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Polar Auxin Transport in *Arabidopsis* Inflorescence Stems

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Contents

1 Introduction

This thesis is about the polar auxin transport in *Arabidopsis thaliana* inflorescence stems. It is made in collaboration with the Plant BioDynamics Laboratory in Leiden, where the experiments mentioned in this thesis were done.
In this thesis we investigate the inter- and intracellular transport of auxin. The reason for this is that we want to know more about how auxin is transported. Is this done by simple diffusion in the cell or is there active transport? Which transporters in the cell membrane play a role and what is their transport capacity? The problem with this is that the auxin molecule, indole-3-acetic acid, is very small and therefore not visible. It can't be made visible either, e.g. by labelling with a fluorescent protein.
Our attempt to learn more about this transport in *Arabidopsis thaliana* is to look at auxin at a macroscopic level. This is possible by making the auxin radioactive. It is not as accurate as looking at visible molecules, but it is accurate enough for this macroscopic level. With modelling we try to fit the obtained experimental results. Assumptions will be made and tested in this thesis by this modelling.
One of the most elaborate articles about this subject is that of G.J. Mitchison, [8], dating back to the 1980s. In the following three decades the mathematical modelling of polar auxin transport in stem segments seems to have stalled. Research seems to have shifted to the molecular biology of the system, with a few exceptions, [3, 5]. This article was used as a starting point and improved at the Plant BioDynamics Laboratory. This thesis is a sub-question of the research that is being done there.
This thesis will differ from most other mathematical theses, because of the biological nature of the subject. As such it is located in the field of mathematical biology. It is meant to be readable for both mathematicians and experimental biologists with some mathematical training.

2 Underlying Information

2.1 Biology

Arabidopsis thaliana is a small flowering plant that, like any other plant, transports auxin, indole-3-acetic acid (IAA), through it's tissue. Auxin is a phytohormone that regulates growth, rates of cell expansion and rates of cell division and establishment and maintenance of pattern during growth and development, like a morphogen, [2, 7]. In this thesis we will look at auxin as a molecule and its function is not relevant.
The transport of auxin is confined to transport channels. One transport channel consists of a single file of cells with an apoplast between every two adjacent cells. In the stem there are around 10 vascular bundles. The cross-sectional area of the stem is around $3,7 \times 10^{-7}$ m^2 of which $0,7 \times 10^{-7}$ m^2 consists of vascular bundles. Around 20 to 30 percent of this area of vascular bundles is expected to consist of transport channels.
IAA is a weak acid, with acidity constant $\mathrm{pK}_a = 4.8$. Thus it is present both in protonated form (IAAH) and anion form (IAA^-) at the same time. In the cell membrane we have PIN-transporters and AUX-transporters to transport IAA through the membrane. PIN-transporters hypothetically transport IAA^- out of the cell and AUX-transporters transport IAA^- into the cell. PIN-transporters are mainly located in the membrane at the basal end of the cell and AUX-transporters are equally distributed across the membrane. The protonated form can only diffuse through the membrane. The different forms of transport are assumed to be linear in the concentration of the solute they transport. That is, we assume that the concentrations if IAA are such that transport rates are in the linear regime. No saturation effect needs to be taken into account.
The fraction of IAA in each form are pH-dependent and can be computed from the Henderson-Hasselbalch equation:

$$\mathrm{pH} = \mathrm{pK}_a + \log_{10} \frac{[A^-]}{[HA]}.$$

The fraction of IAA in anion form as function of pH is then given by

$$f = \frac{1}{1 + 10^{\mathrm{pK}_a - \mathrm{pH}}}.$$

pH	fraction anion	fraction protonated
4	0.1368	0.8632
5	0.6131	0.3869
7	0.9937	0.0063

We assume that the acidity in the cytoplasm and apoplast is buffered and therefore constant. The fraction of auxin in anion form is in a chemical equilibrium. The constant acidity dictates then that the fraction of anion auxin is a constant, f_a for the apoplast and f_c for the cytoplasm of all cells.

There are no known carriers that can transport IAA in either form into a vacuole and it is not likely to go in there by itself either, so the transport of IAA within the cell is exclusively through the cytoplasm.

2.2 Experimental Set-up(s) and Results

Indole-3-acetic acid (IAA) is a small molecule and therefore it is not visible. It can't be made fluorescent either yet. So in the experiments, done in the Plant BioDynamics Laboratory in Leiden, tritium labelled IAA (^{3}H-IAA) is used, so the radioactivity can be measured in order to determine the total amount of auxin in different sections of plant tissue. The tritium is located in the indole ring. (See Figure 1)

Another possibility is using ^{14}C labelled IAA. However, the carbon is typically located in the COOH part of the auxin molecule. (See Figure 1) This part can be split off, so this is not as accurate as tritium, which is in one of the rings and can't be cut off, since not only the radioactivity of the ^{14}C attached to the auxin is measured, but also the radioactivity of the ^{14}C that has been cut off.

