

#### 21 **Abstract**

22 The default growth pattern of primary roots of land plants is directed by gravity. However, roots 23 possess the ability to sense and respond directionally to other chemical and physical stimuli, 24 separately and in combination. Therefore, these root tropic responses must be antagonistic to 25 gravitropism. The role of reactive oxygen species (ROS) in gravitropism of maize and 26 Arabidopsis roots has been previously described. However, which cellular signals underlie the 27 integration of the different environmental stimuli, which lead to an appropriate root tropic 28 response, is currently unknown. In gravity-responding roots, we observed, by applying the ROS-29 sensitive fluorescent dye Dihydrorhodamine-123 and confocal microscopy, a transient 30 asymmetric ROS distribution, higher at the concave side of the root. The asymmetry, detected at 31 the distal elongation zone (DEZ), was built in the first two hours of the gravitropic response and 32 dissipated after another two hours. In contrast, hydrotropically-responding roots show no 33 transient asymmetric distribution of ROS. Decreasing ROS levels by applying the antioxidant 34 ascorbate, or the ROS-generation inhibitor Diphenylene iodonium (DPI) attenuated gravitropism 35 while enhancing hydrotropism. Arabidopsis mutants deficient in Ascorbate Peroxidase 1 (APX1) 36 showed attenuated hydrotropic root bending. Mutants of the root-expressed NADPH oxidase 37 RBOH C, but not *rbohD*, showed enhanced hydrotropism and less ROS in their roots apices 38 (tested in tissue extracts with Amplex Red). Finally, hydrostimulation prior to gravistimulation 39 attenuated the gravistimulated asymmetric ROS and auxin signals that are required for gravity-40 directed curvature. We suggest that ROS, presumably  $H_2O_2$ , function in tuning root tropic 41 responses by promoting gravitropism and negatively regulating hydrotropism.

#### 43 **Introduction**

44 Plants evolved the ability to sense and respond to various environmental stimuli in an integrated 45 fashion. Due to their sessile nature, they respond to directional stimuli such as light, gravity, 46 touch and moisture by directional organ growth (curvature), a phenomenon termed tropism. 47 Experiments on coleoptiles conducted by Darwin in the 1880s revealed that in phototropism, the 48 light stimulus is perceived by the tip, from which a signal is transmitted to the growing part 49 (Darwin and Darwin, 1880). Darwin postulated that in a similar manner, the root tip perceives 50 stimuli from the environment, including gravity and moisture, processes them and directs the 51 growth movement, acting like "the brain of one of the lower animals" (Darwin and Darwin, 52 1880). The transmitted signal in phototropism and gravitropism was later found to be a 53 phytohormone, and its redistribution on opposite sides of the root or shoot was hypothesized to 54 promote differential growth and bending of the organ (Went, 1926; Cholodny, 1927). Over the 55 years, the phytohormone was characterized as indole-3-acetic acid (IAA, auxin) (Kögl et al., 56 1934; Thimann, 1935) and the 'Cholodny-Went' theory was demonstrated for gravitropism and 57 phototropism (Rashotte et al., 2000; Friml et al., 2002). In addition to auxin, second messengers 58 such as  $Ca^{2+}$ , pH oscillations, Reactive Oxygen Species (ROS) and abscisic acid (ABA) were 59 shown to play an essential role in gravitropism (Young and Evans, 1994; Fasano et al., 2001; Joo 60 et al., 2001; Ponce et al., 2008). Auxin was shown to induce ROS accumulation during root 61 gravitropism, where the gravitropic bending is ROS-dependent (Joo et al., 2001; Peer et al., 62 2013).

63 ROS such as superoxide and hydrogen peroxide were initially considered toxic 64 byproducts of aerobic respiration, but currently are known also for their essential role in myriad 65 cellular and physiological processes in animals and plants (Mittler et al., 2011). ROS and 66 antioxidants are essential components of plant cell growth (Foreman et al., 2003), cell cycle 67 control and shoot apical meristem maintenance (Schippers et al., 2016) and play a crucial role in 68 protein modification and cellular redox homeostasis (Foyer and Noctor, 2005). ROS function as 69 signal molecules by mediating both biotic- (Sagi and Fluhr, 2006; Miller et al., 2009) and 70 abiotic- (Kwak et al., 2003; Sharma and Dietz, 2009) stress responses. Joo et al. (2001) reported 71 a transient increase in intracellular ROS concentrations early in the gravitropic response, at the 72 concave side of maize roots, where auxin concentrations are higher. Indeed, this asymmetric 73 ROS distribution is required for gravitropic bending, since maize roots treated with antioxidants,

74 which act as ROS scavengers, showed reduced gravitropic root bending (Joo et al., 2001). The 75 link between auxin and ROS production was later shown to involve the activation of NADPH 76 oxidase, a major membrane-bound ROS generator, via a phosphatidylinositol 3-kinase-77 dependent pathway (Brightman et al., 1988; Joo et al., 2005; Peer et al., 2013). Peer et al. (2013) 78 suggested that in gravitropism, ROS buffer auxin signaling by oxidizing the active auxin, IAA, 79 to the non-active and non-transported form, oxIAA.

80 Gravitropic-oriented growth is the default growth program of the plant, with shoots 81 growing upwards and roots downwards. However, upon exposure to specific external stimuli, the 82 plant overcomes its gravitropic growth program and bends towards or away from the source of 83 the stimulus. For example, as roots respond to physical obstacles or water deficiency. The ability 84 of roots to direct their growth towards environments of higher water potential was described by 85 Darwin and even earlier, and was later defined as hydrotropism (Von Sachs, 1887; Jaffe et al., 86 1985; Eapen et al., 2005).

87 In Arabidopsis, wild-type (WT) seedlings respond to moisture gradients 88 (hydrostimulation) by bending their primary roots towards higher water potential. Upon 89 hydrostimulation, amyloplasts, the starch-containing plastids in root-cap columella cells, which 90 function as part of the gravity sensing system, are degraded within hours and recover upon water 91 replenishment (Takahashi et al., 2003; Ponce et al., 2008; Nakayama et al., 2012). Moreover, 92 mutants with a reduced response to gravity (*pgm1*) and to auxin (*axr1* and *axr2*) exhibit higher 93 responsiveness to hydrostimulation, manifested as accelerated bending compared to WT roots 94 (Takahashi et al., 2002; Takahashi et al., 2003). Recently we have shown that hydrotropic root 95 bending does not require auxin redistribution and is accelerated in the presence of auxin polar 96 transport inhibitors and auxin-signaling antagonists (Shkolnik et al., 2016). These results reflect 97 the competition, or interference, between root gravitropism and hydrotropism (Takahashi et al., 98 2009). However, which cellular signals participate in the integration of the different 99 environmental stimuli that direct root tropic curvature is still poorly understood. Here we sought 100 to assess the potential role of ROS in regulating hydrotropism and gravitropism in Arabidopsis 101 roots.

