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# An integrative model of plant gravitropism linking statoliths position and auxin transport

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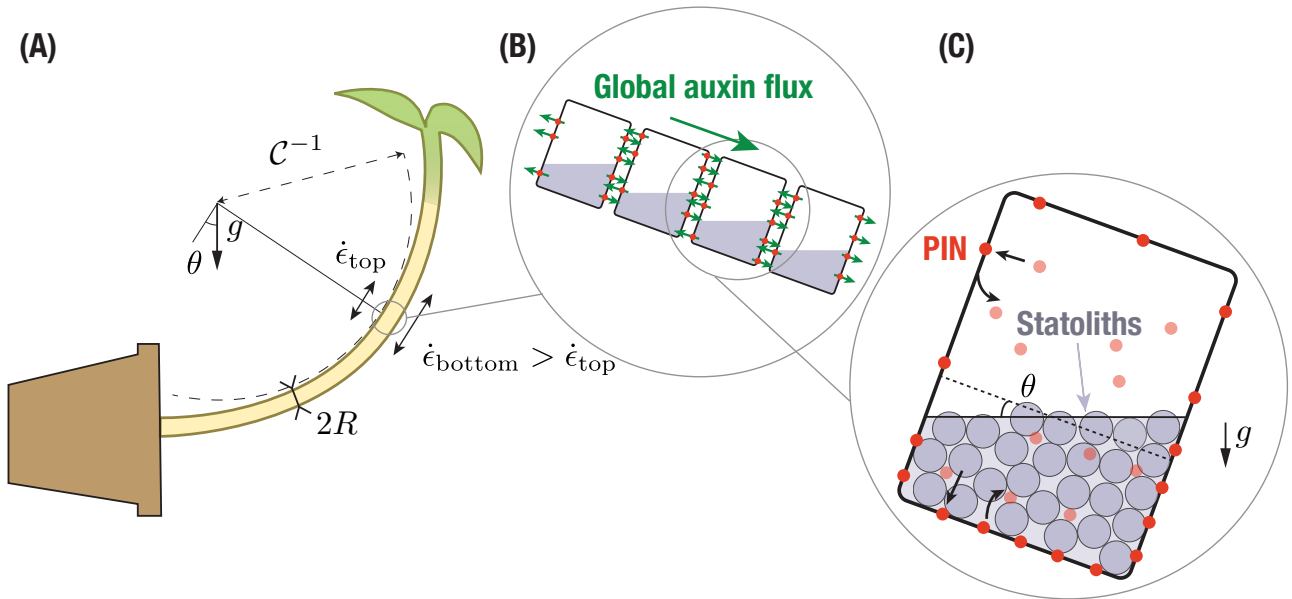
## 2 ABSTRACT

3 Gravity is a major cue for the proper growth and development of plants. The response of  
4 plants to gravity implies starch-filled plastids, the statoliths, which sediments at the bottom of  
5 the gravisensing cells, the statocytes. Statoliths are assumed to modify the transport of the  
6 growth hormone, auxin, by acting on specific auxin transporters, PIN proteins. However, the  
7 complete gravitropic signaling pathway from the intracellular signal associated to statoliths to  
8 the plant bending is still not well understood. In this article, we build on recent experimental  
9 results showing that statoliths do not act as gravitational force sensor, but as position sensor, to  
10 develop a bottom-up theory of plant gravitropism. The main hypothesis of the model is that the  
11 presence of statoliths modifies PIN trafficking close to the cell membrane. This basic assumption,  
12 coupled with auxin transport and growth in an idealized tissue made of a one-dimensional array  
13 of cells, recovers several major features of the gravitropic response of plants. First, the model  
14 provides a new interpretation for the response of a plant to a steady stimulus, the so-called  
15 sine-law of plant gravitropism. Second, it predicts the existence of a gravity-independent memory  
16 process as observed recently in experiments studying the response to transient stimulus. The  
17 model suggests that the timescale of this process is associated to PIN turnover, calling for new  
18 experimental studies.

19 **Keywords:** Plant tropism, Gravity sensing, Auxin signaling, PIN trafficking, Modeling

## 1 INTRODUCTION

20 The detection of gravity by plants and the resulting growth response (gravitropism) offer a fascinating  
21 illustration of a multi-scale perception mechanism in living organisms (Fig. 1) (Mouliia and Fournier,  
22 2009; Morita, 2010; Toyota and Gilroy, 2013). It originates in specific cells, called statocytes, where tiny  
23 starch-accumulating amyloplasts acting as statoliths sediment under gravity at the bottom of the cells  
24 (Fig. 1C). When the plant is inclined, the repositioning of statoliths under gravity induces a relocalisation  
25 of auxin transporters (PIN proteins) at the membrane of statocytes, which generates a lateral transport  
26 of auxin toward the lower side of the shoot or the root (Cholodni–Went hypothesis) (Fig. 1B). In turn,  
27 this asymmetry in auxin concentration induces a differential growth across the plant organ, and thus its  
28 bending toward the gravity vector (Fig. 1A). Since the pioneering works of the Darwins and Sachs on  
29 plant tropisms (Darwin and Darwin, 1880; Sachs, 1887), progress has been made on every step of this  
30 gravitropic signaling pathway. Yet, basic questions remain unanswered. In particular, it is still not clear  
31 how the first physical signal generated by the sedimentation of statoliths is converted into biochemical  
32 signals downstream, to eventually produce the growth response at the plant scale (Nakamura et al., 2019).



**Figure 1.** Multiscale description of gravitropism. At the macroscopic scale (A), the response to gravity of a shoot or a stem is achieved by differential growth across the organ, which induces a curvature of the organ. At the tissue scale (B), differential growth results from a net flux of the auxin across the width (large green arrows), owing to the asymmetric distribution of auxin transporters (PINs, red circles). The local auxin fluxes are shown by the small green arrows. At the cell scale (C), PIN asymmetry results from the asymmetric distribution of the statoliths position after sedimentation under gravity, which modifies PIN trafficking close to the cell membrane.

33 Recently, insights into the sensing mechanism and the transduction pathway have been obtained from  
 34 experiments both at the macroscopic and microscopic levels. First, the gravitropic response to permanent  
 35 stimuli (inclination of the plant), the so-called sine-law of gravitropism (Sachs, 1887; Larsen, 1969; Ino  
 36 et al., 1996; Galland, 2002; Dumais, 2013), was found to depend on the inclination but, surprisingly,  
 37 not on the intensity of gravity (Chauvet et al., 2016). Hence, statocytes behave like inclination sensors  
 38 not force sensors as previously believed. An important consequence is that the initial gravity stimulus  
 39 for gravitropism should be the position of the statoliths within statocytes (Pouliquen et al., 2017). This  
 40 position-sensor hypothesis gained a mechanistic support from the direct observation of statoliths motion  
 41 under gravity stimulation (Bérut et al., 2018). Unlike a pile of macroscopic grains like sand, statoliths were  
 42 found to move and flow at any inclination. This liquid-like behavior comes from the random agitation of  
 43 the statoliths, whose origin is not thermal but arises from the interaction of statoliths with the acto-myosin  
 44 cytoskeleton inside the cell (Sack et al., 1986; Saito et al., 2005; Nakamura et al., 2011). A second insight  
 45 came from dose-response like experiments on wheat coleoptiles, in which the gravity stimulus was applied  
 46 during a transient period only (Chauvet et al., 2019). When the shoots were inclined for short period of  
 47 time, the gravitropic response was found to deviate from the steady response and decay. The transition  
 48 occurred for a time  $\tau_{\text{memory}} \sim 15$  min, which was independent of gravity and much larger than the  
 49 statoliths sedimentation time. This observation suggested the existence of a memory-integration process  
 50 in the gravitropic signaling pathway, independent of the statoliths dynamics, which integrates the initial  
 51 signal induced by statoliths displacement.

52 To account for these observations (position-sensor hypothesis, memory time independent of  $g$ ), Chauvet  
 53 et al. (2019) built a mathematical model of gravitropism in which the gravitropic signal controlling the

54 differential growth was linked to the statoliths position by an integrative process of timescale  $\tau_{\text{memory}}$  (a  
 55 similar approach was used in Meroz et al. (2019)). Once coupled to the statoliths dynamics and the tropic  
 56 growth motion, the model was able to reproduce the transient gravitropic response observed experimentally.  
 57 However, Chauvet et al. (2019)'s model was built on two *ad-hoc* postulates. First, it assumed that the  
 58 relation between the gravitropic signal and the statoliths position is known and given by the sine-law.  
 59 Second, it postulated the existence of the integrative process and time scale  $\tau_{\text{memory}}$ , without explaining  
 60 its origin. The spatio-temporal dynamics of the molecular processes acting between the statoliths and the  
 61 growth response, such as the dynamics of PIN proteins and auxin transport, was not described.

62 The objective of this paper is to fill this gap by building an integrative model of plant gravitropism that  
 63 bridges the different scales of the process: (i) the initial intracellular gravitropic signal encoded in the  
 64 statoliths position, (ii) PINs dynamics at the cellular level, (iii) auxin transport at the tissue level and, finally,  
 65 (iv) differential growth and curvature at the plant organ scale. Previous models of plant gravitropism mainly  
 66 focused either on the macroscopic scale, describing how the complex spatio-temporal evolution of the  
 67 organ shape results from the interplay between differential growth and the slender geometry of the organ  
 68 (Bastien et al., 2013, 2014; Chelakkot and Mahadevan, 2017), or on the tissue level, modeling growth  
 69 mechanics (Dyson et al., 2014) or auxin transport (Band et al., 2012; Fendrych et al., 2018; Retzer et al.,  
 70 2019) in realistic 1D or 3D tissue geometries. In these latter models, the distribution of PINs in response  
 71 to plant inclination was prescribed and not linked to the intracellular dynamics of the statoliths. This is  
 72 precisely the goal of our study. Building on the recent position-sensor hypothesis, we propose a simple but  
 73 generic model of interaction between statoliths and PINs trafficking at the cell membrane, that we couple  
 74 with the classical equations of auxin transport and tissue growth. We then study the gravitropic response  
 75 predicted by the model for steady and unsteady gravity stimuli, comparing the results with the experiments  
 76 of Chauvet et al. (2016) and Chauvet et al. (2019).