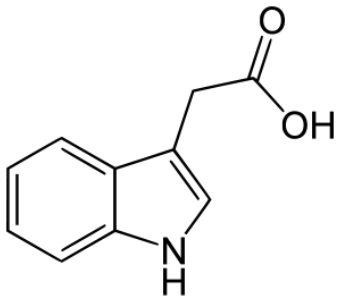


Figure 1: IAA-molecule structure.

Petri dishes filled with molten paraffin, in which grooves between a donor well and receiver well were cut, were used for the experiments. The grooves had a length of 16 mm and in each groove a 16 mm inflorescence stem of the *Arabidopsis* was placed, with the apical side of the stem at the donor well. In the donor well the tritium labelled IAA is added with a concentration of 1×10^{-7} M. The receiver well is filled with neutral buffer and is emptied regularly at relatively short time intervals during the experiments, so the concentration of IAA (tritium labelled and unlabelled) in the receiver well can be considered to remain approximately 0 M during the experiment. The total amount of ^{3}H-IAA taken from the receiver well is measured over time and after 600 minutes the stem is cut in 4 parts of 4 mm and the amount of ^{3}H-IAA in each part is measured.

An example of results of such experiments is shown in Figures 2 and 3. From the slope of the asymptote as $t \to \infty$ in Figure 2 we conclude that that the steady state transport rate of IAA through the stem segment is approximately 9×10^{-3} fmol/s.

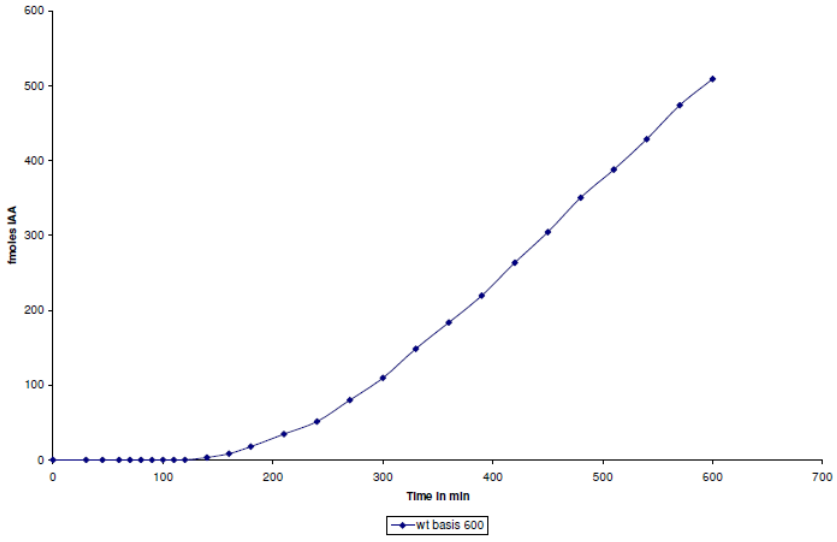


Figure 2: The total cumulative amount of auxin that reached the receiver well as function of time.

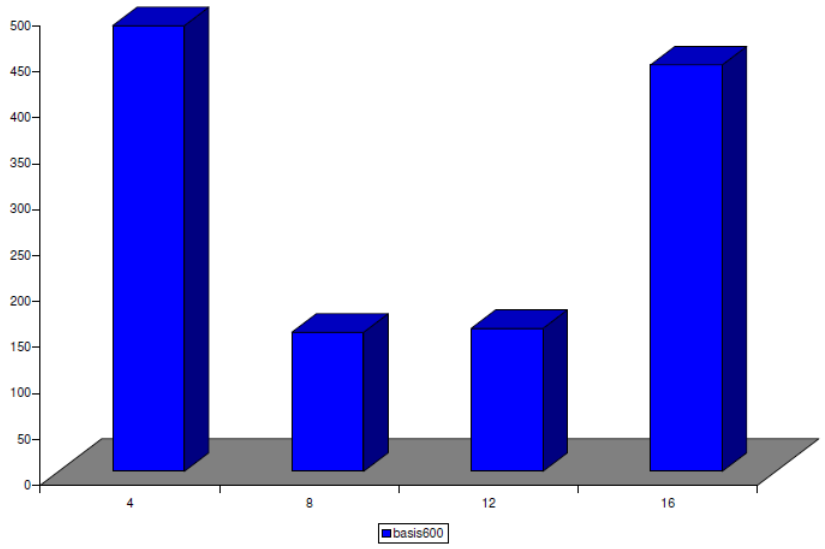


Figure 3: The steady state profile of the total amount of auxin in fmol measured in 4 mm long quarters of the stem.

3 Preparations: Cellular Level Models

It is convenient to do some preparations on cellular level before we continue modelling the entire system.

