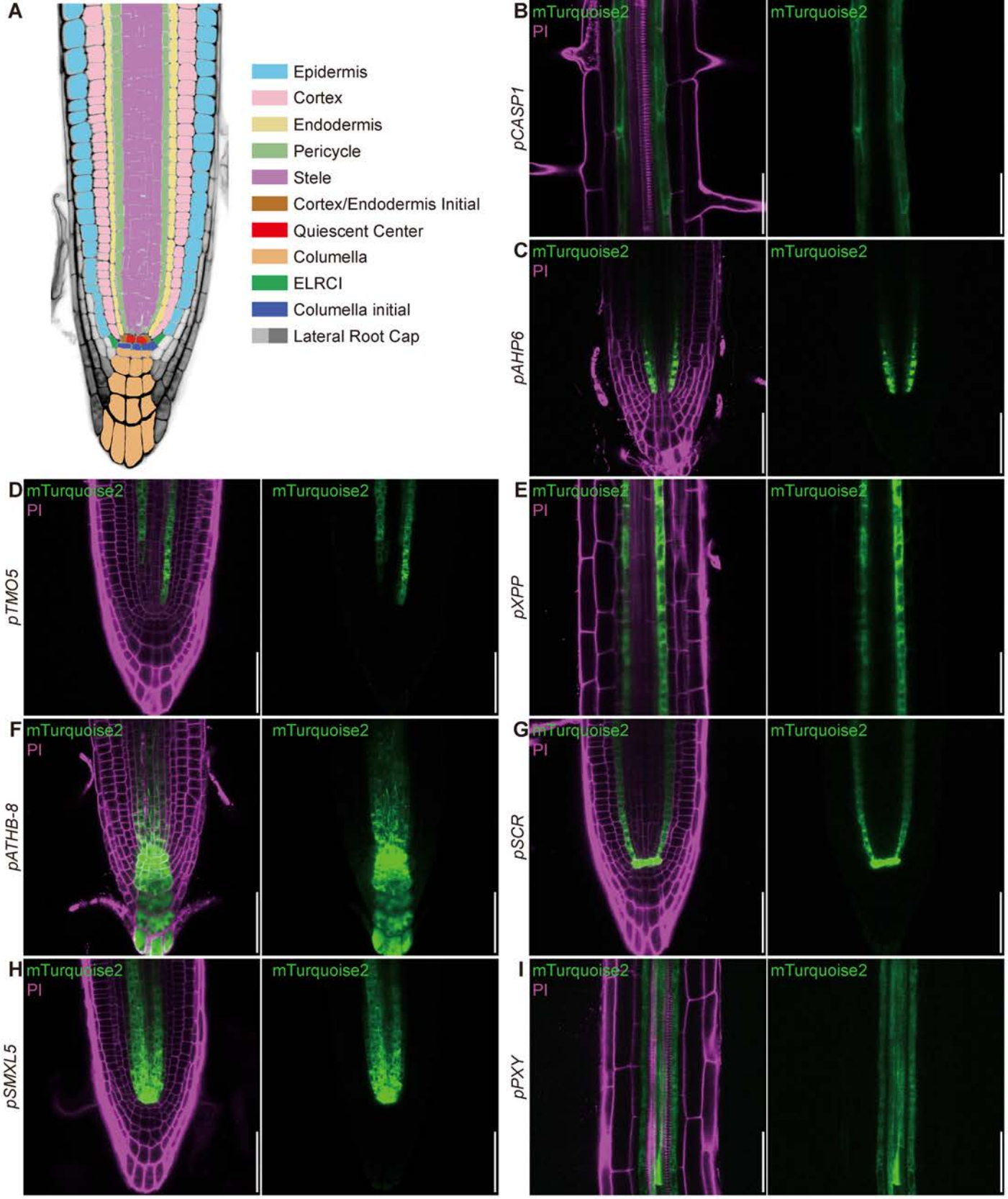

Figure 2. Analysis of induced driver lines in seedling roots. A, Schematic representation of root tissue layers. B-I, Induced driver line roots displaying fluorescence from propidium iodide (PI)-stained cell walls and the mTurquoise2 reporter (see Fig. 1 and Table 1). The indicated promoters mediate expression in the differentiating endodermis (B, pCASPARIAN STRIP MEMBRANE DOMAIN PROTEIN 1 (pCASP1)), phloem precursor cells and adjacent pericycle cells (C, pHISTIDINE PHOSPHOTRANSFER PROTEIN 6 (pAHP6)), xylem precursor cells (D, pTARGET OF MONOPTEROS 5 (pTMO5)), xylem pole pericycle cells (E, pXYLEM POLE PERICYCLE (pXPP)), stele initials, cortex/endodermis initial (CEI) and columella initials (F, pHOMEOBOX GENE 8 (pATHB-8)), endodermis, CEI and quiescent centre (G, pSCARECROW (pSCR)), stele initials, phloem and procambial cells (H, pSMAX1-LIKE 5 (pSMXL5)), and procambial cells (I, pPHLOEM INTERCALATED WITH XYLEM (pPXY)). PI fluorescence is false-coloured in magenta and mTurquoise2 fluorescence in green. Bars = 50 µm.