## 2 MATERIAL AND METHODS

### 77 2.1 Link between gravitropic curvature, differential growth and auxin concentration 78 gradient

79 At the plant scale, the gravitropic response is characterized by the curvature of the organ resulting from  
 80 differential growth, which itself results from auxin gradients (Cholodny–Went hypothesis). The first step  
 81 of the model is thus to relate those three quantities. For a slender organ like a shoot or a stem, the rate of  
 82 change of the local curvature  $\mathcal{C}$  is related to differential growth through the following kinematic relationship:  
 83  $R \frac{d\mathcal{C}}{dt} = \frac{1}{\tau_g} \times \frac{\dot{\epsilon}_{\text{bottom}} - \dot{\epsilon}_{\text{top}}}{2\dot{\epsilon}_{\text{mean}}}$ , where  $R$  is the radius of the organ,  $\dot{\epsilon}_{\text{bottom}} - \dot{\epsilon}_{\text{top}}$  is the difference of growth  
 84 rate between both sides,  $\dot{\epsilon}_{\text{mean}}$  is the mean growth rate and  $\tau_g = \dot{\epsilon}_{\text{mean}}^{-1}$  is the growth timescale (Silk,  
 85 1984; Moulia and Fournier, 2009; Bastien et al., 2013) (Fig. 1). The growth rate of plant cells is known  
 86 to be controlled by auxin, the so-called growth hormone. Auxin stimulates cell elongation by loosening  
 87 cell walls. To the best of our knowledge, the link between the local auxin concentration in walls and the  
 88 local growth rate of cells has not been robustly determined and only the response of the whole tissue to  
 89 an external addition of auxin has been investigated. It is however often assumed that growth is mainly  
 90 controlled by the auxin concentration in the vicinity of the ‘skin’ of the organ, as epidermal tissues are  
 91 stiffer than inner tissues (Kutschera and Niklas, 2007; Dyson et al., 2014). For the sake of simplicity, we  
 92 will here assume that the local growth rate is simply proportional to the local auxin concentration  $c$ ,  $\dot{\epsilon} = kc$   
 93 (Galston and Hand, 1949; Hopkins and Hüner, 2009), such that:

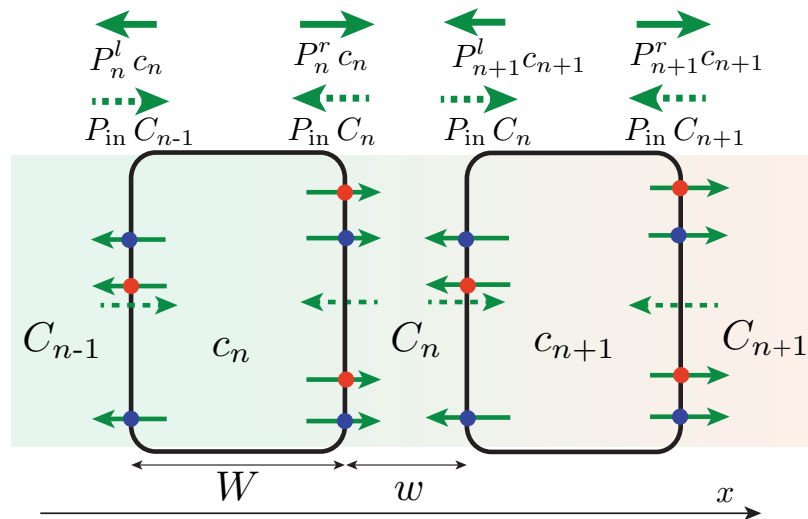
$$R \frac{d\mathcal{C}}{dt} = \frac{1}{\tau_g} \times \frac{c_{\text{bottom}} - c_{\text{top}}}{2c_{\text{mean}}}, \quad (1)$$

94 where  $c_{\text{bottom}}$  and  $c_{\text{top}}$  are the auxin concentrations on both sides of the organ and  $c_{\text{mean}}$  the mean auxin  
 95 concentration. Under this assumption, the dimensionless gravitropic response deduced from the curvature  
 96 dynamics,  $\tilde{\Delta}(t) \equiv R\tau_g \frac{dC}{dt}$ , is equal to the relative auxin gradient across the organ,  $\tilde{\Delta}(t) = \frac{c_{\text{bottom}} - c_{\text{top}}}{2c_{\text{mean}}}$ . The  
 97 goal of the model is to predict how this auxin gradient establishes when the plant is tilted.

## 98 2.2 Auxin transport

99 Auxin transport plays a key role in shaping plants development and, as such, has been the topic of  
 100 extensive research over the past decades. Auxin transport is based on two distinct mechanisms (Goldsmith,  
 101 1977; Hopkins and Hüner, 2009; Runions et al., 2014). On the one hand, auxin in cell walls (mostly in a  
 102 protonated form) enters the neighboring cell passively, or thanks to Aux/Lax influx carriers that are evenly  
 103 distributed throughout the membrane. On the other hand, auxin inside cells (mostly in an anionic form)  
 104 can only exit thanks to active auxin efflux carriers, such as PIN proteins (Krecek et al., 2009) or ABCB  
 105 transporters (Zažímalová et al., 2010). While ABCB are evenly distributed throughout the membrane, PIN  
 106 proteins are usually polarized and can be redistributed in response to external stimuli such as gravity (in  
 107 particular PIN3, which is known to be implied in gravitropic response, see Friml et al. (2002)). Hence, an  
 108 asymmetric distribution of PIN carriers on each side of the cell can generate an active transport of auxin  
 109 from one cell to the other, resulting in a stable auxin gradient.

To model this situation, we provide a simplified description of auxin transport in which the different forms of auxin (proton-associated or not) are not taken into account. The tissue across the shoot or stem (width  $2R$ ) is modeled as a one-dimensional array of  $N$  cells of width  $W$ , separated by a cell wall of width  $w$  (Fig. 1 b and Fig. 2). We denote  $c_n$  the auxin concentration inside the  $n$ -th cell and  $C_n$  the auxin concentration inside the  $n$ -th wall, which are both assumed uniform (the equilibrium time of auxin in each compartment is very fast, about 0.1 s in the cell wall and few s inside the cell taking typical values of auxin



**Figure 2.** One-dimensional, discrete model of auxin transport across the tissue (in reality  $w \ll W$ ). Efflux of auxin (solid green arrow) occurs through efflux carriers (PIN: red circle, ABCB: blue circle), whose distribution (and thus permeabilities  $P_n^{l,r}$ ) can be different on the right and left membrane of the cell. By contrast, influx of auxin (green dotted arrow) occurs with a symmetrical permeability  $P^{\text{in}}$  on both side of the cell. An asymmetry of efflux permeabilities  $P^l \neq P^r$  can generate a net flux of auxin across the tissue, yielding an auxin concentration gradient (background color gradient).

diffusion coefficients, see Kramer et al. (2007)). We also neglect auxin dilution due to cell growth and assume that auxin is neither degraded nor created, as the degradation time of auxin (of the order of the day, see Grieneisen et al. (2012)) is much longer than the minutes to hours timescales we are interested in. The efflux current of auxin (number of auxin molecules per unit time and unit surface) from the  $n$ -th cell to the left wall (resp. right wall) is given by  $P_n^l c_n$  (resp.  $P_n^r c_n$ ), where  $P_n^l$  (resp.  $P_n^r$ ) is the permeability of the left (resp. right) membrane (unit m/s). Conversely, the influx current of auxin from the  $n$ -th wall to both adjacent cells is  $P^{\text{in}} C_n$ , where the influx permeability  $P^{\text{in}}$  is assumed uniform for all cells (see Fig. 2). The time-evolution of the concentration is then:

$$w \frac{dC_n}{dt} = -2P^{\text{in}} C_n + P_n^r c_n + P_{n+1}^l c_{n+1}, \quad (2)$$

$$W \frac{dc_n}{dt} = -(P_n^l + P_n^r) c_n + P^{\text{in}} (C_{n-1} + C_n). \quad (3)$$

110 The cell wall size being much smaller than the cell width ( $w \ll W$ ), the auxin concentration in the cell  
 111 wall can be assumed quasi-steady,  $2P^{\text{in}} C_n \simeq P_n^r c_n + P_{n+1}^l c_{n+1}$ , yielding:

$$2W \frac{dc_n}{dt} = P_{n+1}^l c_{n+1} - P_n^l c_n + P_{n-1}^r c_{n-1} - P_n^r c_n. \quad (4)$$

112 In the following, we assume that the distribution of auxin efflux carriers is the same in each cell, so that  $P^l$   
 113 and  $P^r$  are independent of  $n$ . This is the case of shoot coleoptiles where all cells in the growing region  
 114 are similar and contain statoliths, but not the case of stems like the inflorescence of *Arabidopsis*, where  
 115 statoliths are only present on an external ring in the endodermal cells (the modification of the equation in  
 116 this case of inhomogeneous tissue is given in Appendix A). We also assume that auxin gradients occur  
 117 over a length scale much larger than the cell size. In the continuum limit [ $c_n(t) \rightarrow c(x, t)$ ], equation (4) for  
 118 auxin transport then reduces to an advection-diffusion equation given by:

$$\frac{\partial c}{\partial t} = \mathcal{D} \frac{\partial^2 c}{\partial x^2} - v \frac{\partial c}{\partial x}, \quad (5)$$

119 where  $\mathcal{D} = WP/2$  is the coefficient of diffusion and  $v = \delta P/2$  the advection speed, with  $P = (P^l + P^r)/2$   
 120 and  $\delta P = P^r - P^l$ .