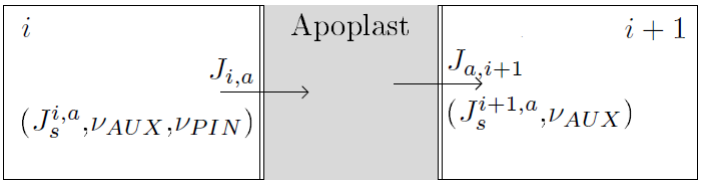
3.1 Effective Number Flux between Adjacent Cells

Between every two cells there is an apoplast. To find an expression for the effective number flux of auxin between cell i and cell $i+1$, we first have to examine the number fluxes between cell i and the apoplast and between the apoplast and cell $i+1$. With the assumption that auxin is homogeneously distributed near the membranes 'connecting' two cells, with the apoplast in between and that the auxin concentration in the apoplast is in quasi-steady state, we can derive the following expressions:

$$\begin{aligned}
\nu_{AUX}(C_a) &= \hat{P}_{in} A f_a C_a \\
\nu_{PIN}(C_i) &= \hat{P}_{ex} A f_c C_i \\
J_s^{i,a}(C_i, C_a) &= \hat{P}_s A(1-f_c) C_i - \hat{P}_s A(1-f_a) C_a \\
&= \hat{P}_s A(1-f_c)\left(C_i - \frac{1-f_a}{1-f_c} C_a\right) \\
J_s^{a,i+1}(C_{i+1}, C_a) &= -\hat{P}_s A(1-f_c)\left(C_{i+1} - \frac{1-f_a}{1-f_c} C_a\right)
\end{aligned}$$

where ν_{AUX}, ν_{PIN}, $J_s^{i,a}$, $J_s^{a,i+1}$ are the number fluxes of the AUX transporters, PIN transporters, diffusion over the left membrane and diffusion over the right membrane respectively, (recall that transport rates were assumed to be in the linear regime),
C_i, C_a, C_{i+1} are the total concentration of auxin (anion and protonated auxin) in cell i, the apoplast and cell $i+1$ respectively, the first and last close to the membrane,
A is the area of the connecting cell membrane,
$\hat{P}_{in}$, $\hat{P}_{ex}$, $\hat{P}_s$ are the effective permeabilities by means of the AUX transporters, PIN transporters and simple diffusion respectively dependent only in the form of auxin they transport, i.e. anion or protonated form.
Let $J_{i,a}(C_i, C_a)$ and $J_{a,i+1}(C_{i+1}, C_a)$ be the total number flux of auxin over the membrane from cell i to the apoplast and from the apoplast to cell $i+1$ respectively, then

$$\begin{aligned}
J_{i,a}(C_i, C_a) &= J_s^{i,a}(C_i, C_a) + \nu_{PIN}(C_i) - \nu_{AUX}(C_a) \\
&= \hat{P}_s A(1-f_c)\left(C_i - \frac{1-f_a}{1-f_c} C_a\right) + \hat{P}_{ex} A f_c C_i - \hat{P}_{in} A f_a C_a \\
J_{a,i+1}(C_{i+1}, C_a) &= \nu_{AUX}(C_a) + J_s^{a,i+1}(C_{i+1}, C_a) \\
&= \hat{P}_{in} A f_a C_a - \hat{P}_s A(1-f_c)\left(C_{i+1} - \frac{1-f_a}{1-f_c} C_a\right)
\end{aligned}$$



The assumption is made that C_a is in quasi-steady state, $C_a^\star$. From this follows

$$\begin{aligned}
J_{i,a}(C_i, C_a^\star) &= J_{a,i+1}(C_{i+1}, C_a^\star) \\
\hat{P}_s A(1-f_c)\left(C_i - \frac{1-f_a}{1-f_c}C_a^\star\right) & \\
+\hat{P}_{ex} A f_c C_i - \hat{P}_{in} A f_a C_a^\star &= \hat{P}_{in} A f_a C_a^\star \\
& \quad -\hat{P}_s A(1-f_c)\left(C_{i+1} - \frac{1-f_a}{1-f_c}C_a^\star\right) \\
\hat{P}_s A(1-f_c)(C_i + C_{i+1}) + \hat{P}_{ex} A f_c C_i &= 2\hat{P}_{in} A f_a C_a^\star + 2\hat{P}_s A(1-f_a) C_a^\star \\
\hat{P}_s(1-f_c)(C_i + C_{i+1}) + \hat{P}_{ex} f_c C_i &= (2\hat{P}_{in} f_a + 2\hat{P}_s(1-f_a)) C_a^\star \\
C_a^\star &= \frac{\hat{P}_s(1-f_c)(C_i + C_{i+1}) + \hat{P}_{ex} f_c C_i}{2\hat{P}_{in} f_a + 2\hat{P}_s(1-f_a)}
\end{aligned}$$