#### 102 **Results**

# 103 **Different spatial and temporal ROS patterns occur in roots in response to hydrostimulation**  104 **and gravistimulation**

105 In order to investigate the role of ROS signals in tropic responses we first assessed the spatial 106 distribution of ROS in Arabidopsis roots responding to gravitropic stimulation. WT Arabidopsis 107 seedlings grown vertically on agar-based medium (Materials and Methods) were gravistimulated 108 by a 90º rotation, and monitored for their ROS distribution by applying Dihydrorhodamine-123 109 (DHR), a rhodamine-based fluorescent probe mostly sensitive to  $H_2O_2$  (Gomes et al., 2005) that 110 is often used in monitoring intracellular, cytosolic ROS (Royall and Ischiropoulos, 1993; Crow, 111 1997; Douda et al., 2015). DHR staining was detected in the columella, lateral root cap, 112 epidermal layer of elongation zone (EZ) and the vasculature, and was weaker at the meristematic 113 zone (Fig.1). This pattern is similar to previously reported staining patterns obtained by  $H_2O_2$ -114 specific dyes in primary roots of Arabidopsis (Dunand et al., 2007; Tsukagoshi et al., 2010; Chen 115 and Umeda, 2015) and of other plant species (Ivanchenko et al., 2013; Xu et al., 2015). One to 116 two hours post gravistimulation, a ROS asymmetric distribution, higher at the concave (bottom 117 side of the root) was apparent in the epidermal layer of the distal elongation zone (DEZ), where 118 the bending initiates (Fig.1 A). The asymmetric ROS distribution dissipated after another two 119 hours (Fig.1 A, D), in accordance with previous reports (Joo et al., 2001; Peer et al., 2013).

120 To study ROS dynamics during hydrotropic growth, WT seedlings were introduced into a 121 moisture gradient in a closed CaCl<sub>2</sub>-containing chamber (herein referred to as the CaCl<sub>2</sub> / dry 122 chamber) as previously described (Takahashi et al., 2002; Kobayashi et al., 2007; Shkolnik et al., 123 2016). Under this system root bending upon hydrostimulation initiates at a region more distant 124 from the root tip compared to root bending by gravitropism. The distances of curvature from the 125 root tip for hydrotropism and gravitropism were  $601.2 \pm 18.1$  μm and  $365.1 \pm 13.1$  μm, 126 respectively (mean  $\pm$  SE), 2 h post stimulation ( $n=29$ ). We therefore designated the region of 127 gravitropic bending initiation as the distal elongation zone (DEZ) and the region of hydrotropic 128 bending initiation as the central elongation zone (CEZ), in accordance with previous definitions 129 (Fasano et al., 2001; Massa and Gilroy, 2003). Furthermore, during the hydrotropic response, the 130 root tip keeps facing downwards in response to gravity, where a slight curvature is detected in 131 the DEZ (Fig.1 B, 1, 2 and 4 hours, concave side is indicated). Interestingly, during hydrotropic 132 growth, ROS do not form an asymmetric distribution pattern at the DEZ, in contrast to the 133 gravity-induced ROS asymmetric distribution (Fig.1 B, D). However, asymmetric distribution of

134 ROS appears at the CEZ, where the hydrotropic root curvature takes place and detected ROS 135 levels are lower (Fig.1 B, D). This unequal distribution of ROS appears, however, also in roots 136 that were subjected to non-hydrostimulating conditions (obtained by adding distilled water to the 137 bottom the chamber), which do not undergo hydrotropic bending (Fig.1 C). Under these 138 experimental conditions, a higher ROS level was measured at the side of the root facing the agar 139 medium (Fig.1 C, arrowhead). The CEZ-located asymmetric distribution is not dynamic, and is 140 maintained throughout the first four hours of the hydrotropic response without a significant 141 change in the ratio level between the two sides of the root (Fig.1 B, D). We suspected that this 142 asymmetric distribution of ROS may be caused by the mechanical tension formed as the root 143 bends around the agar bed. To further test this, we used the split-agar / sorbitol system (Materials 144 and Methods) for assessing ROS distribution during hydrotropism. In this experimental system, 145 no asymmetric ROS distribution could be detected in response to hydrostimulation in the DEZ or 146 CEZ (Fig.1 E, D). Moreover, we detected no changes in the overall intensity of DHR 147 fluorescence at the indicated time points in both hydrostimulated and gravistimulated roots 148 (Supplemental Fig.S1). Collectively, these results depict distinct dynamics and spatial patterns of 149 ROS distribution during gravitropic and hydrotropic responses, which may imply different roles 150 of ROS in these tropic responses. We note that strong DHR fluorescence is detected in the root 151 vasculature above the CEZ at all time points, similar to previous reports (Tsukagoshi et al., 2010; 152 Chen and Umeda, 2015).

#### 153 **ROS tune root tropic responses**

154 To assess the possible role of ROS in hydrotropism compared to gravitropism, we tested whether 155 ROS scavenging molecules or ROS-generation inhibitors affect hydrotropic growth. As 156 described previously, the antioxidant ascorbic acid (ascorbate) has an inhibitory effect on root 157 gravitropism (Joo et al., 2001; Peer et al., 2013). Indeed, our results show gravitropic bending 158 inhibition in the presence of 1 mM ascorbate, a concentration that we found to significantly 159 reduce ROS level at the root tip (Supplemental Fig.S2). Root curvature in control conditions was 160 64.9  $\pm$  2.6 degrees, whereas in the presence of ascorbate only 49.1  $\pm$  5.2 degrees (mean  $\pm$  SE) 8 h 161 post gravistimulation (*P*=0.011, Student's *t* test for independent measurements), without 162 differences in root growth rates (Supplemental Fig.S3). In contrast, application of 1 mM 163 ascorbate accelerated hydrotropic root bending. Root curvature in the CaCl<sub>2</sub> / dry chamber was  $164$   $27.2 \pm 2.6$  degrees in control conditions whereas in the presence of ascorbate curvature was 39.3 165  $\pm$  3.5 degrees (mean  $\pm$  SE) 2 h post hydrostimulation (*P*=0.01, Student's *t* test for independent 166 measurements), and reduced root growth rate by 29.4% (Fig.2 A, B). The same trend was 167 apparent when 1 mM of the antioxidant N-Acetyl-Cysteine was applied (not shown).