121 The advective part of equation (5), which is responsible for auxin transport from one side to the other and  
 122 thus to the differentiated growth and the curvature of the organ, is entirely controlled by the asymmetry of  
 123 efflux permeabilities  $\delta P$ . Since ABCB carriers are evenly distributed, this asymmetry comes solely from  
 124 the asymmetry of PINs distribution between the right and left side of the cells:

$$\delta P = P^r - P^l = \frac{1}{S} \left( \alpha \int_S [PIN]_{\text{right}} - \alpha \int_S [PIN]_{\text{left}} \right), \quad (6)$$

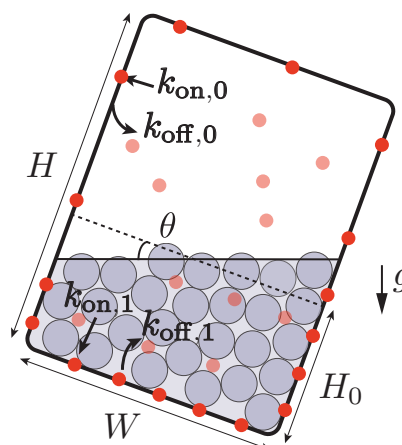
125 where  $\alpha$  is the conductance of a single PIN carrier (unit  $\text{m}^3/\text{s}$ ),  $S$  the lateral surface of the cells and  
 126  $[PIN]$  the surface concentration of PINs attached to the membrane. In the following, we assume that the  
 127 efflux permeability due to ABCB carriers is much larger than the efflux permeability due to PINs, such  
 128 that  $P = (P^l + P^r)/2 \simeq (1/S)\beta \int [ABCB]$ , where  $\beta$  is the conductance of a single ABCB carrier, is  
 129 independent of PINs concentration. This enables us to take a constant coefficient of diffusion  $\mathcal{D}$  in the

130 model, which simplify the results without affecting much the conclusions.

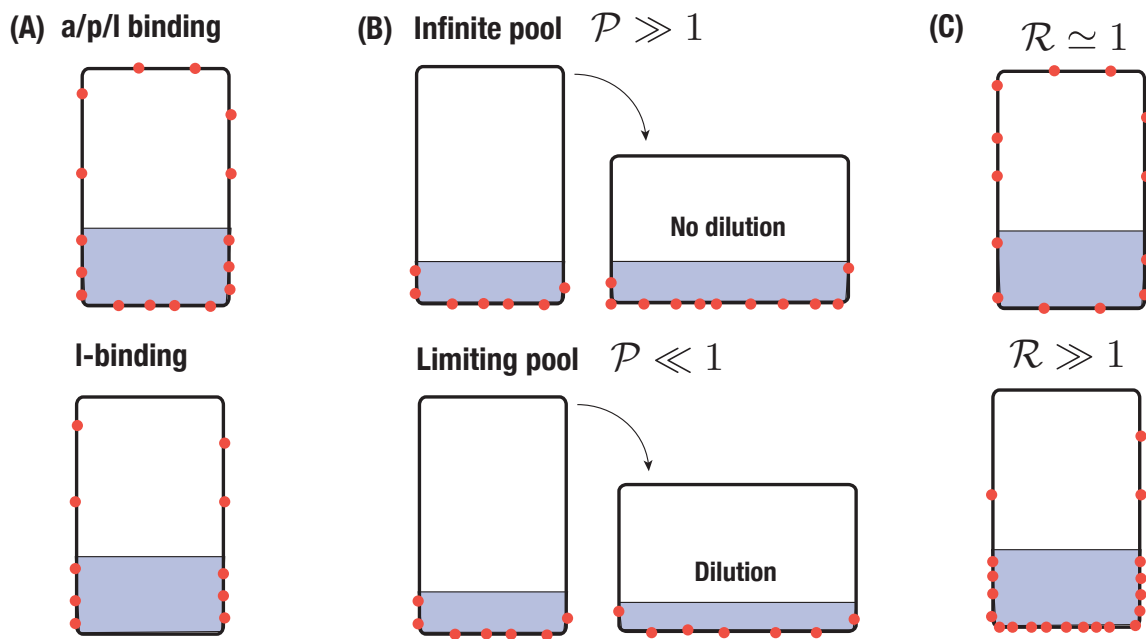
### 131 132 **2.3 Coupling PIN dynamics to statoliths position: biased efflux at cell scale**

133 The previous section relates auxin transport to the asymmetry of PINs distribution at the cellular level.  
134 We now model how this asymmetry emerges when the plant is tilted under gravity. Recently, it has been  
135 demonstrated that the relevant gravitropic stimulus for graviperception is the statoliths position within  
136 the statocytes (position-sensor hypothesis), and not their weight as previously believed (Chauvet et al.,  
137 2016; Pouliquen et al., 2017). Statoliths have also been identified as key actors in the relocalisation of  
138 PIN-proteins in response to change of gravity direction (Nakamura et al., 2019). Yet, how statoliths  
139 position is detected and read to modify PIN polarity remains largely unknown. PINs trafficking involves  
140 synthesis in the endoplasmic reticulum, degradation in the vacuole and recycling (Kleine-Vehn and Friml,  
141 2008). Recycling is achieved by endocytosis, i.e., the deallocation of PIN proteins formerly attached to  
142 the cell membrane toward the cytoplasm inside a vesicle, or by exocytosis, i.e., the reallocation of the  
143 vesicle-carried PINs from the cytoplasm back to the cell membrane.

144 Following the position-sensor hypothesis, we assume that the presence of statoliths, either through direct  
145 steric constraints or through indirect molecular signaling, modify the trafficking of PIN proteins, so that  
146 PINs tend to enter the cell membrane preferentially on places where statoliths are in contact with it. This  
147 mechanism is formalized as follows. The endocytosis rate of PINs,  $d[PIN]_i/dt|_{\text{endo}} = -k_{\text{off},i}[PIN]_i$   
148 where  $[PIN]_i$  is the surface concentration of PIN attached to the membrane, is assumed to depend on the  
149 presence of statoliths, with  $i = 0$  if no statoliths are present and  $i = 1$  if they are (see Fig. 3). Similarly,  
150 the rate of exocytosis is written as  $d[PIN]_i/dt|_{\text{exo}} = +k_{\text{on},i}[PIN]_{\text{vol}}$ , where  $[PIN]_{\text{vol}}$  is the volumic  
151 concentration of PINs molecules inside the cell of volume  $WS$ . Two cases will be distinguished in the  
152 model, depending on whether PINs can attach to any side of the cell ("apical/basal/lateral binding") or  
153 only on lateral sides ("lateral binding") (see Fig. 4A). Assuming that the total number  $N_{\text{tot}}$  of PINs is  
154 conserved during gravistimulation (Kleine-Vehn et al., 2010) leads to the following set of equations for the  
155 PIN concentration attached to the membrane,  $[PIN]_{i=0,1}$ :



**Figure 3.** Interaction between PIN trafficking and statoliths position. The rate of reallocation  $k_{\text{on}}$  and deallocation  $k_{\text{off}}$  of PINs (bold red circles: PINs attached to the cell membrane, light red circles: PINs in bulk) depends on the presence of statoliths (grey). When the cell is tilted, the asymmetric distribution of the position of the statoliths induces a bias in the distribution of the PINs attached to the membrane.



**Figure 4.** Sketch of different scenario of PIN-binding. PINs are represented in red and the region with statoliths in grey. **(A)** Apical/basal/lateral-binding vs lateral-binding. **(B)** Infinite pool versus limiting pool. In the first case, the surface density of PINs is conserved whereas in the second one, the total number of PINs is conserved. **(C)** Low sensitivity of PIN to statoliths ( $\mathcal{R} \simeq 1$ ) or high sensitivity ( $\mathcal{R} \gg 1$ ).

$$\begin{aligned} \frac{d[PIN]_0}{dt} &= -k_{\text{off},0} [PIN]_0 + k_{\text{on},0} \left( \frac{N_{\text{tot}} - (S_0[PIN]_0 + S_1[PIN]_1)}{WS} \right), \\ \frac{d[PIN]_1}{dt} &= -k_{\text{off},1} [PIN]_1 + k_{\text{on},1} \left( \frac{N_{\text{tot}} - (S_0[PIN]_0 + S_1[PIN]_1)}{WS} \right), \end{aligned} \quad (7)$$

156 where  $S_1$  (resp.  $S_0$ ) denotes the total surface in contact (resp. not in contact) with statoliths in case of  
 157 apical/basal/lateral binding, or only the lateral surfaces in contact (resp. not in contact) with statoliths in  
 158 the lateral binding case.

159 The form of equation (7) shows that two regimes can be distinguished, depending on whether  $W$  is large  
 160 or small compared to  $k_{\text{on}}/k_{\text{off}}$ . The first regime, called ‘infinite-pool’ regime in the following, corresponds  
 161 to the case where  $Wk_{\text{off}}/k_{\text{on}}$  is so large that binding is only limited by  $k_{\text{off}}$ . The second regime, called  
 162 ‘limiting-pool’ regime, corresponds to the opposite situation where the total number of attached carriers  
 163 is almost equal to  $N_{\text{tot}}$ :  $S_0[PIN]_0 + S_1[PIN]_1 \simeq N_{\text{tot}}$  (see Fig. 4B). Finally, we note that in writing  
 164 equation (7), we have neglected the diffusion of PINs inside the membrane. This is justified since, over the  
 165 time scales we are interesting in (running from minutes to one hour), PINs diffuse only over a distance  
 166 of about few micrometers, which is much smaller than the cell size (taking  $0.1 \mu\text{m}^2 \text{ min}$  for the diffusion  
 167 coefficient of a PIN, see Kleine-Vehn et al. (2011)).

168 Equations (1, 5, 7) represent a complete model describing the time-evolution of the gravitropic response  
 169 once the statoliths is known, from the PIN localization to auxin transport and bending of the plant. In



170 the following, we study the predictions of the model for a steady and transient stimulus. Table 1 and 2  
171 summarizes all the physical quantities and dimensionless parameters defined from the model.