Define

$$\begin{aligned}
P_s &:= \hat{P}_s(1-f_c) \\
P_{in} &:= \hat{P}_{in} f_a \\
P_{ex} &:= \hat{P}_{ex} f_c \\
\tilde{R} &:= \frac{1-f_a}{1-f_c},
\end{aligned}$$

then we get

$$C_a^\star = \frac{P_s(C_i + C_{i+1}) + P_{ex} C_i}{2P_{in} + 2P_s \tilde{R}}.$$

Since our quasi-steady state assumption implies that

$$J_{i,a}(C_i, C_a^\star) = J_{a,i+1}(C_{i+1}, C_a^\star)$$

we can define $J_{i,i+1} := J_{i,a}(C_i, C_a^\star) = J_{a,i+1}(C_{i+1}, C_a^\star)$ as the total number flux of auxin between cell i and $i+1$.

We get

$$\begin{aligned}
J_{i,i+1} &= J_{i,a}(C_i, C_a^\star) \\
&= \hat{P}_s A(1-f_c)\left(C_i - \frac{1-f_a}{1-f_c}C_a^\star\right) + \hat{P}_{ex}Af_cC_i - \hat{P}_{in}Af_aC_a^\star \\
&= P_sA(C_i - \tilde{R}C_a^\star) + P_{ex}AC_i - P_{in}AC_a^\star \\
&= P_sA\left(C_i - \tilde{R}\frac{P_s\,(C_i + C_{i+1}) + P_{ex}C_i}{2P_{in} + 2P_s\tilde{R}}\right) + P_{ex}AC_i \\
&\quad -P_{in}A\frac{P_s\,(C_i + C_{i+1}) + P_{ex}C_i}{2P_{in} + 2P_s\tilde{R}} \\
&= \frac{1}{2P_{in}+2P_s\tilde{R}}[(2P_{in}+2P_sR)P_sAC_i - P_sA\tilde{R}(P_s(C_i+C_{i+1})+P_{ex}C_i) \\
&\quad +(2P_{in} + 2P_s\tilde{R})P_{ex}AC_i - P_{in}A(P_s(C_i + C_{i+1}) + P_{ex}C_i)] \\
&= \frac{A}{2P_{in} + 2P_s\tilde{R}}[(P_s^2\tilde{R}) + P_sP_{in} + P_sP_{ex}\tilde{R} + P_{in}P_{ex})C_i \\
&\quad -(P_s^2\tilde{R} + P_sP_{in})C_{i+1})] \\
&= \frac{A}{2P_{in} + 2P_s\tilde{R}}[(P_{in} + P_s\tilde{R})(P_s + P_{ex})C_i - (P_{in} + P_s\tilde{R})P_sC_{i+1}] \\
&= \frac{1}{2}P_sA\left[\frac{P_s + P_{ex}}{P_s}C_i - C_{i+1}\right] \\
&= -PA(C_{i+1} - RC_i),
\end{aligned}$$

where

$$\begin{aligned}
P &= \frac{1}{2}P_s \\
&= \frac{1}{2}\hat{P}_s(1-f_c)
\end{aligned}$$

and

$$\begin{aligned}
R &= \frac{P_s + P_{ex}}{P_s} \\
&= 1 + \frac{\hat{P}_{ex}f_c}{\hat{P}_s(1-f_c)}.
\end{aligned}$$

Mitchison, [8], assumes the expression

$$J_{i,i+1} = pC_i + q(C_i - C_{i+1})$$

for these fluxes. Thus,

$$q = PA, \qquad p = PA(R-1).$$

Since the values of P and R may not be the same at the beginning and end of the stem, e.g. due to damage to cells caused by cutting process, we get

$$\begin{aligned} J_{i,i+1} &= -\frac{1}{2}P_s A\left(C_{i+1} - \frac{P_s + P_{ex}}{P_s}C_i\right) \\ &= -PA(C_{i+1} - RC_i), \qquad i \in \{1, 2, \ldots, N-1\} \\ J_{in} &= -P_{in}A(C_1 - R_{in}C_d) \\ J_{out} &= -P_{out}A(C_r - R_{out}C_N) \\ &\overset{C_r=0}{=} P_{out}R_{out}AC_N \end{aligned} \tag{1}$$

where C_d is the concentration of auxin in the donor well and C_r the concentration in the receiver well.
Note that this last P_{in} is not the same P_{in} as used before. The $P_{in} = \hat{P}_{in}f_a$ will not return, since our expressions of $J_{i,i+1}$, J_{in} and J_{out} are not dependent of this P_{in}, so from now on every P_{in} will be the one as in (1).