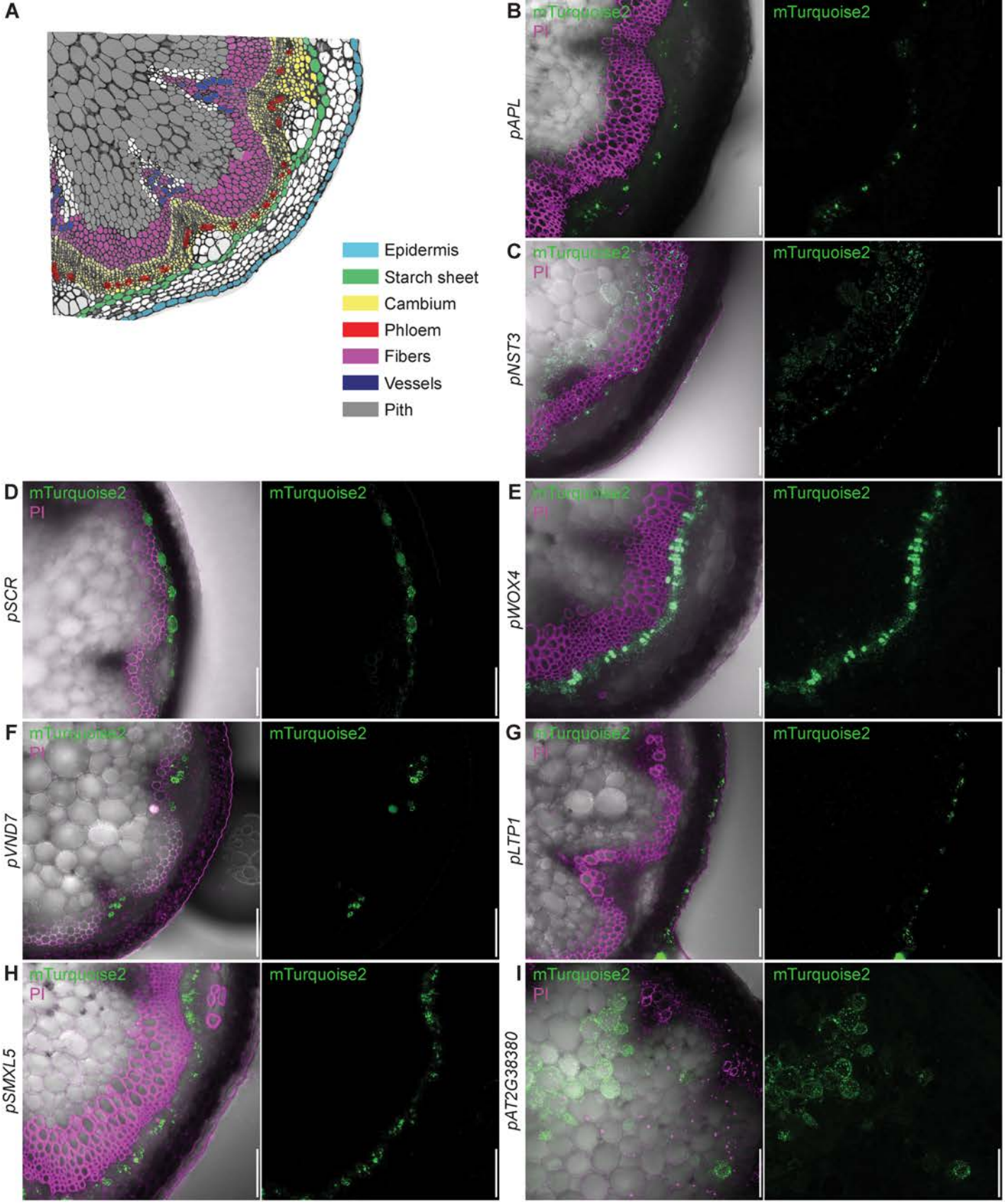

Figure 3. Analysis of induced driver lines in the stem. A, Schematic representation of inflorescence stem tissue layers. B-I, Induced driver line stems displaying fluorescence from propidium iodide (PI)-stained cell walls and the mTurquoise2 reporter (see Fig. 1 and Table 1). The promoters mediate expression in differentiated phloem (B, *pALTERED PHLOEM DEVELOPMENT*, (*pAPL*)), xylem fibres and interfascicular fibres (C, *pNAC SECONDARY WALL THICKENING PROMOTING 3* (*pNST3*)), starch sheath (D, *pSCR*), cambium (E, *pWUSCHEL RELATED HOMEOBOX 4* (*pWOX4*), xylem vessels (F, *pVASCULAR-RELATED NAC-DOMAIN PROTEIN 7* (*pVND7*), epidermal cells (G, *pLIPID TRANSFER PROTEIN 1* (*pLTP1*)), the incipient phloem (H, *pSMXL5*), and pith (I, *pAT2G38380*). PI fluorescence is false-coloured in magenta and mTurquoise2 fluorescence in green. Bars = 50 µm.