168 To further study the effect of ascorbate metabolism on hydrotropism we tested mutants 169 deficient in the most abundant cytosolic ascorbate peroxidase, Ascorbate Peroxidase 1 (APX1) 170 (Davletova et al., 2005). *apx1-2* seedlings exhibited attenuated hydrotropic bending compared to 171 WT. Root curvature in the CaCl<sub>2</sub> / dry chamber of WT was  $72.0 \pm 2.8$  degrees whereas that of 172 *apx1-2* was  $55.8 \pm 3.5$  degrees (mean  $\pm$  SE) 5 h post hydrostimulation (*P*=9.6  $*$  10<sup>-4</sup>, Student's *t* 173 test for independent measurements), with no differences in their growth rates (Fig.2 C, D). These 174 results were reproduced using the split-agar / sorbitol system in which the ascorbate was 175 supplemented to the sorbitol agar slice, allowing diffusion of the chemicals towards the root tip 176 so that the exposure to ascorbate occurs while a water potential gradient is formed (Takahashi et 177 al., 2002; Antoni et al., 2016) (Supplemental Fig.S4 A, B). These data strongly suggest that the 178 reduced ability to scavenge cytosolic  $H_2O_2$  inhibited root hydrotropic bending. Unlike ascorbate-179 treated seedlings, gravitropic bending was not impaired or promoted in the *apx1-2* mutant 180 (supplemental Fig.S7).

#### 181 **ROS generation by NADPH oxidase has opposite effects on different root tropic responses**

182 To further study the roles of ROS in root tropisms, we tested the effects of diphenylene iodonium 183 (DPI), an inhibitor of NADPH oxidase and other flavin-containing enzymes (Foreman et al., 184 2003), on hydrotropic- and gravitropic-bending kinetics and the corresponding ROS distribution 185 patterns in primary roots. NADPH oxidase is a plasma membrane-bound enzyme that produces 186 superoxide  $(O_2^{\text{-}})$  to the apoplast (Sagi and Fluhr, 2006). Superoxide is rapidly converted to 187 H2O2, which may enter the cell passively or through aquaporins (Miller et al., 2010; Mittler et 188 al., 2011). Application of DPI accelerated hydrotropic root bending but attenuated gravitropic 189 root bending (Fig.3). In response to hydrostimulation, root bending was accelerated in the 190 presence of DPI, showing  $86.3 \pm 2.1$  degrees curvature (mean  $\pm$  SE) in the CaCl<sub>2</sub> / dry chamber 191 after only 4 h, even though root growth rate was inhibited by 65.3% (Fig.3). This result was 192 reproduced using the split-agar / sorbitol system (Supplemental Fig.S4 A).

193 Fluorescent ROS staining of DPI-treated roots revealed elimination of ROS from the 194 epidermal layer of the EZ and further along the root, where ROS at the outer layers (epidermis 195 and cortex) seemed to drop down and the remaining ROS appeared in the vasculature and its 196 surrounding layers (Fig.4 A, B). ROS elimination at the outer root cell layers was previously

197 described for hydroxyphenyl fluorescein (HPF)-staining upon DPI treatment (Dunand et al., 198 2007). Along with decreased fluorescence at the EZ, we detected an increase of DHR 199 fluorescence intensity at the meristematic zone of DPI-treated roots (Fig.4). Dunand et al. (2007) 200 used nitroblue tetrazolium (NBT) for assessing extracellular  $O_2$ <sup> $\sim$ </sup> levels in Arabidopsis root tips, 201 and detected a decrease in NBT intensity upon DPI treatment. Since the DHR probe is mostly 202 sensitive to cytosolic  $H_2O_2$  (Gomes et al., 2005), our results do not contradict previously reported 203 results.

204 Gravistimulated seedlings that were pre-treated for 2 h with DPI showed less ROS 205 accumulation and consequently no ROS asymmetric distribution in the epidermal layer of the 206 EZ, resulting in a delayed gravitropic response (Fig.4 C). Similarly, seedlings that were 207 hydrostimulated in the presence of DPI showed elimination of ROS from the epidermal layer at 208 the bending region, which became more proximal to the root tip (Fig.4 D). Interestingly, the 209 gravity-directed curvature of the root tip, which occurs during hydrotropic root bending, 210 appeared to be attenuated in ascorbate- and DPI-treated seedlings (Fig.2 A, Fig.4 D). This 211 finding demonstrates again the negative effect of ROS elimination on root gravitropism, also in 212 combination with a hydrotropic response.

#### 213 **Hydrotropism is affected by root NADPH oxidase**

214 To further assess the inhibitory effect of ROS generation by NADPH oxidase on root 215 hydrotropism we tested transposon-insertion mutants of the plant NADPH oxidase - RBOH 216 (Respiratory Burst Oxidase Homolog) gene family, which consists of 10 members in 217 Arabidopsis. These can be divided into three classes based on their tissue-specificity: RBOH D 218 and F are highly expressed throughout the plant, RBOH A-G and I are expressed mostly in roots, 219 and RBOH H and J express specifically in pollen (Sagi and Fluhr, 2006). RBOH C has been 220 intensively studied, and its activity in ROS production in trichoblasts is essential for root hair 221 elongation and mechanosensing (Foreman et al., 2003; Monshausen et al., 2009). It is expressed 222 in trichoblasts and in the epidermal layer of the EZ (Foreman et al., 2003), though its role in the 223 EZ is still unclear (Monshausen et al., 2009). When hydrostimulated in the CaCl<sub>2</sub> / dry chamber 224 or in the split-agar / sorbitol systems, *rbohC* seedlings exhibited accelerated hydrotropic bending. 225 Measured in the CaCl<sub>2</sub>/ dry chamber, root curvature in WT was  $46.4 \pm 3.1$  degrees compared to 226 64.2  $\pm$  3.5 degrees in *rbohC* (mean  $\pm$  SE) 2 h post hydrostimulation (*P*=5.1  $\ast$  10<sup>-4</sup>, student's *t* 227 test for independent measurements) with no difference in growth rate compared to WT (Fig.5 A,