3.2 Intracellular Transport

Diffusion is in all directions and not just in one. We have to deal with the three dimensions of the cells. Assume that the cells are cylindrical, with a cylindrical vacuole in the middle. Let l be the length of one cell, $l - 2\delta$ $(0 < \delta < \frac{l}{2})$ the length of the vacuole, R the radius of the cells and $R - d(x)$ the radius of the vacuoles at point x in the cell. From this follows that the non-vacuole part of the radius equals $R - (R - d(x)) = d(x)$. Let $A(x)$ be the cross section of the cytoplasm at x, i.e. $A(x) = \{(x, y, z) | R - d(x) < \sqrt{y^2 + z^2} < R\}$.

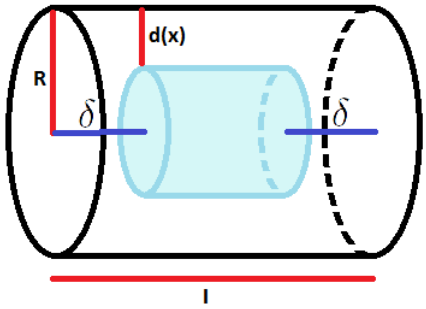


Figure 4: The mathematical abstraction of a cell in a transport channel of *Arabidopsis*.

Let $C_i(x, y, z, t)$ be the concentration of auxin in cell i in point (x, y, z) at time t. A change to cylindrical coördinates is convenient:

$$\tilde{C}_i(x, r, \theta, t) = C_i(x, y, z, t)$$

The cylinder is invariant under rotation around the x-axis, so if the flux of auxin over the boundaries is rotationally symmetric, then $\tilde{C}_i$ is independent of θ:

$$\hat{C}_i(x, r, t) = \tilde{C}_i(x, r, \theta, t)$$

Now we can simplify our three-dimensional cell to a two-dimensional cell (see figure 5).

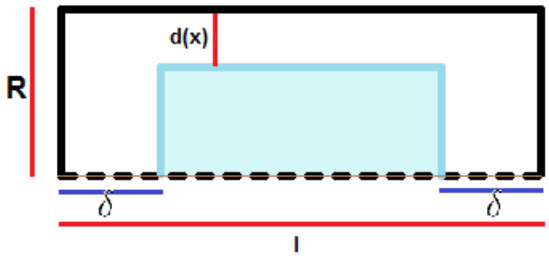


Figure 5: The two-dimensional simplification of the three-dimensional geometry presented in Figure 4 given that the concentration of auxin within the cells is independent of θ.

We assume that there is no flux through the lateral area of the cell membrane and no flux through the vacuole membrane. From this assumptions we get that

$$\frac{\partial \hat{C}_i}{\partial r}(R - d(x)) = 0 \quad \text{and} \quad \frac{\partial \hat{C}_i}{\partial r}(R) = 0. \tag{2}$$

Figure 6 illustrates this.

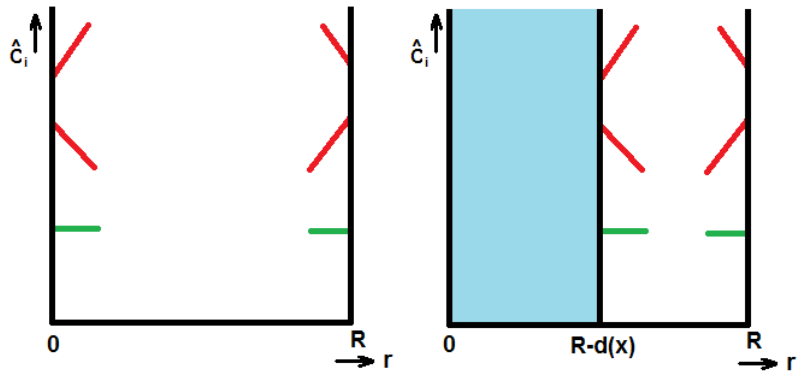


Figure 6: The independency of θ yields that $\frac{\partial \hat{C}_i}{\partial r}(0) = \frac{\partial \hat{C}_i}{\partial r}(R - d(x)) = 0$ for $0 < x < \delta$ and $l - \delta < x < l$ (left figure). The absence of flux through both the lateral area of the cell membrane and vacuole membrane yield that $\frac{\partial \hat{C}_i}{\partial r}(R - d(x)) = 0$ for $\delta < x < l - \delta$ (right figure) and $\frac{\partial \hat{C}_i}{\partial r}(R) = 0$ (both left and right figure).