### 3 RESULTS

#### 172 3.1 Steady gravitropic response: revisiting the sine-law

173 We first study the gravitropic response predicted by our model in the case of a steady inclination of  
174 the plant  $\theta$ , for long timescales when the system reaches a steady state. This situation corresponds to the  
175 usual protocol for measuring the sensitivity of plant to gravity under steady condition, when the plant is  
176 suddenly inclined to a fixed angle  $\theta$  and its curvature (or tip angle) measured over time. After a transient,  
177 the rate of change of curvature is found to be constant (Chauvet et al., 2016), which enables to measure the  
178 steady gravitropic response  $\tilde{\Delta}^{\text{steady}}(\theta) = R\tau_g \frac{dC}{dt}$  (see Material and Methods) for each imposed angle  $\theta$ .  
179 For many plants, this relationship between the gravitropic response and the inclination angle has sine-like  
180 shape (the response is null for  $\theta = 0^\circ$  or  $\theta = 180^\circ$  and maximal for  $\theta = 90^\circ$ ) and is called the ‘sine-law’  
181 in the literature (Sachs, 1887; Larsen, 1969; Iino et al., 1996; Galland, 2002; Dumais, 2013). Below, we  
182 determine the steady gravitropic response  $\tilde{\Delta}^{\text{steady}}(\theta)$  predicted by the model (eqs. 1, 5, 7) and compare  
183 with measurements of the sine-law obtained previously for wheat coleoptiles over a wide range of angles  
184 (Chauvet et al., 2016).

185 In the steady regime, the auxin transport equation (eq. 5) reduces to:  $dJ/dx = 0$ , where  $J = \mathcal{D}(dc/dx) -$   
186  $vc$  is the auxin flux. For impermeable boundaries at  $x = 0$  and  $x = 2R$ , the flux is null and the auxin  
187 concentration profile is given by:

$$c(x) = c_{\text{mean}} \frac{\text{Pe} \times \exp\left(\frac{\text{Pe} \cdot x}{2R}\right)}{\exp(\text{Pe}) - 1}, \quad (8)$$

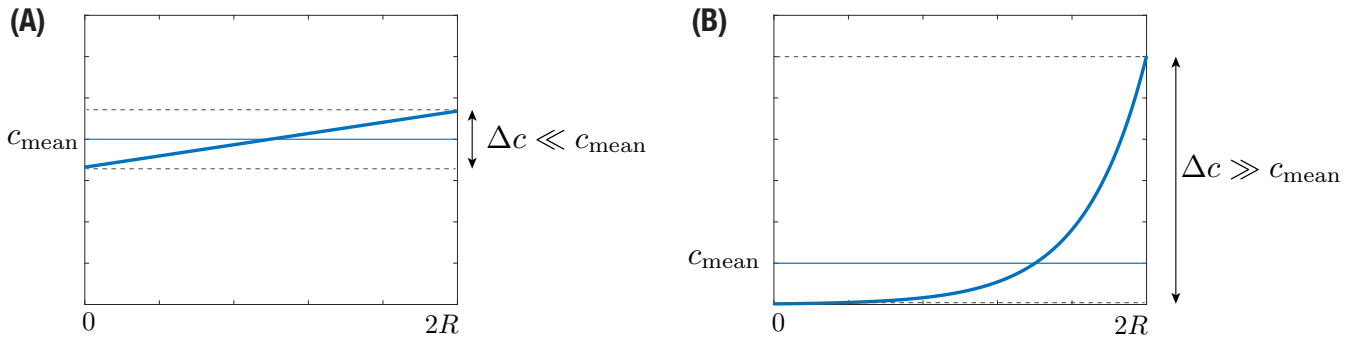
188 where  $c_{\text{mean}} = (1/2R) \int_0^{2R} c(x)dx$  is the mean concentration of auxin and Pe is the Peclet number  
189 comparing advection to diffusion and given by:

$$\text{Pe} \equiv \frac{2Rv}{\mathcal{D}} = N \frac{\delta P}{P} = N \frac{\alpha \left( \int_S [PIN]_{\text{right}} - \int_S [PIN]_{\text{left}} \right)}{\beta \int [ABCB]}. \quad (9)$$

190 For  $\text{Pe} \ll 1$ , the profile is linear and the auxin level in the middle of the stem is unchanged, whereas for  
191  $\text{Pe} \gg 1$  the profile is strongly asymmetric with most auxin concentrated on the right, corresponding to the  
192 lower side of the shoot (Fig. 5). From this steady profile of auxin, the gravitropic response can be computed  
193 as  $\tilde{\Delta}^{\text{steady}} = \frac{c(x=2R) - c(x=0)}{2c_{\text{mean}}}$  (eq. 1), which gives:

$$\tilde{\Delta}^{\text{steady}} = \frac{\text{Pe}}{2}. \quad (10)$$

194 In the steady state, the gravitropic response of the plant is thus given by the value of the Peclet number.  
195 Previous measurements in various plant species representative of land angiosperm showed that  $\tilde{\Delta}^{\text{steady}}$  is  
196 typically of the order 1 (Chauvet et al., 2016) (for e.g. in wheat coleoptile, the maximal value of  $\tilde{\Delta}^{\text{steady}}$   
197 obtained for a 90 degrees inclination is about 0.7), meaning that the Peclet number is typically of the  
198 order 1. Therefore, the auxin profile across the shoot is expected to be close to linear (Fig. 5A) (and not  
199 a pronounced exponential, Fig. 5B). A consequence is that growth, which was assumed proportional to  
200 the auxin concentration, varies also linearly from one side of the shoot to the other during the gravitropic  
201 response.



**Figure 5.** Stationary auxin profile for (A) small and (B) large Peclet number.

202 The next step to determine  $\tilde{\Delta}^{\text{steady}}$  is to compute the Peclet number given by equation (9), i.e., the relative  
 203 distribution of PIN between the left and right side of the cell. In the steady regime, the concentration of PIN  
 204 attached to a membrane not covered by statoliths ( $[PIN]_0^{\text{steady}}$ ), or covered by statoliths ( $[PIN]_1^{\text{steady}}$ ), is  
 205 given by (see eq. 7):

$$\begin{aligned}
 [PIN]_0^{\text{steady}} &= \frac{N_{\text{tot}}}{S} \left( \frac{k_{\text{off},0}W}{k_{\text{on},0}} + \frac{1}{S} \left[ S_0 + \frac{k_{\text{on},1} k_{\text{off},0}}{k_{\text{on},0} k_{\text{off},1}} S_1 \right] \right)^{-1}, \\
 [PIN]_1^{\text{steady}} &= \frac{N_{\text{tot}}}{S} \left( \frac{k_{\text{off},1}W}{k_{\text{on},1}} + \frac{1}{S} \left[ S_1 + \frac{k_{\text{on},0} k_{\text{off},1}}{k_{\text{on},1} k_{\text{off},0}} S_0 \right] \right)^{-1}.
 \end{aligned} \tag{11}$$

206 Noting  $S_i^l$  (resp.  $S_i^r$ ) the surface of the left (resp. right) side of the cell not covered ( $i = 0$ ) or covered ( $i = 1$ )  
 207 by statoliths, we have  $\int_S [PIN]_{\text{right}} - \int_S [PIN]_{\text{left}} = [PIN]_0^{\text{steady}} (S_0^r - S_0^l) + [PIN]_1^{\text{steady}} (S_1^r - S_1^l)$ .  
 208 Finally, since  $S_0^l + S_1^r = S_0^r + S_1^l = S$ , where  $S$  is the lateral surface of the cells and using equation (9),  
 209 we have:

$$\tilde{\Delta}^{\text{steady}} = \frac{\alpha N (\mathcal{R} - 1) (S_1^r - S_1^l) [PIN]_0^{\text{steady}}}{2\beta \int [ABCB]}, \tag{12}$$

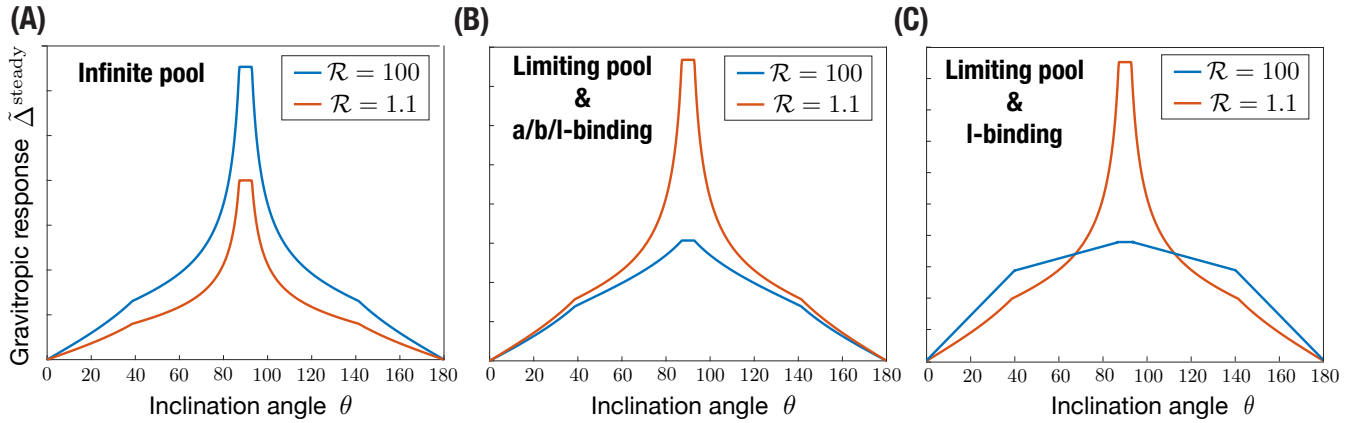
210 with

$$[PIN]_0^{\text{steady}} = \frac{N_{\text{tot}}}{S} \frac{1}{\mathcal{R}} \left( \mathcal{P} + \frac{S_1}{S} \left( 1 + \frac{S_0}{S_1 \mathcal{R}} \right) \right)^{-1}, \tag{13}$$

211 and:

$$\mathcal{R} = \frac{[PIN]_1^{\text{steady}}}{[PIN]_0^{\text{steady}}} = \frac{k_{\text{on},1} k_{\text{off},0}}{k_{\text{on},0} k_{\text{off},1}}, \quad \mathcal{P} = \frac{W k_{\text{off},1}}{k_{\text{on},1}}. \tag{14}$$