228 B; Supplemental Fig.S4 C; Supplemental movie 1). We then examined the hydrotropic response 229 of seedlings deficient in RBOH D, which has the highest expression levels among the RBOHs. 230 RBOH D is expressed in all plant tissues but mainly in stems and leaves and is known as a key 231 factor in ROS systemic signaling (Sagi and Fluhr, 2006; Miller et al., 2009; Suzuki et al., 2011). 232 Interestingly, *rbohD* seedlings did not exhibit significantly-different hydrotropic bending kinetics 233 or root growth rates compared to WT (Fig. 5 A, B; Supplemental Fig.S4 C; Supplemental movie 234 2). DHR staining revealed no significant difference in ROS spatial patterns in gravistimulated 235 nor hydrostimulated (using the CaCl<sub>2</sub> / dry chamber or split-agar / sorbitol system) roots of the 236 RBOH mutants, compared to WT (Supplemental Fig.S5-S8). Therefore, to better characterize 237 endogenous ROS levels in root tissues of wt and *rbohc* and *rbohd* mutants, we applied Amplex 238 red for determination of  $H_2O_2$  content in tissue extracts (Materials and Methods). When 239 examining extracts from whole seedlings, we observed a 68% and 77% reduction in  $H_2O_2$  levels 240 in *rbohD* and *rbohC*, respectively, compared to WT (Fig.5 D). We then examined extracts from 241 excised root apices (1-2 mm from tip) and observed a relatively similar  $H_2O_2$  content in WT and 242 *rbohD* roots, while *rbohC* mutants showed a 57% reduction in  $H_2O_2$  content compared to WT 243 (Fig.5 C). These results are consistent with the tissue-specific expression pattern of the two 244 RBOHs, as RBOH C is highly expressed in roots, while RBOH D is not (Sagi and Fluhr, 2006) 245 and with the accelerated hydrotropic phenotype of *rbohC* compared to *rbohD* and wt. Their 246 different expression patterns could also be visualized in the high-resolution spatiotemporal map 247 (Brady et al., 2007) of the eFP browser (Winter et al., 2007).

248 The acceleration in hydrotropic root bending of *rbohC* is however weaker compared with 249 that of DPI-treated WT seedlings (measured in the CaCl<sub>2</sub> / dry chamber, root curvature in *rbohC* 250 was  $75.41\pm2.19$  degrees and root curvature of DPI treated seedlings was  $86.31\pm2.11$  degrees 251 after 4 h of hydrostimulation, while WT and DMSO-treated WT roots exhibited  $63.27\pm2.38$  and 252 62.67±3.17 degrees in that time, respectively). These results may indicate partial functional 253 redundancy with other root-expressed RBOHs, or involvement of other DPI-sensitive enzymes in 254 this tropic growth. When treated with DPI, *rbohC* roots presented the same hydrotropic bending 255 kinetics as WT roots (not shown). Unlike DPI-treated seedlings, RBOH C- and RBOH D-256 deficient mutants did not show inhibition or acceleration in their gravitropic growth 257 (Supplemental Fig.S8) nor weakened gravity-directed curvature of the root tip during 258 hydrotropic growth (Fig.5) and gravitropic ROS asymmetric distribution as in WT 259 (Supplemental Fig.S7). These results may be explained by functional redundancy between the

260 root-expressed RBOH family members, as well as by compensation of ROS signaling by 261 mechanisms involved specifically in gravitropism.

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### 263 **Hydrotrostimulation attenuates the gravitropic ROS and auxin signals**

264 In order to test a possible direct link between hydrotropism and gravitropism through ROS, we 265 challenged WT seedlings with combined stimuli using the split-agar / sorbitol method (Fig.6 A). 266 The split-agar system allows slow and controlled exposure of the root tips to increasing osmotic 267 pressure, and by rotation of the chamber allows changes in the gravity vector (Fig.6 A). After 0-2 268 h of hydrostimulation, 1 h of gravistimulation induced a clear asymmetric ROS distribution at 269 the bending EZ. After 3 h of hydrostimulation, 1 h of gravistimulation generated a weak 270 asymmetric ROS distribution (Fig.6 B, C). Strikingly, following 4 h of hydrostimulation, 1 h of 271 gravistimulation failed to generate an asymmetric ROS distribution, and gravity-directed root 272 bending was not observed (Fig.6 B, C). These results indicate that as the osmotic stress stimulus 273 increases and promotes hydrotropic curvature, gravistimulation is not sufficient to evoke typical 274 ROS asymmetric distribution, and growth towards higher water potential is favorable. Indeed, 275 with increasing hydrostimulation time from 0 to 4 hr prior to gravistimulation, gravitropic 276 curvature decreased (Fig.6 D). Four hrs of hydrostimulation prevented gravitropic curvature as 277 roots responded only to the hydrotropic stimulus (depicted as a negative curvature angle in Fig.6 278 D).

279 Subsequently, in order to assess whether the attenuation of the ROS signal of 280 gravistimulated roots following hydrostimulation is associated with the attenuation of auxin 281 distribution, roots of DII-VENUS-expressing transgenic seedlings (Brunoud et al., 2012) were 282 gravistimulated for 1 h following exposure to an osmotic gradient for 0, 2 or 4 h (Supplemental 283 Fig.S9). With this auxin reporter, lower levels of DII-VENUS fluorescence indicate higher levels 284 of auxin. In agreement with the ROS signal dynamics, we observed asymmetric auxin 285 distribution in the lower part of the root tip (concave) in roots that were gravistimulated with no 286 prior hydrostimulation, or following 2 h of hydrostimulation (Supplemental Fig.S9), as 287 previously demonstrated in graviresponding roots (Band et al., 2012). However, 288 hydrostimulation for 4 h prior to gravistimulation impaired the generation of an auxin gradient 289 across the root tip (Supplemental Fig.S9). Based on the known relationship between auxin and 290 ROS in gravistimulation, these results may suggest that hydrotropic stimulation attenuates the

291 gravitropic ROS signal through the interruption of auxin distribution. However, we cannot 292 exclude the possibility that hydrostimulation attenuates gravistimulated ROS and auxin 293 distribution through independent signaling pathways that are yet to be elucidated.

## 294 **Discussion**

295 In order to perform hydrotropic bending, a root must overcome its gravity-directed growth 296 (Eapen et al., 2005; Takahashi et al., 2009). Our results suggest opposite roles for ROS in 297 hydrotropic and gravitropic growth behaviors. When treated with ascorbate, an antioxidant, or 298 DPI, an inhibitor of NADPH oxidase and other flavin-containing enzymes (Foreman et al., 299 2003), Arabidopsis primary roots exhibit opposite changes in their bending kinetics in response 300 to the different stimulations, namely, delay in gravitropism and acceleration in hydrotropism 301 (Fig.2, 3 ,Supplemental Fig. S3 and Supplemental Fig.S4). The antagonism between these two 302 responses was shown previously for the agravitropic pea mutant (*ageotropum*), whose lack of 303 gravity response contributes to its hydrotropic responsiveness (Takahashi and Suge, 1991). 304 Amyloplast degradation at early stages of a hydrotropic response may also be a mechanism by 305 which the root eliminates its sense of gravity in order to perform non-gravitropic growth 306 (Takahashi et al., 2003; Ponce et al., 2008). When examining the ROS and auxin patterns in 307 response to combined stimuli by first applying hydrostimulation and afterwards applying both 308 hydro- and gravistimulation, we observed a reduction in gravity-directed ROS-asymmetry and 309 auxin-gradient when the duration of hydrostimulation is increased (Fig.6, Supplemental Fig.S9). 310 We therefore conclude that during hydrotropic growth, the root actively attenuates gravitropic 311 auxin and ROS signaling to overcome gravitropic growth.