We define the longitudinal density of total IAA as

$$\begin{aligned} u_i(x,t) &:= \iint_{A(x)} C_i(x,y,z,t)\ dydz \\ &= \iint_{A(x)} \hat{C}_i(x,r,t)\ dydz \\ &= \int_0^R \int_0^{2\pi} \hat{C}_i(x,r,t) r\ d\theta dr \\ &= \int_0^R 2\pi \hat{C}_i(x,r,t) r\ dr \\ &\overset{\star}{=} 2\pi \int_{R-d(x)}^R \hat{C}_i(x,r,t) r\ dr. \end{aligned}$$

$\star$: *There is no auxin in the vacuole.*

For intracellular diffusion we know

$$\frac{\partial \hat{C}_i}{\partial t} = D\left(\frac{\partial^2 \hat{C}_i}{\partial x^2} + \frac{\partial^2 \hat{C}_i}{\partial r^2} + \frac{1}{r}\frac{\partial \hat{C}_i}{\partial r}\right),$$

where D is the effective diffusivity, so for intracellular diffusion we get

$$\begin{aligned}
\frac{\partial u_i}{\partial t} &= 2\pi \int_{R-d(x)}^{R} \frac{\partial \hat{C}_i}{\partial t} r \; dr \\
&= 2\pi \int_{R-d(x)}^{R} D \left(\frac{\partial^2 \hat{C}_i}{\partial x^2} + \frac{\partial^2 \hat{C}_i}{\partial r^2} + \frac{1}{r} \frac{\partial \hat{C}_i}{\partial r} \right) r \; dr \\
&= 2\pi D \left(\int_{R-d(x)}^{R} \frac{\partial^2 \hat{C}_i}{\partial x^2} r \; dr + \underbrace{\int_{R-d(x)}^{R} \frac{\partial^2 \hat{C}_i}{\partial r^2} r \; dr}_{(\&)} + \int_{R-d(x)}^{R} \frac{\partial \hat{C}_i}{\partial r} \; dr \right),
\end{aligned}$$

where

$$\begin{aligned}
(\&) &= \left[\frac{\partial \hat{C}_i}{\partial r} r \right]_{R-d(x)}^{R} - \int_{R-d(x)}^{R} \frac{\partial \hat{C}_i}{\partial r} \; dr \\
&\overset{(2)}{=} - \int_{R-d(x)}^{R} \frac{\partial \hat{C}_i}{\partial r} \; dr.
\end{aligned}$$

So

$$\begin{aligned}
\frac{\partial u_i}{\partial t} &= 2\pi D \int_{R-d(x)}^{R} \frac{\partial^2 \hat{C}_i}{\partial x^2} r \; dr \\
&= D \frac{\partial^2}{\partial x^2} \left(2\pi \int_{R-d(x)}^{R} \hat{C}_i(x, r, t) r \; dr \right) \\
&= D \frac{\partial^2 u_i}{\partial x^2}. \qquad (3)
\end{aligned}$$

For intracellular diffusion and active transport in longitudinal direction we know

$$\frac{\partial \hat{C}_i}{\partial t} = D \left(\frac{\partial^2 \hat{C}_i}{\partial x^2} + \frac{\partial^2 \hat{C}_i}{\partial r^2} + \frac{1}{r} \frac{\partial \hat{C}_i}{\partial r} \right) - \mathbf{v} \nabla C_i,$$

where $\mathbf{v}$ is the transport velocity vector field, but we don't know anything about the $\mathbf{v}$-field. There may be active transport within the cell, as there should be in large (5 cm) *Chara* and *Nitella* cells, [2, 9]. The precise mechanism there is not yet known, nor is there particular evidence that such transport exists in the much smaller *Arabidopsis* transport cells (~ 100 μm). In order to be able to proceed investigations, we make the simplest imaginable phenomenological modification of (3) that effectively includes active transport, namely

$$\frac{\partial u_i}{\partial t} = D \frac{\partial^2 u_i}{\partial x^2} - v \frac{\partial u_i}{\partial x}. \qquad (4)$$

Now we have one-dimensional equations for the auxin transport within the cells by intracellular diffusion only and for transport within the cells for both intracellular diffusion and active transport.

4 Cell Array Models

Now we have made the necessary preparations we will proceed with modelling the entire system. This entire system consist of an array of cells.

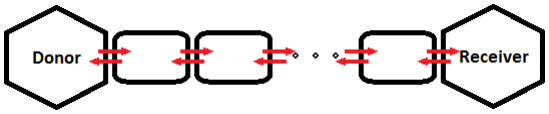


Figure 7: Cartoon of the experimental set-up.

4.1 Fast Homogenization within Cells

As a first and easiest approach we assume that the concentration of auxin will be equally distributed within the cells very fast. This assumption might not be realistic, because the transport within the cell might not be so fast that the concentration can be considered homogeneous at all times. When you assume homogeneity every molecule of auxin effects the concentration everywhere in the cell and so the length of the cells doesn't play any role in the intracellular transport velocity when this assumption is made. However when the total number of cells will become very large, the length of the cells will become very small. In this case the transport can be considered to be instantaneous, since both ends of the cells are very close to each other. This approximates a situation where there is fast homogenization within the cells and thus this might give some useful results.
With the expressions of number fluxes and the assumption of fast homogenization within the cells the change of the concentration in time for each cell can now easily be described. We get