212 The expressions (12–14) show that the steady gravitropic response is proportional to  $(\mathcal{R} - 1)(S_1^r - S_1^l)$ .  
 213 For  $\theta > 0$  as in figure 1, the difference  $(S_1^r - S_1^l)$  is positive since statoliths sediment toward the right  
 214 side of the cell. Therefore, to obtain a ‘normal’ gravitropic response ( $\tilde{\Delta}^{\text{steady}} > 0$ , i.e., a larger auxin  
 215 concentration at the bottom side of the shoot), the ratio  $\mathcal{R}$  must be larger than 1. The parameter  $\mathcal{R}$  is the  
 216 ratio between the concentration of PINs in a zone with statolith and in a zone without statolith, hence the  
 217 larger  $\mathcal{R}$ , the more PINs in the region with statoliths compared to region without statolith (see Fig 4C). The  
 218 other main parameter controlling the gravitropic response is the pool number  $\mathcal{P}$  characterizing the ratio of

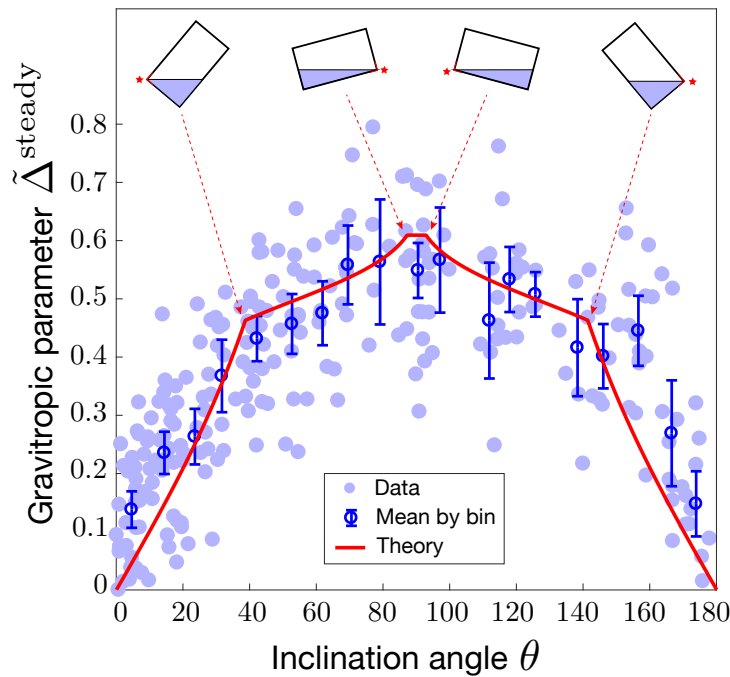


**Figure 6.** Steady gravitropic response  $\tilde{\Delta}^{\text{steady}}$  (arbitrary amplitude) as a function of the inclination angle  $\theta$ , for  $\mathcal{R}$  either large or close to 1, in the case of **(A)** infinite pool ( $\mathcal{P} \gg 1$ ), **(B)** limiting pool ( $\mathcal{P} \ll 1$ ) with apical/basal/lateral binding, **(C)** limiting pool ( $\mathcal{P} \ll 1$ ) with lateral binding only. Note that in the case of an infinite pool, results are the same in the a/b/l-binding or l-binding case. Geometrical parameters used are  $H_0 = 4d$ ,  $W = 10d$ ,  $H = 25d$  where  $d$  stands for the diameter of a statolith.

219 endocytosis to exocytosis, where  $\mathcal{P} \gg 1$  corresponds to the infinite-pool regime and  $\mathcal{P} \ll 1$  corresponds  
 220 to the limiting-pool regime (see Fig 4B).

221 Once  $\mathcal{R}$  and  $\mathcal{P}$  are set, the final step is to compute how the different surfaces covered (and not covered)  
 222 by the statoliths vary as function of the inclination angle  $\theta$ . To this end, one has to know the final position of  
 223 statoliths when a cell is tilted. Recently, we addressed this question and showed that statoliths at the bottom  
 224 of statocytes behave like an effective liquid on long timescale, due to the agitation of statoliths by the cell  
 225 activity (Bérut et al., 2018). Therefore, the final free surface of the statoliths pile is horizontal, as sketched  
 226 in figure 3. This key feature of the flowing behavior of statoliths allows us to reduce the computation of the  
 227 surfaces touched or not by the statoliths ( $S_{0,1}^{r,l}$ ,  $S_0$  and  $S_1$  in eqs. 12, 13) to a purely geometrical problem,  
 228 which depends on three parameters: the angle of inclination  $\theta$ , the aspect ratio of the cell  $H/W$  and the  
 229 initial aspect ratio of the statolith pile  $H_0/W$  (see Fig. 3). The corresponding relationships are given in  
 230 Appendix B.

231 Figure 6 presents the typical steady gravitropic response  $\tilde{\Delta}^{\text{steady}}(\theta)$  predicted by the model (eqs. 12, 13,  
 232 14) as a function of  $\theta$ , in the case of an infinite pool ( $\mathcal{P} \gg 1$ ) or a limiting pool ( $\mathcal{P} \ll 1$ ), and for two  
 233 extreme values of  $\mathcal{R}$ :  $\mathcal{R} \simeq 1$  (red curve, low influence of statoliths on PIN binding) and  $\mathcal{R} \gg 1$  (blue curve,  
 234 strong influence of statoliths on PIN binding). The geometry used for the cell aspect ratio and the statoliths  
 235 pile ratio is taken from experimental observations of wheat coleoptile statocytes, with a typical aspect ratio  
 236  $H/W = 2.5$  and  $H_0/W = 1/2.5$ . In the infinite pool regime (Fig. 6A), the gravitropic response presents  
 237 a convex shape with a strong peak close to  $90^\circ$  whatever the value of  $\mathcal{R}$ , in disagreement with the usual  
 238 sine-law shape. The amplitude of this peak in this regime also strongly depends on the cell geometry: the  
 239 more elongated the cell, the higher the peak because in this case more lateral surface is available for PIN  
 240 attachment without any PIN dilution (see Fig 4B). By contrast, in the limiting-pool regime (Fig. 6B,C),  
 241 the response strongly depends on  $\mathcal{R}$ , the peak at  $90^\circ$  being much smaller for  $\mathcal{R} \gg 1$  than for  $\mathcal{R} \simeq 1$ .  
 242 Interestingly, the response in this case also depends on whether PIN can attach on every sides of the cell  
 243 (apical/basal/lateral binding) or only on the lateral sides (lateral binding case), as attachment to the ‘useless’  
 244 apical and basal sides contribute to deplete PIN from the available pool. Overall, we see that only one  
 245 case is compatible with the concave ‘sine-law’ shape observed experimentally: a limiting pool of PIN with  
 246 lateral binding and  $\mathcal{R} \gg 1$  (blue curve in Fig. 6C).



**Figure 7.** Modified sine-law  $\tilde{\Delta}^{\text{steady}}$  as a function of the inclination angle  $\theta$ . Comparison between the model prediction for  $\mathcal{P} \ll 1$  (limiting pool) and l-binding (eq. 15 with  $\mathcal{R} = 25$  and  $\mathcal{A} = 1.3$ , red line) and experiments on wheat coleoptiles (symbols, Chauvet et al. (2016)). Geometrical parameters used in the model for the statocyte are  $H_0 = 4d$ ,  $W = 10d$ ,  $H = 25d$  where  $d$  stands for the diameter of a statolith. Error bars are the mean value of the data by binning the  $[0,180]$  interval into 20 boxes.

247 In the following, we thus assume that PIN recycling occurs in the limited-pool regime ( $\mathcal{P} \gg 1$ ), with  
 248 lateral binding only. In this limit, and using expression of the surfaces given in Appendix B, the steady  
 249 gravitropic response given by equations (12, 13, 14) can be written as:

$$\tilde{\Delta}^{\text{steady}}(\theta) = \frac{1}{2} \mathcal{A}(\mathcal{R} - 1) \begin{cases} \frac{W \tan \theta}{2H + 2(\mathcal{R} - 1)H_0} & \text{if } W \tan \theta < 2H_0 \\ \frac{\sqrt{2H_0 W \tan \theta}}{2H + (\mathcal{R} - 1)\sqrt{2H_0 W \tan \theta}} & \text{if } 2H_0 < W \tan \theta < H^2/(2H_0) \\ \frac{1}{\mathcal{R} + 1} & \text{else} \end{cases} \quad (15)$$

250 with  $\mathcal{A} = \frac{\alpha N_{\text{tot}} N}{\beta \int [ABC B]}$ . The different conditions stand for cases where statoliths are totally absent of the  
 251 left side, or totally covering the right side (see Fig. 7). Once the geometry of the cell and of the statoliths  
 252 pile are fixed, the predicted gravitropic response depends on two dimensionless parameters:  $\mathcal{R}$  and  $\mathcal{A}$ .  
 253 Figure 7 presents the experimental measurements of the ‘sine-law’ obtained by Chauvet et al. (2016) on  
 254 wheat coleoptiles, together with the best fit of the data using a least-square method. Reasonable agreement  
 255 between theory and experiments is obtained with  $\mathcal{R} \simeq 25$  (or larger values as the shape converges in this  
 256 case) and  $\mathcal{A} \simeq 1.3$ . It is interesting to note that within our position-sensor framework, the predicted steady  
 257 gravitropic response is not a simple ‘sine-law’, but rather a piece-wise curve with an overall concave shape.  
 258 This law is also not universal and can be affected by several anatomical and physiological properties, such  
 259 as the geometry of the cell  $H/W$ , the amount of statoliths  $H_0/W$ , or the molecular signaling machinery  
 260 (embedded in the parameters  $\mathcal{R}$  and  $\mathcal{A}$ ).