312 In gravitropism, auxin is required for ROS production (Joo et al., 2005; Peer et al., 2013). 313 In contrast, neither auxin redistribution nor auxin signaling are required for hydrotropic bending 314 (Shkolnik et al., 2016). Moreover, inhibition of polar auxin transport or Transport Inhibitor 315 Response (TIR)-dependent signaling accelerate hydrotropism (Shkolnik et al., 2016). Consistent 316 with these observations, asymmetric distribution of ROS was not detected in the DEZ during 317 hydrotropism. In gravitropism, however, both an auxin gradient at the lateral root cap, and ROS 318 asymmetric distribution at the DEZ are formed transiently. Collectively, these results 319 demonstrate the antagonism between hydro- and gravitropism with respect to auxin- and ROS-320 signaling.

321 Asymmetric ROS distribution was however observed in the CEZ of hydrostimulated  $322$  roots in the CaCl<sub>2</sub> / dry chamber system, and its asymmetry ratio level has not changed during 323 the measured time points (Fig.1 B, D). This asymmetric pattern, i.e., higher ROS levels at the 324 side of the root that is in contact with the agar medium, was also present in roots that were 325 exposed to non-hydrostimulating conditions and do not perform hydrotropic bending (Fig.1 C, 326 D). Therefore, this non-transient unequal distribution of ROS in the CEZ may be a result of 327 mechanosensing-induced ROS (Monshausen et al., 2009) at the region where the root detaches 328 from the agar medium. Indeed, no ROS asymmetry was observed in roots exposed to a water-329 potential gradient in the split-agar / sorbitol system (Fig.1 E,D), where the root does not 330 encounter mechanical tension by the agar due to bending. Therefore it is clear that hydrotropism 331 does not involve asymmetric distribution of ROS. Yet, it attenuates gravity-directed asymmetric 332 ROS distribution.

333 In addition to their roles as intracellular signaling molecules, ROS function in several 334 apoplastic processes, including cell wall rigidification that is thought to restrict cell elongation 335 (Hohl et al., 1995; Monshausen et al., 2007). It is tempting to hypothesize that in gravitropism, 336 the higher levels of ROS in the concave side of the root promote root bending by inhibition of 337 cell elongation at this side. However, this hypothesis fails to explain the opposite effects of 338 antioxidants and ROS-generator inhibitors on gravi- and hydrotropism, as differential cell 339 elongation is needed in both cases.

340 In this study, we show that ROS, presumably cytosolic  $H_2O_2$  in the epidermal layer of the 341 root EZ, negatively regulate hydrotropic bending. The activity of RBOH C was characterized as 342 essential for this process, since *rbohC* mutants showed accelerated hydrotropic root bending and 343 lower levels of  $H_2O_2$  in the root apex (Fig.5). This, however, does not exclude the possible 344 contribution of other root-expressed RBOHs or other flavin-containing enzymes to the process. 345 The localization of ROS-generating enzymes of the RBOH family has substantial effects on the 346 tissue-specific ROS levels and the consequent hydrotropic root curvature, as it appears that in 347 mutants deficient in RBOH D, which is expressed throughout the plant but mostly in leaves and 348 stems (Suzuki et al., 2011) ROS levels in the root apex and hydrotropic curvature were similar to 349 those of WT (Fig.5, Supplemental Fig.S3). As for ROS scavenging enzymes, we detected a weak 350 hydrotropic root bending in *apx1-2* mutants (Fig.2, Supplemental Fig.S3), which lack the 351 function of the abundant cytosolic  $H_2O_2$ -scavenging enzyme APX1 and are thus expected to 352 accumulate higher  $H_2O_2$  levels in all plant tissues. Peroxidases were shown to play an important

353 role in root development and growth control (Dunand et al., 2007) by modifying  $O_2$  to H<sub>2</sub>O<sub>2</sub> at 354 the transition-to-elongation zone (Tsukagoshi et al., 2010). Our observations are consistent with 355 this ROS type-specific accumulation pattern, and add a new aspect to the role of  $H_2O_2$  at the root 356 EZ.

357 The phytohormone abscisic acid (ABA) was previously reported as a positive regulator of 358 root hydrotropism. Arabidopsis mutants deficient in ABA-sensitivity (*abi2-1*) and ABA-359 biosynthesis (*aba1-1*) were reported as less responsive to hydrostimulation, whereas ABA 360 treatment rescued the delayed hydrotropic phenotype of *aba1-1* (Takahashi et al., 2002). ABA-361 signaling involves the activation of Pyrabactin Resistance/PYR1-like (PYR/PYL) receptors that 362 mediate the inhibition of clade A phosphatases type 2C (PP2C), which are negative regulators of 363 the pathway (Antoni et al., 2013). The involvement of this pathway in root hydrotropism was 364 demonstrated recently, as a *pp2c*-quadruple mutant exhibited an ABA-hypersensitive phenotype 365 and consequently enhanced hydrotropic response, while a mutant deficient in six PYR/PYL 366 receptors exhibited insensitivity to ABA treatment and to hydrotropic stimulation (Antoni et al., 367 2013). Since ABA was shown to induce stomata closure through the activation of the NADPH 368 oxidases RBOH D and RBOH F (Kwak et al., 2003), it is tempting to hypothesize that ABA 369 activates ROS production in root-expressed NADPH oxidases during hydrotropic growth. A 370 candidate mediator for this process may be PYL8, since PYL8-deficient mutants (*pyl8-1* and 371 *pyl8-2*) exhibited a non-redundant ABA-insensitive root growth when treated with ABA, and 372 transcriptional fusion of PYL8 (*ProPYL8:GUS*) revealed its expression in the stele, columella, 373 lateral root cap and root epidermis cells (Antoni et al., 2013). The latter expression region 374 overlaps with that of RBOH C (Foreman et al., 2003). However, distinguished from their role in 375 stomata closure, ROS negatively regulate hydrotropism and thus may function in a negative 376 feedback to ABA signaling. Antagonism between ROS and ABA also appears in seed 377 germination, as  $H_2O_2$  breaks ABA-induced seed dormancy in several plant species (Sarath et al., 378 2007).