$$\begin{aligned}
\frac{dC_i}{dt} &= \frac{J_{i-1,i}}{V} - \frac{J_{i,i+1}}{V} \\
&= \frac{J_{i-1,i} - J_{i,i+1}}{V}, \qquad i \in \{2, 3, \ldots, N-1\} \\
\frac{dC_1}{dt} &= \frac{J_{in} - J_{1,2}}{V} \\
\frac{dC_N}{dt} &= \frac{J_{N-1,N} - J_{out}}{V}
\end{aligned}$$

where V is the volume of the cell.
Substituting (1) gives us the change of concentration in time for each cell:

$$\begin{aligned}
\frac{dC_i}{dt} &= \frac{-PA(C_i - RC_{i-1}) + PA(C_{i+1} - RC_i)}{V}, \qquad i \in \{2, 3, \ldots, N-1\} \\
\frac{dC_1}{dt} &= \frac{-P_{in}A(C_1 - R_{in}C_d) + PA(C_2 - RC_1)}{V} \\
\frac{dC_N}{dt} &= \frac{-PA(C_N - RC_{N-1}) + P_{out}R_{out}AC_N)}{V}
\end{aligned} \tag{5}$$

A simulation in Matlab gives the results in Figure 8. Parameter values were taken as described in Appendix A.
As you can see in Figure 8 the stem fills up very fast. This is the effect of the

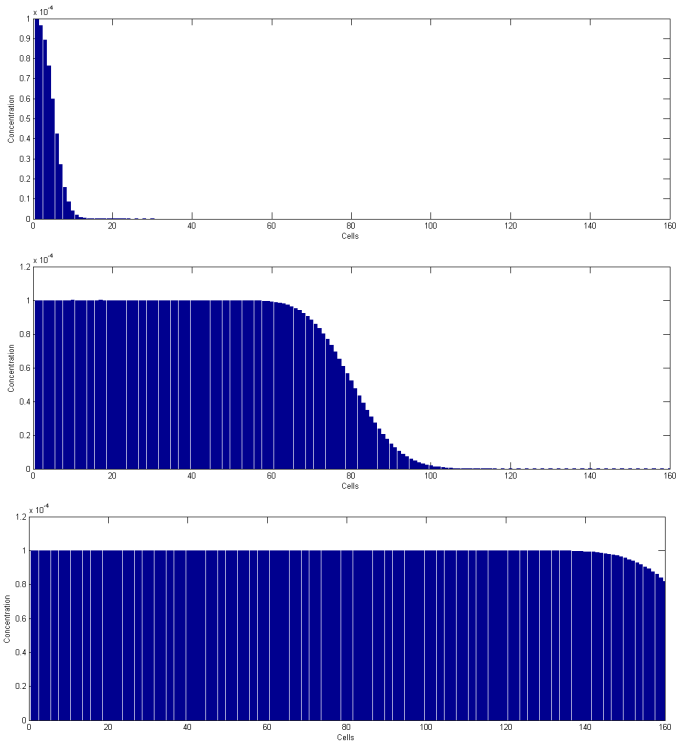


Figure 8: Concentration of auxin in mol in the cells of the stem at t=20 (upper figure), t=200 (middle figure) and t=400(bottom figure).

instantaneous transport of auxin within the cells. This is too fast to match the experiment. We will make a continuum approximation of the cell array model in Section 4.3.
To assess the validity of the homogenization assumption, we shall consider the case of intracellular diffusion and active transport.

4.2 A Model with Intracellular Diffusion and Active Transport

When there is no equal distribution of auxin within the cells the concentration of the apical end of the cells can differ from the concentration on the basal end of the cell. Modifying (5) to this case gives

$$\begin{aligned}
\frac{dC_i}{dt} &= \frac{-PA(C_i^a - RC_{i-1}^b) + PA(C_{i+1}^a - RC_i^b)}{V}, \qquad i \in \{2, 3, \ldots, N-1\} \\
\frac{dC_1}{dt} &= \frac{-P_{in}A(C_1^a - R_{in}C_d) + PA(C_2^a - RC_1^b)}{V} \\
\frac{dC_N}{dt} &= \frac{-PA(C_N^a - RC_{N-1}^b) + P_{out}R_{out}AC_N^b}{V},
\end{aligned}$$

where C_i^a and C_i^b are the concentrations at the apical end of the cell and the basal end of the cell respectively.
By definition we have

$$\begin{aligned}
C_i(t) &= \frac{1}{V}\int_0^l u_i(x,t)\ dx \\
C_i^a(t) &= \frac{u_i(0,t)}{A} \\
C_i^b(t) &= \frac{u_i(l,t)}{A}.
\end{aligned}$$