### 261 3.2 Transient gravitropic response: dose-response law

262 The previous results deal with the steady gravitropic response obtained when the gravity stimulus (the  
263 angle of inclination  $\theta$  of the plant) is permanent. We now turn to the study of the transient gravitropic  
264 response, i.e., when the system has not yet reached the steady state. This situation typically corresponds  
265 to ‘dose-response’ like experiments, in which the gravity stimulus is applied during a transient time  $\Delta T$   
266 only. Using such protocol on wheat coleoptiles, Chauvet et al. (2019) revealed the existence of an intrinsic  
267 ‘memory’ time  $\tau_{\text{memory}}$  in the gravitropic response. For  $\Delta T \gg \tau_{\text{memory}}$ , the response was constant and  
268 equal to the steady response  $\tilde{\Delta}^{\text{steady}}$ . However, for  $\Delta T \lesssim \tau_{\text{memory}}$ , the response was smaller and became  
269 proportional to  $\Delta T$  (Fig. 8). The memory time  $\tau_{\text{memory}} \sim 15$  min identified in these experiments was  
270 longer than the sedimentation time of statoliths ( $\sim 2$  min) but shorter than the growth timescale (hours). It thus  
271 reflects a temporal process in the gravitropic signaling pathway that remains to be identified. We address  
272 below this question in the framework of the model.

273 The set of equations (5)-(7) give a complete description of the transient gravitropic response (we assume  
274 that sedimentation of statoliths is fast enough that the surfaces in equation 7 can be computed from their  
275 equilibrium values – see Appendix B). Two different typical times control the dynamics:  $\tau_{\text{aux}}$ , describing  
276 the transport of auxin across the tissue of length  $2R$ , and  $\tau_{\text{PIN}}$ , describing the dynamics of PIN at molecular  
277 scale. The time scale associated to auxin transport  $\tau_{\text{aux}}$  can be estimated using equation (5) for a constant  
278 coefficient of diffusion  $\mathcal{D}$  and transport velocity  $v$  (i.e., PIN distribution). In this case, relaxation towards  
279 the stationary profile (eq. 8) is exponential and occurs on a time scale set by the inverse of the shortest  
280 non-vanishing eigen-mode of equation (5) (Mohsen and Baluch, 1983):

$$\tau_{\text{aux}} = \frac{1}{\pi^2 + (\text{Pe}^2/4)} \times \frac{(2R)^2}{\mathcal{D}} = \frac{1}{\pi^2 + (\text{Pe}^2/4)} \times \frac{(2R)\text{Pe}}{v} \quad (16)$$

281 Estimating the Peclet number from the steady gravitropic response ( $\text{Pe} = 2\tilde{\Delta}^{\text{steady}} \approx 1$ , see Fig. 7), and  
282 the auxin transport speed  $v$  from measurements of the speed of auxin pulses in plant tissues ( $v \simeq 3 \mu\text{m/s}$ ,  
283 Goldsmith (1977); Rashotte et al. (2003)), gives  $\tau_{\text{aux}} \simeq 30$  s (taking  $2R \sim 1$  mm). This is much shorter  
284 than the memory time  $\tau_{\text{memory}} \sim 15$  min evidenced in dose-response experiments, and even shorter than  
285 the statoliths sedimentation time. This suggests that the dynamics of the gravitropic response is controlled  
286 by  $\tau_{\text{PIN}}$ , rather than by the auxin diffusion time  $\tau_{\text{aux}}$ .

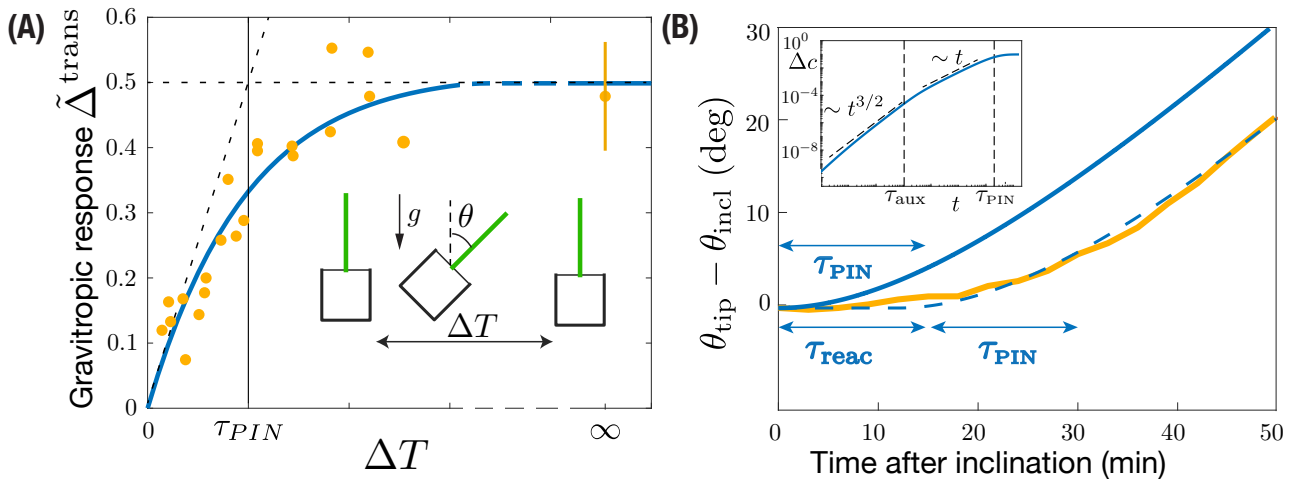
287 The time scale  $\tau_{\text{PIN}}$  is set by the slowest characteristic time of the system (eq. 7) describing PIN dynamics.  
288 From the eigenvalues of this linear system, two timescales are obtained, which are solutions of:

$$\begin{aligned} &\tau^{-2} - (k_{\text{off},0} + k_{\text{off},1} + [k_{\text{on},0}S_0 + k_{\text{on},1}S_1]/WS)\tau^{-1} \\ &+ (k_{\text{off},0} + k_{\text{on},0}S_0/WS)(k_{\text{off},1} + k_{\text{on},1}S_1/WS) - k_{\text{on},0}k_{\text{on},1}S_0S_1/W^2S^2 = 0. \end{aligned} \quad (17)$$

289 In the limiting pool case ( $WSk_{\text{off},i}/k_{\text{on},i}S_i \ll 1$ ), the two solutions are:

$$\tau_1 = \frac{WS}{k_{\text{on},0}S_0 + k_{\text{on},1}S_1} \quad \text{and} \quad \tau_2 = \frac{k_{\text{on},0}S_0 + k_{\text{on},1}S_1}{k_{\text{off},0}k_{\text{on},1}S_1 + k_{\text{off},1}k_{\text{on},0}S_0}, \quad (18)$$

290 with  $\tau_1 \ll \tau_2$ . Therefore, the slowest timescale of the gravitropic signaling pathway, which sets  $\tau_{\text{memory}}$ ,  
291 should be given by  $\tau_{\text{PIN}} = \tau_2$ . Note that when preferential attachment in region with statoliths is achieved via  
292 a strongly increased attachment rate ( $k_{\text{on},1} \gg k_{\text{on},0}$ ), and not by change of detachment rate ( $k_{\text{off},0} \simeq k_{\text{off},1}$ ),  
293 then  $\tau_{\text{PIN}} = k_{\text{off}}^{-1}$ . Conversely, if it is achieved by decreased detachment rate ( $k_{\text{off},0} \gg k_{\text{off},1}$ ) and not by



**Figure 8.** Gravitropic response to a transient inclination (dose-response like protocol). **(A)** Maximal gravitropic response reached during the dynamics as function of the inclination time  $\Delta T$  for  $\theta = 45^\circ$ . The blue solid line is the model prediction using  $\tau_{PIN} = 13$  min ( $\tau_{aux}/\tau_{PIN}$  and  $\tau_1/\tau_{PIN} \ll 1$ , other parameters are fixed as in Fig. 7). Symbols correspond to the aggregation results of (Chauvet et al., 2019) under  $1g$  and  $3g$ . **(B)** Evolution of the tip angle after an inclination  $\theta = 50^\circ$  predicted by the model with the same parameters (blue solid line) and in the experiments of Chauvet et al. (2016) (orange thick line). The predicted model must be shifted by a constant time  $\tau_{reac} = 13$  min to match the experimental curve (dashed blue line). Inset: early time behavior of the gravitropic response predicted by the model in log-log scale.

294 change of attachment rate ( $k_{on,0} \simeq k_{on,1}$ ), then  $\tau_{PIN} = k_{off,0}^{-1}(1 + S_1/S_0) \simeq k_{off,0}^{-1}$ . Remarkably, in this last  
 295 case, the equilibration time of PIN is not controlled by the slowest rate of detachment ( $k_{off,1}$ ), but by the  
 296 fastest one ( $k_{off,0}$ ), due to the limiting pool.

297 To check these predictions, we solve the model for a transient gravitropic stimulus that reproduces the  
 298 protocol of Chauvet et al. (2019). The inclination  $\theta$  is set to  $45^\circ$  for a transient time  $\Delta T$  and then put back  
 299 to zero, the gravitropic response being defined as the maximal auxin gradient reached during the dynamics:  
 300  $\tilde{\Delta}^{trans} = \text{MAX}[\frac{c_{bottom}(t) - c_{top}(t)}{2c_{mean}}]$ . Figure 8A compares the experimental data of Chauvet et al. (2019) with  
 301 the prediction of the model for  $\tau_{aux}/\tau_{PIN} \ll 1$ , using the parameters  $\mathcal{R}$  and  $\mathcal{A}$  already fixed by the steady  
 302 response (see Fig. 7). Good agreement is obtained using  $\tau_{PIN} = 13$  min as the only fitting parameter. This  
 303 result shows that  $\tau_{PIN}$  is playing the role of the memory time evidenced by the experiments of Chauvet et al.  
 304 (2019). If  $\Delta T \ll \tau_{PIN}$ , PIN transporters have not enough time to rearrange before the end of the stimulus,  
 305 and the response is weak. Conversely if  $\Delta T \gg \tau_{PIN}$ , PINs have time to rearrange and reach their steady  
 306 repartition before the end of the stimulus, and the response is maximal, similar to the one of a permanent  
 307 stimulus.