379 In the context of integration of environmental stimuli by the root tip (Darwin and Darwin, 380 1880), we suggest that ROS, presumably cytosolic hydrogen peroxide, fine tune root tropic 381 responses by acting as positive regulators of gravitropism and as negative regulators of 382 hydrotropism. Root hydrotropism and gravitropism differ in several aspects, such as the time of 383 response (Eapen et al., 2005), the region of bending initiation (reported in this study), the 384 involvement of auxin (Kaneyasu et al., 2007; Shkolnik et al., 2016) and the effect of ROS on the

385 response kinetics. In order to elucidate the effects of ROS on tropic responses, their downstream

386 effectors in gravitropism and hydrotropism need to be characterized.

## 387 **Materials and Methods**

### 388 **Plant material and growth conditions**

389 Wild type Arabidopsis thaliana (Col-0) and T-DNA/Transposon insertion mutants: *rbohC* (*rhd2*), 390 *rbohD* (Miller et al., 2009) and *apx1-2* (SALK\_000249) (Suzuki et al., 2013) were used in this 391 research. For vapor sterilization, seeds were put inside a desiccator next to a glass beaker 392 containing 25 ml water, 75 ml bleach and 5 ml HCl for 2 h. Sterilized seeds were sown on 12 x 393 12 cm squared Petri dishes, containing 2.2 gr/L Nitsch & Nitsch medium (Duchefa Biochemie 394 B.V., Haarlem, the Netherlands) titrated to pH 5.8, 0.5 % (w/v) sucrose supplemented with 1 %  $395$  (w/v) plant agar (Duchefa) and vernalized for one day in  $4^{\circ}$  C in dark. Plates were put vertically 396 in a growth chamber at 22° C and day light (100  $\mu$ E m<sup>-2</sup> sec<sup>-1</sup>) under 16/8 light/dark photoperiod. 397 The root hair-deficient phenotype of *rbohC* was observed when grown on pH 5-titrated growth 398 medium. Treatments with 10 µM DPI (Diphenyleneiodonium chloride, Sigma) dissolved in 399 Dimethyl Sulfoxide (DMSO), 1 mM Sodium Ascorbate (Sigma) dissolved in distilled water and 400 1 mM N-acetyl-cysteine (Acros organics) dissolved in distilled water were performed by 401 applying these chemicals in the agar medium. Ascorbate treatment for DHR staining was 402 performed by transferring seedlings onto 1 mm Whatman filter paper 0.25 X Murashige and 403 Skoog medium (MS) (Murashige and Skoog, 1962) and the indicated ascorbate concentrations.

## 404 **Hydrotropic stimulation assays**

405 A CaCl<sub>2</sub> dry chamber was designed based on a previously described system (Takahashi et al., 406 2002; Kobayashi et al., 2007; Shkolnik et al., 2016) with the following modifications: Plates 407 were prepared as described in 'Plant material and growth conditions' with or without 408 supplemented chemicals, as indicated. The medium was cut 6 cm from the bottom and 5-7 day-409 old seedlings were transferred to the cut medium, such that approximately 0.2 mm of the primary 410 root tip was bolting from the agar into air. Twelve ml of 40 % CaCl<sub>2</sub> (w/v) (Duchefa) were put at 411 the bottom of the plate, which was then closed, sealed with Parafilm and placed vertically under 412 30  $\mu$ E m<sup>-2</sup> sec<sup>-1</sup> white light. As control, non-hydrostimulating conditions were achieved by 413 adding 20 ml of distilled water to the bottom of the plate. In this system, the roots were exposed 414 to the supplemented chemical at the beginning of the experiment. Hydrostimulation was 415 performed also using the previously described split-agar method (Takahashi et al., 2002; Antoni

416 et al., 2016). Ascorbate, DPI or DMSO (control) were added directly to the sorbitol containing 417 gel slice. Root tips were imaged at indicated time points using Nikon D7100 camera equipped 418 with AF-S DX Micro NIKKOR 85 mm f/3.5G ED VR lens (Nikon, Tokyo, Japan). For root 419 curvature measurements and supplemental movies of the humidity-gradient system, plates were 420 faced ~45 ° to the lens, and multiple photos with changing focus were obtained using Helicon 421 remote software, and stacked using Helicon focus software (www.heliconsoft.com). Root 422 curvature and growth were analyzed using ImageJ software 1.48V (Wayne Rasband, NIH, USA).

## 423 **Gravitropic stimulation assay**

424 Five to seven-day-old seedlings were transferred to a standard medium, or ascorbate containing 425 medium, following one hour of acclimation at original growth orientation before the plates were 426 90º rotated. For DPI treatment, seedlings were pre-treated in DMSO or 10 µM DPI-containing 427 media for 2 h, then transferred to another plate containing standard medium, followed by 30 min 428 acclimation at the original growth orientation before the plates were rotated by 90º.

### 429 **Confocal microscopy**

430 For ROS detection, seedlings were immersed in 86.5 µM [0.003% (w/v)] Dihydrorhodamine-123 431 (Sigma) dissolved in Phosphate Buffer Saline (PBS x 1, pH 7.4) for 2 or 5 min, after hydrotropic 432 or gravitropic stimulation assays. Fluorescent signals in roots were imaged with a Zeiss LSM 433 780 laser spectral scanning confocal microscope (Zeiss, http://corporate.zeiss.com), with a 10X 434 air (EC Plan-Neofluar 10x/0.30 M27) objective. Acquisition parameters were as follows: master 435 gain was always set between 670 and 720, with a digital gain of 1, excitation at 488 nm (2%) and 436 emission at 519-560 nm. Signal intensity was quantified as mean grey value using ImageJ 437 software. Confocal images were pseudo-colored using the RGB look-up table of the ZEN 438 software, for easier detection of the fluorescent signal distribution in the root. Imaging of DII-439 VENUS expressing roots was performed as previously described (Shkolnik et al., 2016).