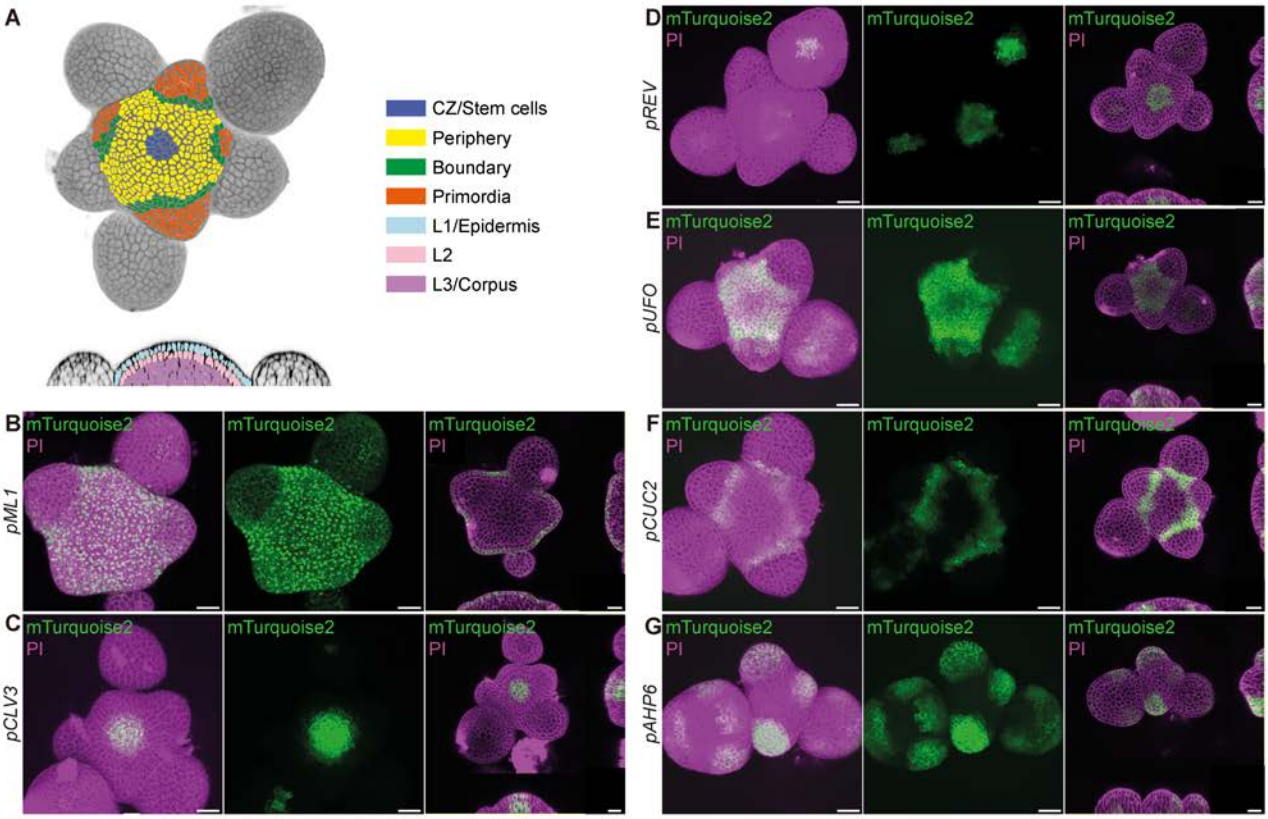

Figure 4. Analysis of induced driver lines in the shoot apical meristem (SAM). A, Schematic representation of cell identity domains in the SAM. B-G, Induced driver line stems displaying fluorescence from propidium iodide (PI)-stained cell walls and the mTurquoise2 reporter (see Fig. 1 and Table 1). The left and middle panels are maximum projections of confocal stack, the right panels consist of a single median confocal xy section and xz and yz view of the stack. The indicated promoters mediate expression in the L1 layer/epidermis (B, *pMERISTEM LAYER 1* (*pML1*)), the stem cell domain (C, *pCLV3*), the central zone (D, *pREVOLUTA* (*pREV*)), the peripheral zone (E, *pUNUSUAL FLOWER ORGANS* (*pUFO*)), the boundary domain (F, *pCUP-SHAPED COTYLEDON* (*pCUC2*)), and organ primordia (G, *pAHP6*). PI fluorescence is false-coloured in magenta and mTurquoise2 fluorescence in green. Bars = 20 µm.