308 We finish our analysis by investigating the full temporal dynamics of the gravitropic response after a  
 309 sudden inclination  $\theta = 50^\circ$ . Figure 8B presents the time evolution of the shoot curvature  $\mathcal{C}(t)$  (or similarly  
 310  $\theta_{tip}(t)$  for small curvatures) predicted by the model for  $\tau_{PIN} = 13$  min (blue curve), together with the  
 311 experimental data of Chauvet et al. (2016) (yellow curve). The time scale of the curvature change  $\tau_{PIN}$  is  
 312 well captured by the model. However, to match the experiments, the model has to be shifted in time by a  
 313 constant time  $\tau_{reac} \approx 13$  min. Such delay or reaction time of the gravitropic response after the stimulus was  
 314 already noticed by Chauvet et al. (2019), but does not seem to be captured by the model. Actually, a careful  
 315 analysis of the temporal behavior of the model (assuming  $\tau_1 \ll \tau_{aux} \ll \tau_{PIN} = \tau_2$ ) shows that the auxin  
 316 gradient at early times increases as  $\Delta c \sim t^{3/2}$  (so that  $\mathcal{C} \propto \int_0^t \Delta c dt \propto t^{5/2}$ ) as long as  $t < \tau_{aux}$ , before

317 varying as  $\Delta c \sim t$  for  $\tau_{\text{aux}} < t < \tau_{\text{PIN}}$  (Inset of Fig. 8B). These scaling laws are thus not compatible with  
 318 a very flat initial response.

## 4 DISCUSSION

319 In this paper, we have derived a multi-scale model of plant gravitropism which links the different steps of  
 320 the gravitropic signaling pathway: (i) the initial intracellular perception of gravity by statoliths, (ii) the  
 321 transduction of this physical signal into a biochemical signal through the reorganization of PINs at the  
 322 membrane of statocytes, (iii) the intercellular signal transmission via auxin transport and (iv) asymmetric  
 323 organ growth. The main originality of the model lies in the mechanistic link we propose between the  
 324 statoliths position and the dynamics of PINs, based on the recent position-sensor hypothesis (Pouliquen  
 325 et al., 2017). This basic assumption coupled to auxin transport and growth in an idealized tissue made of a  
 326 one-dimensional array of cells recovers several major features of the gravitropic response of plants.

### 327 4.1 A new interpretation of the sine-law of plant gravitropism

328 The first main result concerns the steady gravitropic response to a permanent gravity stimulus,  $\tilde{\Delta}^{\text{steady}}(\theta)$ .  
 329 For many plants, this response takes the form of an inclination-dependent law with a sine-like shape, called  
 330 for this reason the sine-law (Sachs, 1887; Larsen, 1969; Iino et al., 1996; Galland, 2002; Dumais, 2013).  
 331 This sine-law has long been interpreted in terms of a force sensor mechanism, for the projected weight of the  
 332 statoliths on the lateral surface of the cell varies with the sine of the inclination angle (Audus, 1969; Barlow,  
 333 1995). However, recent experiments showing that the response is independent of the gravity intensity  
 334 have dismissed this force-sensing hypothesis, calling for a new interpretation of the sine law (Chauvet  
 335 et al., 2016; Pouliquen et al., 2017). A key result of the model is that it predicts an inclination-dependent  
 336 steady gravitropic response  $\tilde{\Delta}^{\text{steady}}(\theta)$  without invoking a force-based mechanism. In the model, the initial  
 337 gravitropic stimulus is the statoliths position at the cell membrane, not their weight. Since statoliths behave  
 338 on long time like a liquid (Bérut et al., 2018), their position in steady state is a purely geometrical cue,  
 339 which depends only on the cell inclination. As a result, the steady response predicted by the model depends  
 340 on the inclination but not on the gravity intensity, in agreement with the observations.

341 In the model, the actual shape of the gravitropic response  $\tilde{\Delta}^{\text{steady}}(\theta)$  is never a pure sine law. It depends  
 342 on several parameters, related either to geometric factors, such as the aspect ratios of the statocytes and of  
 343 the sedimented statoliths pile, or to molecular processes: intensity of coupling between statoliths position  
 344 and PINs through parameter  $\mathcal{R}$ ; ratio of endocytosis to exocytosis through parameter  $\mathcal{P}$ ; ratio between  
 345 the conductance of PIN carriers to the total conductance of auxin transporters through parameter  $\mathcal{A}$ . For  
 346 elongated cells and shallow statoliths piles such as those of wheat coleoptile statocytes, the shape of the  
 347 response tends to be sine-like only in the case of a strong coupling between the statoliths and PINs ( $\mathcal{R} \gg 1$ ),  
 348 and for a number of PINs conserved along the cell membrane (limiting pool regime,  $\mathcal{P} \ll 1$ ). This latter  
 349 assumption is common in models of auxin transport (Runions et al., 2014; Retzer et al., 2019), while the  
 350 strong coupling assumption is compatible with the large asymmetry in PINs localization observed upon  
 351 gravity stimulation (Friml et al., 2002; Harrison and Masson, 2008; Kleine-Vehn et al., 2010). Interestingly,  
 352 although gravity is absent from the model, the gravitropic response depends on the amount of statoliths  
 353 through the geometrical aspect ratio of the statoliths pile  $H_0/W$ . The model could thus account for previous  
 354 experiments using starch-less and starch-excess mutants, which showed a modified gravitropic response  
 355 when the number of statoliths is changed (Kiss et al., 1997; Vitha et al., 2007; Pouliquen et al., 2017).  
 356 Finally, it is worth noting that the model assumes that the statoliths form a static pile at the bottom of  
 357 the cell, while statoliths actually exhibit a dynamic and random agitation due to the interaction with the  
 358 cytoskeleton (Sack et al., 1986; Saito et al., 2005; Nakamura et al., 2011; Bérut et al., 2018). We might  
 359 expect this agitation to reduce the averaged contact time between the statoliths and the cell membrane,

360 thereby decreasing the coupling between statoliths and PINs. It would be interesting to extend the model in  
361 order to incorporate such effect of agitation on the gravitropic response. The model could then be compared  
362 with the behavior of agravitropic mutants in *Arabidopsis thaliana* like *sgr9*, whose weaker response is  
363 likely associated to an abnormally strong agitation of the statoliths (Nakamura et al., 2011).

364 Overall, our model suggests that the classical sine-law of plant gravitropism might not be universal, as its  
365 shape and amplitude could depend on several anatomical and physiological parameters. Full measurements  
366 of the gravitropic response of plants over a wide range of inclination are scarce and mostly performed on  
367 shoot coleoptiles. It would be interesting to perform systematic measurements of the sine-law on other  
368 plant organs (root, stem), to see if the shape of the sine-law is affected by different statocyte geometries  
369 and tissue organization.

#### 370 **4.2 The gravity-independent memory process in dose-response laws is likely** 371 **associated to PIN dynamics**

372 The second main result of our study concerns the gravitropic response to a transient gravity stimulus.  
373 For a sudden inclination applied at time  $t = 0$ , the model predicts that the response reaches the steady  
374 response  $\tilde{\Delta}^{\text{steady}}(\theta)$  only after a time large compared to a 'memory' timescale  $\tau_{\text{memory}}$ , corresponding to  
375 the slowest timescale introduced in the model. Therefore, when a stimulus is applied only during a transient  
376 time  $\Delta T < \tau_{\text{memory}}$ , a weaker gravitropic response is predicted, following a dose-response like law. In the  
377 model, the memory time is not associated with the sediment time of the statoliths, which is assumed to be  
378 much shorter than the other timescales of the gravitropic signaling pathway (a valid assumption for a gravity  
379 intensity like Earth gravity). Our model is therefore compatible with the recent experiments of Chauvet  
380 et al. (2019) performed on wheat coleoptiles, which show a dose-like behavior of the gravitropic response  
381 with a memory time  $\tau_{\text{memory}}$  independent of gravity. The model also provides the explicit origin of this  
382 memory process, which was postulated in Chauvet et al. (2019). In the model, two different processes can  
383 lead to the temporal filtration of the initial signal associated with statoliths position: auxin transport across  
384 the tissue and the dynamics of PIN turnover at the molecular scale. Our study suggests that the limiting  
385 process is actually controlled by PIN dynamics ( $\tau_{\text{memory}} = \tau_{\text{PIN}}$ ), auxin transport being too fast to account  
386 for the memory time measured experimentally ( $\sim 10\text{-}20$  min). Interestingly, visualization of the PIN3  
387 auxin efflux carrier in root columella cells after a sudden change in the gravity vector indicates a time scale  
388 of about 10 min for complete relocation (Friml et al., 2002), a duration very close to the memory time  
389 measured by (Chauvet et al., 2019). Although our model successfully captures the existence and origin  
390 of a gravity-independent memory process in the signaling pathway, it is not able to describe the delay  
391 time  $\tau_{\text{reaction}} \sim 10$  min observed between the application of the stimulus and the first gravitropic response  
392 (Chauvet et al., 2019). This delay may have different origins: the time needed to reorganize the cytoskeleton  
393 implied in the transport of PIN carriers, the time needed by a PIN to go from the pool towards the plasma  
394 membrane, or the time of incorporation of a PIN into the membrane. It is worth noting that a similar  
395 timescale of about 10 min was identified in the gravity-sensing columella cells for the internalization of  
396 PIN3 from the plasma membrane into vesicles (Kleine-Vehn et al., 2010). Further experiments combining  
397 a transient stimulus with pharmacological and genetic approaches would be needed to confirm the key role  
398 of the PIN turnover timescale in the gravitropic response. Besides, it would be interesting to see what is the  
399 influence of this hierarchy of time-scales on the response of a plant to oscillatory stimulus (e. g. wind) or  
400 on the dynamic competition between gravitropism and proprioception (Bastien et al., 2013).