## 440 **Determination of H2O2 in tissue extracts**

441 Whole seedlings ( $n = 20$  seedlings) and root apices (1-2 mm from root tip,  $n = 60$  seedlings) 442 were frozen in liquid nitrogen and homogenized in Phosphate Buffer Saline (PBS x 1, pH 7.4) 443 (600 µl for whole seedlings and 150 µl for root apices), centrifuged in 10,000 g for 5 min in  $4^{\circ}$  C 444 and the supernatant was used as the tissue extract.  $H_2O_2$  levels in the extracts were measured 445 using the Amplex red assay kit (Molecular Probes, Invitrogen) according to the manufacturer's 446 protocol, with 3 biological repeats and two technical replicates. Samples were measured with a

- 447 Synergy HT fluorescence plate reader (BioTek) using 530/590 nm excitation/emission filters.
- 448 Protein levels in the extracts were determined using the Bradford reagent (Bio-Rad). The 449 absorbance was read in the same plate reader using a 595 nm filter. Fluorescence reads were then
- 450 normalized to the protein amount.

#### **Statistical analysis**

- 452 Results were analyzed using MS Excel ToolPak and R version 3.1.1.
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#### **Supplemental materials**

- **Figure S1**: Relative DHR fluorescence intensity in gravistimulated and hydrostimulated roots.
- **Figure S2**: ROS level is reduced by ascorbate.
- **Figure S3**: The antioxidant ascorbate impedes root gravitropic response.
- **Figure S4**: Hydrostimulation using the split-agar / sorbitol method.
- **Figure S5**: ROS distribution during hydrotropic growth in WT, *rbohC* and *rbohD* mutants.
- **Figure S6**: ROS distribution in hydrostimulated WT, *rbohC* and *rbohD* mutants using the split-
- 461 agar / sorbitol system.
- **Figure S7**: ROS distribution in gravistimulated WT, *apx1-2*, *rbhoC* and *rbhoD* mutants.
- **Figure S8**: *rbohC* and *rbohD* exhibit normal gravitropic growth compared to WT.
- **Figure S9**: Auxin distribution in gravistimulated root tips with or without prior 465 hydrostimulation.
- **Video movie-1**: Hydrotropism of *rbohC* mutant compared to wt.
- **Video Movie-2**: Hydrotropism of *rbohD* mutant compared to wt.
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## 474 **Figure Legends**

475

476 **Figure 1**: ROS spatial and temporal distribution patterns during root gravitropism and 477 hydrotropism. A, B, C and E) Confocal microscopy of 5-day old seedlings stained with 478 Dihydrorhodamin-123 (DHR), a ROS-sensitive fluorescent dye. Images were pseudo-colored, 479 red indicates higher ROS-dependent fluorescence intensity. Scale bars, 100 µm. DEZ, Distal 480 Elongation Zone, CEZ, Central Elongation Zone (designated according to Fasano et al., 2001). 481 White lines next to the root mark defined root zones. *g* represents gravity vector, Ψ represents 482 water potential gradient. Concave and convex sides of the root are indicated. Arrowheads point 483 to regions where the fluorescence signal distributes unevenly between the two sides of the root. 484 A) Under gravistimulation, an asymmetric distribution of ROS was apparent 2 h post stimulation 485 and dissipated after another 2 h. This asymmetry was detected at the DEZ where higher ROS 486 levels were observed at the concave side of the root. B) Under hydrostimulation, ROS distribute 487 asymmetrically at the CEZ however maintain symmetric distribution at the DEZ. C) The 488 asymmetric ROS pattern at the CEZ was also observed in roots that were exposed to non-489 hydrostimulating conditions and do not bend hydrotropically. The higher ROS level was 490 observed at the side that is in contact with the agar medium. D) Quantification of DHR 491 fluorescence, measured at the epidermal layer in two regions of the root EZ (in the DEZ of 492 gravistimulated roots and in the DEZ and CEZ of hydrostimulated roots). The data is presented 493 as the ratio between the signal at the concave and the convex sides of the root. Error bars 494 represent mean  $\pm$  SE (3 biological independent experiments, 14 $\leq$ n $\leq$ 23). \*\*p $\leq$  0.01, Student's t-495 test versus start time. E) Roots were hydrostimulated for the indicated times using the split-agar / 496 sorbitol system. F) Quantification of DHR fluorescence, measured at the DEZ epidermal layer 497 (200  $\mu$ m above apex) and CEZ (600  $\mu$ m above apex). The data is presented as the ratio between 498 the signal at the concave and the convex sides of the root. Error bars represent mean  $\pm$  SE (3) 499 biological independent experiments, n=20). No significant difference was found among different 500 hydrostimulation times (Tukey-HSD post hoc-test  $(P < 0.05)$ ).

502 **Figure 2**: Ascorbate accelerates root hydrotropic growth, and a mutant deficient in APX1 shows 503 attenuated hydrotropic bending. A) Seedlings performing hydrotropic bending 2.5 h post 504 hydrostimulation in the presence or absence of 1 mM sodium ascorbate. In both A and C) g 505 represents gravity vector, Ψ represents water potential gradient, Scale bar, 1 mm. B) Root 506 curvature kinetics and growth rate of ascorbate-treated hydrostimulated seedlings. Root 507 curvature was measured at 1 h interval for 7 h following hydrostimulation. Root growth rate was 508 determined by measuring the length at the beginning and at the end of the experiment. Error bars 509 represent mean  $\pm$  SE (3 biological independent experiments, 10 seedlings each). \*p <0.05, 510 Student's t-test for independent measurements. C) Root hydrotropic bending of WT and *apx1-2*, 511 5 h post hydrostimulation. D) Root curvature kinetics and growth rate of *apx1-2* and WT 512 hydrostimulated seedlings. Root curvature and root growth rate were measured as described in 513 B).

514

515 **Figure 3**: Application of DPI, an NADPH oxidase inhibitor, accelerates hydrotropism while 516 delaying gravitropism. A) Application of 10 µM Diphenyleneiodonium (DPI) to the growing 517 medium promotes hydrotropic curvature (first two left panels), and impedes gravitropic 518 curvature (two right panels). Images were taken 2 h post hydrostimulation (scale bar, 1 mm) and 519 12 h post gravistimulation (scale bar, 5 mm). *g* represents gravity vector, Ψ represents water 520 potential gradient. B) Root curvature was measured at 1 h interval for 6 h following 521 hydrostimulation and at 2 h interval for 12 h following gravistimulation. Error bars represent 522 mean ± SE (3 biological independent experiments, 10 seedlings each). C) DPI inhibits root 523 growth in both physiological assays. Root growth rate was determined by measuring length at 524 the beginning and at the end of the experiment. Error bars represent mean  $\pm$  SE (3 biological 525 independent experiments, 10 seedlings each). \*\*p<0.01, t-test for independent measurements.