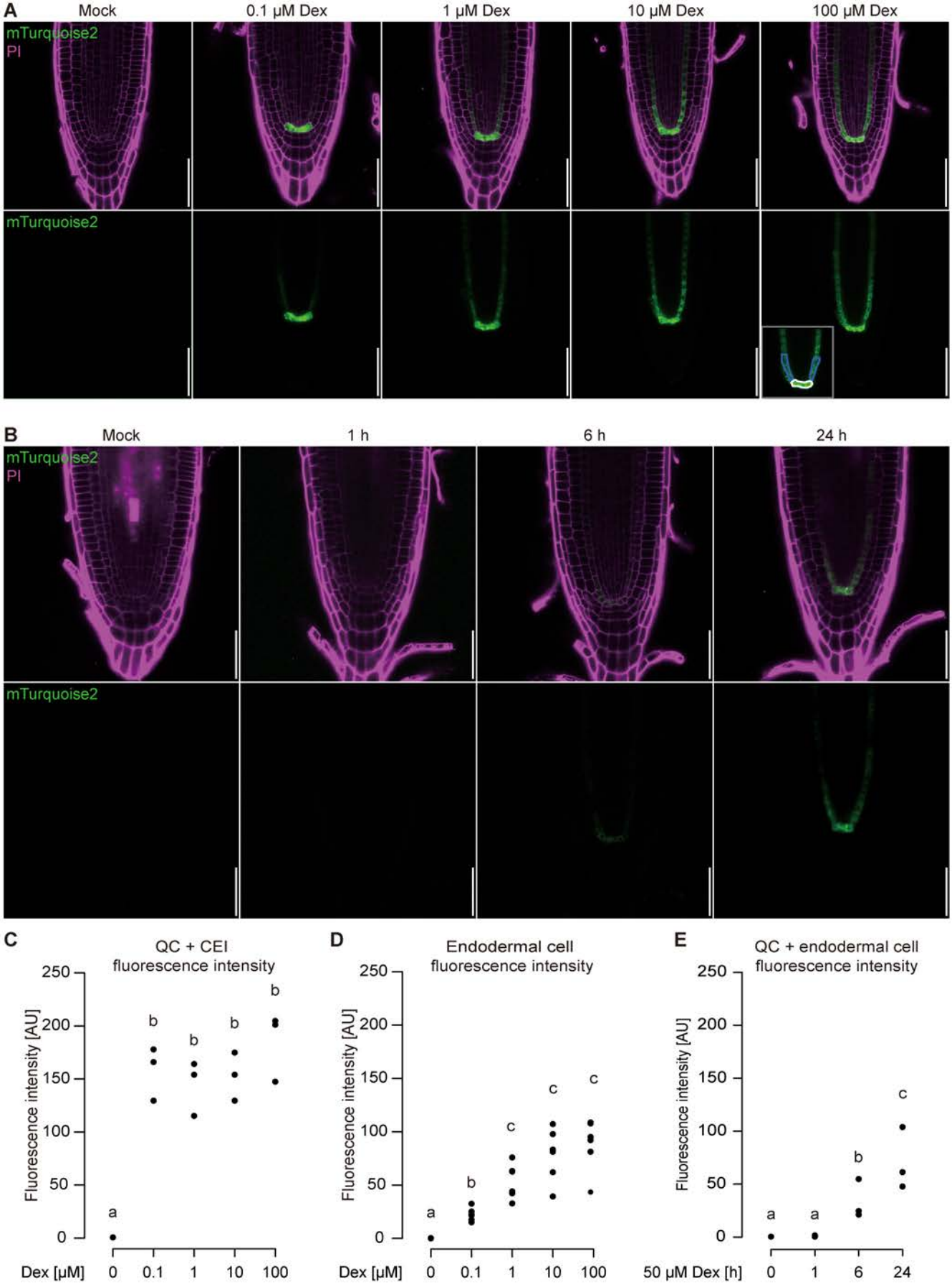

Figure 5. Dose-response and time course analysis of driver line seedling roots. A, The *pSCR* driver line was grown on 0, 0.1, 1, 10 and 100 µM Dex and imaged five DAG. B, Time-course of *pSCR* driver line induction for 1, 6 and 24 hours with 10 µM Dex. C, Quantification of the mTurquoise2 fluorescence intensity dose-response in quiescent centre cells and CEI (cells outlined in white in panel A). D, Quantification of mTurquoise2 fluorescence intensity of the first 3 endodermal cells after the CEI (cells outlined in blue in panel A). E, quantification of the induction time-course (B) in quiescent centre cells, CEI and the first 3 endodermal cells. Significant differences in (C, D, and E) are based on the results of a two-tailed t test with $p < 0.05$, $p < 0.01$, $p < 0.001$, n=3-6 roots each. Bars = 50 µm.