#### 401 **4.3 Back to the statoliths/PIN coupling assumption**

402 We conclude by discussing the possible origin of the coupling between statoliths and PINs, which is  
403 at the core of our model. Although the respective roles of statoliths and PIN auxin transporters in plant



404 gravitropism are well established, the link between the two is still not clear (see Nakamura et al. (2019)  
 405 for a recent review of the possible molecular actors involved). In our model, we have used a very general  
 406 hypothesis for this coupling based on the recent finding that the relevant gravitropic stimulus is the statoliths  
 407 position inside the gravisensing cells (Chauvet et al., 2016; Pouliquen et al., 2017; Bérut et al., 2018).  
 408 We have postulated that statoliths in contact with the cell membrane bias the exocytosis and endocytosis  
 409 rate of PIN recycling, therefore inducing an asymmetry of PIN distribution when statoliths reposition  
 410 in response to plant inclination. Our results suggest that this interaction between PINs and statoliths is  
 411 strong, as large values of the parameter  $\mathcal{R}$  are needed to match the experimental gravitropic response.  
 412 This interaction between statoliths and PINs could involve a complex molecular pathway that remains  
 413 to be unveiled (Strohm et al., 2014). However, more direct mechanisms of interaction could occur. For  
 414 example, statoliths could modify PIN vesicle-mediated transportation to the membrane by modifying the  
 415 architecture of the actin cytoskeleton. Another possibility would be that internalization of PINs from the  
 416 membrane is reduced by the presence of statoliths, for example by simple steric effects. Indeed, direct  
 417 visualizations reveal a length scale of  $\sim 1 \mu\text{m}$  for the endosome formation, which is not far from statolith  
 418 size (Kleine-Vehn et al., 2010). Interestingly, such direct interaction of statoliths and the cytoskeleton  
 419 machinery was put forward as an explanation of gravitropism in rhizoids and protonemata, such as the  
 420 single-cell alga *Chara* (Sievers et al., 1996). A last possibility could be that PINs cluster in regions where  
 421 there is no statolith, while they do not cluster when statoliths are present. Indeed, for a conserved number  
 422 of PIN proteins, clustering reduces the efflux efficiency, as this diffusion process scales not linearly but  
 423 as the square-root of the number of carriers (Bénichou and Voituriez, 2014; Valet et al., 2019). Such a  
 424 clustering has been highlighted by Kleine-Vehn et al. (2011), but, to our knowledge, no comparison has  
 425 been done between regions of the membrane in contact or not in contact with statoliths. Further studies  
 426 would be needed to discriminate between these molecular mechanisms.

## CONFLICT OF INTEREST STATEMENT

427 The authors declare that the research was conducted in the absence of any commercial or financial  
 428 relationships that could be construed as a potential conflict of interest.

## AUTHOR CONTRIBUTIONS

429 N.L., O.P., and Y.F. designed research. N.L. built and analyzed the model with inputs from O.P. and Y.F.  
 430 N.L., O.P., and Y.F. wrote the paper..

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## APPENDIX A: CASE OF STATOLITHS ONLY PRESENT ON A RING

436 Let be a central region between  $l$  and  $2R - l$  with no statolith (and constant efflux rate  $P_0$ ). We can redo the  
 437 calculation leading to eq. (4) in this geometry. Clearly, equations will be similar in each region, with  $v = 0$  in  
 438 the central one. We have to take care to the continuity of the flux at the jonction of each regions. We can show  
 439 that  $J(l) = (P + \delta P)c(l^-) - P_0c(l^+)$  and  $J(2R - l) = P_0c((2R - l)^-) - Pc((2R - l)^+)$ . At steady state, we

440 thus get a jump of auxin concentration:  $c(l^+) = (P+\delta P)/P_0 c(l^-)$  and  $c((2R-l)^+) = P_0/P c((2R-l)^-)$ .  
 441 In the limit of small Peclet number, we thus get  $\Delta c/c = (P_0/P)(vl/\mathcal{D})$ .

**APPENDIX B: EXPRESSION OF THE GEOMETRIC PARAMETERS AS A FUNCTION OF  $\theta$**

We give here the value of the surfaces  $S_i^{r,l}(\theta)$  that are necessary to compute the Peclet number as a function of the angle (see eq. 15). As statoliths are solid, the shaded area in Fig. 3 is conserved and is thus equal to  $H_0W$ . We note  $\theta_1 = \arctan 2H_0/W$  the angle for which the horizontal level meets the lower left corner, and  $\theta_2 = \arctan H^2/(2H_0W)$  the one for which it meets the upper right one (we assume  $H_0 < H/2$ ). Elementary geometry calculations give:

$$S_0^l = \begin{cases} H - H_0 + \frac{W \tan \theta}{2} & \text{if } \theta < \theta_1 \\ H & \text{else} \end{cases} \tag{19}$$

$$S_1^l = \begin{cases} H_0 - \frac{W \tan \theta}{2} & \text{if } \theta < \theta_1 \\ 0 & \text{else} \end{cases} \tag{20}$$

$$S_0^r = \begin{cases} H - H_0 - \frac{W \tan \theta}{2} & \text{if } \theta < \theta_1 \\ H - \sqrt{2H_0W \tan \theta} & \text{if } \theta_1 < \theta < \theta_2 \\ 0 & \text{else} \end{cases} \tag{21}$$

$$S_1^r = \begin{cases} H_0 + \frac{W \tan \theta}{2} & \text{if } \theta < \theta_1 \\ \sqrt{2H_0W \tan \theta} & \text{if } \theta_1 < \theta < \theta_2 \\ H & \text{else} \end{cases} \tag{22}$$

In the case of apical binding, this leads to

$$S_0 = \begin{cases} 2(H - H_0) & \text{if } \theta < \theta_1 \\ 2H - \sqrt{2H_0W \tan \theta} & \text{if } \theta_1 < \theta < \theta_2 \\ H & \text{else} \end{cases} \tag{23}$$

$$S_1 = \begin{cases} 2H_0 & \text{if } \theta < \theta_1 \\ \sqrt{2H_0W \tan \theta} & \text{if } \theta_1 < \theta < \theta_2 \\ H & \text{else} \end{cases} \tag{24}$$

442 In the case of apical/basal/lateral binding, the expressions for the total surfaces are slightly modified due to  
 443 attachment at apical and basal side.

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Physical quantities	Definition	Unit
$R$	radius of the organ	(m)
$\mathcal{C}$	bending curvature of the organ	(m <sup>-1</sup> )
$W$	cell width	(m)
$w$	cell wall width	(m)
$H$	cell height	(m)
$H_0$	statolith pile height before inclination	(m)
$S$	cell lateral surface	(m <sup>2</sup> )
$S_{0,1}$	total surface of the cell not (0) or (1) in contact with statoliths	(m <sup>2</sup> )
$S_0^{l,r}$	surface of the left ( $l$ ) or right ( $r$ ) side of the cell not in contact with statoliths	(m <sup>2</sup> )
$S_1^{l,r}$	surface of the left ( $l$ ) or right ( $r$ ) side of the cell in contact with statoliths	(m <sup>2</sup> )
$\dot{\epsilon}$	growth rate	(s <sup>-1</sup> )
$\tau_g$	$\tau_g = \dot{\epsilon}_{\text{mean}}^{-1}$ growth timescale	(s)
$c$	auxin concentration inside the cell	(mol m <sup>-3</sup> )
$C$	auxin concentration in the cell wall	(mol m <sup>-3</sup> )
$P^{l,r}$	auxin efflux permeability of the left ( $l$ ) or right ( $r$ ) side of the cell	(m <sup>-1</sup> )
$P^{\text{in}}$	auxin influx permeability	(m <sup>-1</sup> )
$\alpha$	conductance of a single PIN carrier	(m <sup>3</sup> s <sup>-1</sup> )
$\beta$	conductance of a single ABCB carrier	(m <sup>3</sup> s <sup>-1</sup> )
$P$	$P = \frac{P^l + P^r}{2} = \frac{1}{S} \beta \int [ABCB]$	(m <sup>-1</sup> )
$\delta P$	$\delta P = P^r - P^l = \frac{1}{S} \left( \alpha \int_S [PIN]_{\text{right}} - \alpha \int_S [PIN]_{\text{left}} \right)$	(m <sup>-1</sup> )
$\mathcal{D}$	auxin coefficient of diffusion $\mathcal{D} = \frac{WP}{2}$	(m <sup>2</sup> s <sup>-1</sup> )
$v$	auxin advection speed $v = \frac{\delta P}{2}$	(m <sup>-1</sup> )
$k_{\text{off},0,1}$	endocytosis rate when statoliths are (1) or are not (0) in contact with the membrane	(s <sup>-1</sup> )
$k_{\text{on},0,1}$	exocytosis speed when statoliths are (1) or are not (0) in contact with the membrane	(m s <sup>-1</sup> )
$\tau_{\text{aux}}$	timescale for auxin transport across the tissue $\tau_{\text{aux}} = \frac{1}{\pi^2 + (\text{Pe}^2/4)} \times \frac{(2R)^2}{\mathcal{D}}$	(s)
$\tau_{\text{PIN}}$	timescale for PIN turnover $\tau_{\text{PIN}} = \frac{k_{\text{on},0}S_0 + k_{\text{on},1}S_1}{k_{\text{off},0}k_{\text{on},1}S_1 + k_{\text{off},1}k_{\text{on},0}S_0}$	(s)

**Table 1.** List of dimensional quantities in the model with their definition and unit.

Dimensionless parameters	Definition	Meaning
$\theta$		Inclination of the plant
$N$		Number of cells across the tissue
$N_{\text{tot}}$		Total number of PIN carriers per cell
$\tilde{\Delta}$	$\tilde{\Delta} = \frac{c_{\text{bottom}} - c_{\text{top}}}{2c_{\text{mean}}}$	Gravitropic response
$\text{Pe}$	$\text{Pe} = \frac{2Rw}{\mathcal{D}}$	Peclet number comparing auxin advection to diffusion
$\mathcal{A}$	$\mathcal{A} = \frac{\alpha N_{\text{tot}} N}{\beta \int [\text{ABCB}]}$	Effect of PIN conductance vs ABCB conductance on auxin transport
$\mathcal{R}$	$\mathcal{R} = \frac{[\text{PIN}]_1^{\text{steady}}}{[\text{PIN}]_0^{\text{steady}}} = \frac{k_{\text{on},1} k_{\text{off},0}}{k_{\text{on},0} k_{\text{off},1}}$	Intensity of statoliths/PINs coupling
$\mathcal{P}$	$\mathcal{P} = \frac{W k_{\text{off},1}}{k_{\text{on},1}}$	Ratio of endocytosis to exocytosis (pool number)

**Table 2.** List of the dimensionless parameters used in the model with their definition and meaning.