526 **Figure 4**: DPI eliminates ROS levels at the epidermal layer of the root elongation zone and 527 elevates ROS levels at the meristematic zone. A, C and D) DHR fluorescence (in A, over bright 528 field, in C and D, fluorescent channel only) of seedlings treated for 2 h with 10  $\mu$ M DPI or 529 DMSO for control. Scale bars, 100 µm in all confocal images. *g* represents gravity vector, Ψ 530 represents water potential gradient. A) Images of unstimulated roots, pre-treated for 2 h with 10 531 µM DPI or DMSO. DHR signal is more intense and penetrates to the deeper root layers due to 532 longer incubation in the dye (5 minutes). Images are representatives of n=23 seedlings. B) DHR 533 fluorescence intensity of seedlings treated with DPI or DMSO for 2 h, measured at the epidermal 534 layer of the EZ and at the meristematic zone. Error bars represent mean  $\pm$  SE (3 biological 535 independent experiments, n=23 seedlings in total). \*p<0.05, \*\*p<0.01, t-test for independent 536 measurements. C) Seedlings pre-treated with DPI for 2 h were gravistimulated, and show less 537 ROS accumulation and asymmetrical distribution at the EZ. Images shown here are of a more 538 extraneous section of the root, where the differences between DPI-treatment and control are 539 highly detectable. Images are representatives of  $n = 11$  seedlings. D) Seedlings that were 540 hydrostimulated for 2 h on a DPI containing medium showing elimination of the signal from the 541 epidermal layer at the bending region, which became more proximal to the root tip. Images are 542 representatives of  $n = 20$  seedlings.

543 **Figure 5**: *rbohC*, but not *rbohD*, show accelerated hydrotropic bending and lower ROS levels in 544 the root apex. A) Root hydrotropic growth of WT, *rbohC* and *rbohD*, 2 h post hydrostimulation. 545 Scale bar, 1 mm. g represents gravity vector, Ψ represents water potential gradient. B) Root 546 curvature kinetics and growth rates. Root curvature was measured at 1 h interval for 7 hours 547 following hydrostimulation. Root growth rate was determined by measuring length at the 548 beginning and at the end of the experiment. Error bars represent mean  $\pm$  SE (3 biological 549 independent experiments, 10 seedlings each). Statistical difference in root curvature was tested 550 for 2 and 5 h post hydrostimulation. C) Determination of H2O2 content in root apices (1-2 mm 551 from tip) and whole seedlings (D) of WT, *rbohD* and *rbohC*, measured by the Amplex red assay 552 (Materials and Methods). The fluorescent reads were normalized to the amount of extracted 553 protein, measured by the Bradford assay. Error bars represent mean  $\pm$  SD (3 biological repeats 554 with two technical replicates. for root apices,  $n = 60$ , for whole seedlings,  $n = 20$ ). The higher y-555 scale in C is a result of normalization to ten-fold lower protein level extracted from root apices. 556 In B, C and D) Means with different letters are significantly different (p < 0.05, Tukey HSD 557 adjusted comparisons).

558 **Figure 6**: Hydrotropism abrogates the gravitropic ROS signal. A) Schematic presentation of the 559 assay applied to test ROS distribution at root tips of hydrostimulated seedlings and a combined 560 gravistimulation with hydrostimulation. B) Roots were hydrostimulated for the indicated times 561 and then gravistimulation for 1 h, stained with Dihydrorhodamin-123 (DHR) and imaged using a 562 confocal microscope (Materials & Methods). Images are presented as pseudo color. Scale bar, 563 100  $\mu$ m. C) Quantification of DHR fluorescence, measured at the DEZ epidermal layer (200  $\mu$ m 564 above apex). The data is presented as the ratio between the signal at the concave and the convex

- 565 sides of the root. Error bars represent mean  $\pm$  SE (3 biological independent experiments, n=20).
- 566 D) Root curvature of 1 h gravistimulated seedlings following hydrostimulation for the indicated
- 567 times. The 1 h gravitropic curvature following 0, 2, 3 and 4 h hydrosimulation was  $14.42^{\circ}$  ±
- 568 1.27,  $9.16^{\circ} \pm 0.76$ ,  $6.33^{\circ} \pm 0.78$  and  $-3.14^{\circ} \pm 2.03$ , respectively. Error bars represent mean  $\pm$  SE
- 569 (3 biological independent experiments, n=15). Negative value means curvature against the
- 570 gravity vector direction. In A and B, Ψ and g represent the water potential gradient and gravity
- 571 vector, respectively. ROS images of hydrostimulated roots for the same indicated times, without
- 572 gravistimulation are shown in Fig. 1 E. In C and D, letters above bars represent statistically
- 573 significant differences by Tukey-HSD post hoc-test  $(P < 0.05)$ .
- 574

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CaCl<sub>2</sub> / dry chamber

Split-agar / sorbitol





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Pubmed: [Author and Title](http://www.ncbi.nlm.nih.gov/pubmed?term=Antoni R%2C Dietrich D%2C Bennett MJ%2C Rodriguez PL %282016%29 Hydrotropism%3A Analysis of the Root Response to a Moisture Gradient%2E Environ Responses Plants Methods Protoc 3%2D9&dopt=abstract) CrossRef: [Author and Title](http://search.crossref.org/?page=1&rows=2&q=Antoni R, Dietrich D, Bennett MJ, Rodriguez PL (2016) Hydrotropism: Analysis of the Root Response to a Moisture Gradient. Environ Responses Plants Methods Protoc 3-9) Google Scholar: [Author Only](http://scholar.google.com/scholar?as_q=&num=10&as_occt=any&as_sauthors=Antoni&hl=en&c2coff=1) [Title Only](http://scholar.google.com/scholar?as_q=Hydrotropism: Analysis of the Root Response to a Moisture Gradient.&num=10&btnG=Search+Scholar&as_epq=&as_oq=&as_eq=&as_occt=any&as_publication=&as_yhi=&as_allsubj=all&hl=en&lr=&c2coff=1) [Author and Title](http://scholar.google.com/scholar?as_q=Hydrotropism: Analysis of the Root Response to a Moisture Gradient.&num=10&btnG=Search+Scholar&as_occt=any&as_sauthors=Antoni&as_ylo=2016&as_allsubj=all&hl=en&c2coff=1)

**Antoni R, Gonzalez-Guzman M, Rodriguez L, Peirats-Llobet M, Pizzio GA, Fernandez MA, De Winne N, De Jaeger G, Dietrich D, Bennett MJ, et al (2013) PYRABACTIN RESISTANCE1-LIKE8 plays an important role for the regulation of abscisic acid signaling in root. Plant Physiol 161: 931-941**

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