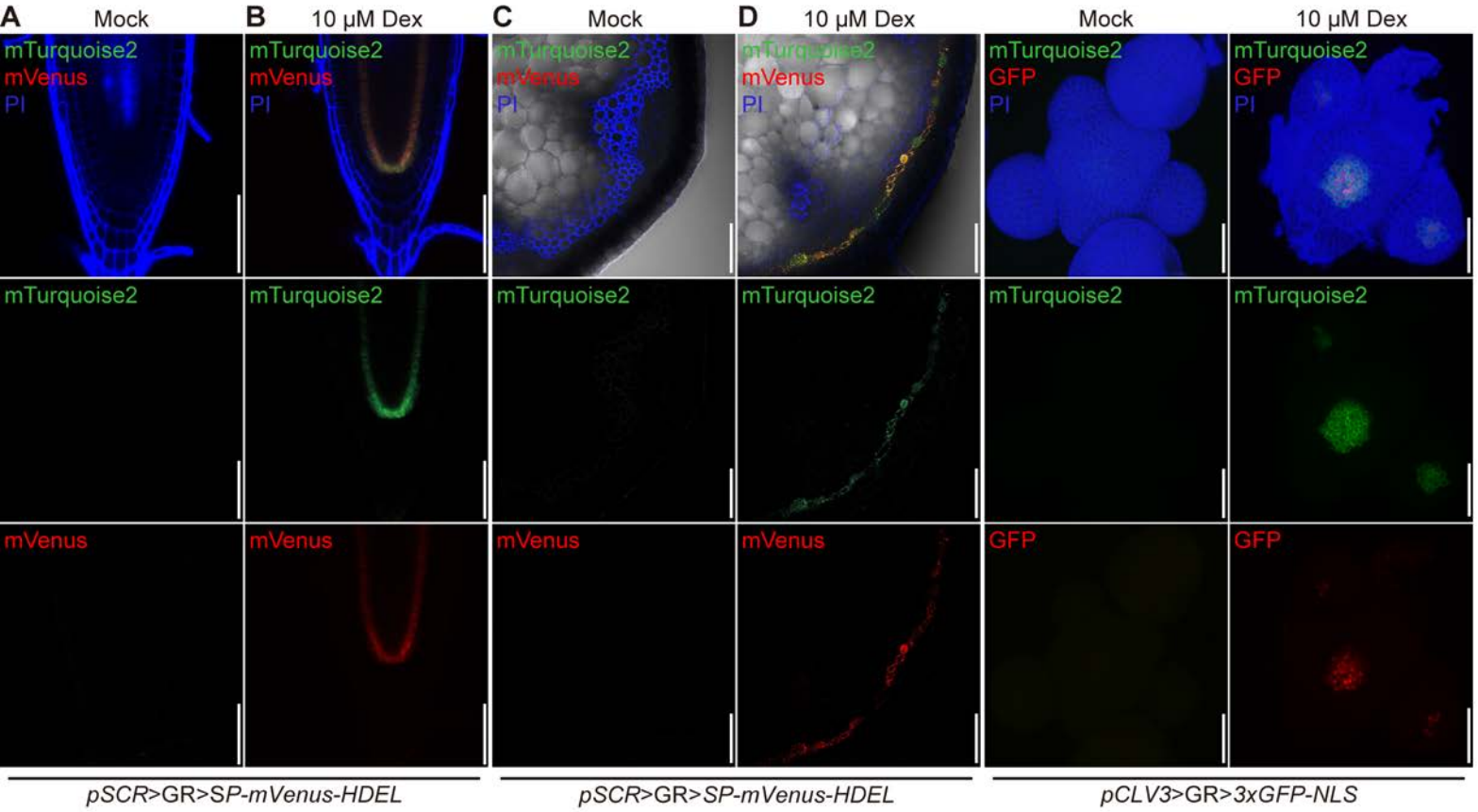

Figure 6. Induction of mTurquoise2 and mVenus/3xGFP fluorescence in the root, stem and SAM of F1 plants from a driver line-effector line cross. Cells are counter-stained with PI (which, in the stem, highlights lignified vessel elements and fibres). Fluorescence channels are false-coloured. Bars = 50 µm for the root and the stem, 40 µm for the SAM.

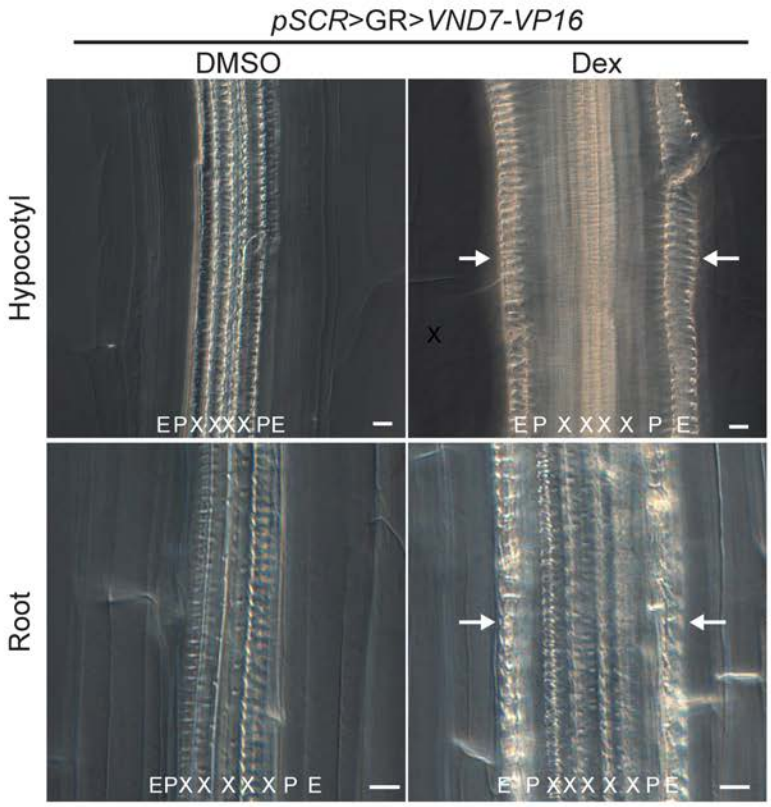

Figure 7. Cell-type specific induction demonstrates the efficacy of trans-activation. Plants expressing VND7-VP16 as an effector in the endodermal cells (*pSCR*>GR>*VND7-VP16*) show ectopic vessel formation (white arrows) after 5 days of Dex induction in both root and hypocotyl endodermis, in contrast to DMSO-treated plants. The spiral secondary cell wall thickening was observed after fixing and clearing the samples and visualized by DIC (differential interference contrast microscope). E = endodermis, P = pericycle, X = xylem. Bars = 20 μm.

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