Within the cells we have (4). It follows that

$$\frac{1}{V}\int_0^l D\frac{\partial^2 u_i}{\partial x^2} - v\frac{\partial u_i}{\partial x}\ dx = \frac{-P(u_i(0,t) - Ru_{i-1}(l,t)) + P(u_{i+1}(0,t) - Ru_i(l,t))}{V}.$$

Modifying (1) to this case gives

$$\begin{aligned}
J_{i,i+1} &= -P(u_{i+1}(0) - Ru_i(l)), \qquad i \in \{1, 2, \ldots, N-1\} \\
J_{in} &= -P_{in}(u_1(0) - R_{in}AC_d) \\
J_{out} &= P_{out}R_{out}u_N(l). \qquad (6)
\end{aligned}$$

We get

$$\begin{aligned}
\frac{\partial u_i}{\partial t}(0,t) &= J_{i-1,i} - \left(-D\frac{\partial u_i}{\partial x}(0,t) + vu_i(0,t)\right) \\
\frac{\partial u_i}{\partial t}(l,t) &= -D\frac{\partial u_i}{\partial x}(0,t) + vu_i(0,t) - J_{i,i+1}.
\end{aligned}$$

Simulating this is not as easy as when auxin is equally distributed within the cells, because in this case we have a concatenation of partial differential equations. Numerical simulation was not within the scope of this thesis. Instead we consider the steady state solution of these these cases, that can be approached analytically. See Chapter 5.

4.3 A Continuum Approximation for fast Homogenization

With the previous derivatives we can examine how the model works with a large number of cells in a fixed macroscopic stem length (i.e. small length of the cells). When the cells become very small the model approaches a continuum. We expect an equation of the form

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} - v\frac{\partial u}{\partial x} \tag{7}$$

where D is the effective diffusivity constant and v the velocity.
Rewriting (5) gives

$$\begin{aligned}
\frac{dC_i}{dt} &= \frac{-PA(C_i - RC_{i-1}) + PA(C_{i+1} - RC_i)}{V} \\
&= \frac{PA}{V}(RC_{i-1} - (1+R)C_i + C_{i+1}) \\
&= \frac{PA}{V}([RC_{i+1} - 2RC_i + RC_{i-1}] + [(1-R)C_{i+1} + (R-1)C_i]) \\
&= \frac{PAR}{V}\Delta x^2\left[\frac{C_{i+1} - 2C_i + C_{i-1}}{\Delta x^2}\right] + \frac{PA(1-R)}{V}\Delta x\left[\frac{C_{i+1} - C_i}{\Delta x}\right] \qquad (8)
\end{aligned}$$

where Δx is the length of the cells.
When $N \to \infty$ (i.e. $\Delta x \to 0$) then, formally,

$$\begin{aligned}
\frac{C_{i+1} - 2C_i + C_{i-1}}{\Delta x^2} &\to \frac{\partial^2 C_i}{\partial x^2} \\
\frac{C_{i+1} - C_i}{\Delta x} &\to \frac{\partial C_i}{\partial x}.
\end{aligned}$$

It follows from (7) and (8) that

$$D = \lim_{\Delta x \to 0} \frac{PAR}{V}\Delta x^2$$

and

$$v = \lim_{\Delta x \to 0} \frac{PA(R-1)}{V}\Delta x.$$

Assume that $V = A\Delta x$, then

$$\begin{aligned}
D &= \lim_{\Delta x \to 0} \frac{PAR}{A\Delta x}\Delta x^2 \\
&= \lim_{\Delta x \to 0} PR\Delta x \\
&= \lim_{\Delta x \to 0} \frac{1}{2}P_s\frac{P_s + P_{ex}}{P_s}\Delta x \\
&= \lim_{\Delta x \to 0} \frac{1}{2}(\hat{P}_s(1 - f_c) + \hat{P}_{ex}f_c)\Delta x
\end{aligned}$$

and

$$\begin{aligned} v &= \lim_{\Delta x \to 0} \frac{PA(R-1)}{A\Delta x}\Delta x \\ &= \lim_{\Delta x \to 0} P(R-1) \\ &= \lim_{\Delta x \to 0} \frac{1}{2} P_s \left(\frac{P_s + P_{ex}}{P_s} - 1 \right) \\ &= \lim_{\Delta x \to 0} \frac{1}{2} \hat{P}_{ex} f_c. \end{aligned}$$

When we change the length of our cells, we want that the proportions of the thickness of the membrane compared to the entire length of the cell stays the same. $\hat{P}_s$ is the effective permeability by means of diffusion. This is dependent on the thickness of the membrane, d_m, and the diffusivity constant of the membrane, D_m. d_m is dependent on the length of the cell. In order to keep the same proportions we have that $d_m = c\Delta x$, where c is the proportion of the thickness of the cell membrane compared to the cell length. D_m is not dependent on. We have $\hat{P}_s = C\frac{D_m}{d_m} = C\frac{D_m}{c\Delta x}$, where C is the partitioning coefficient.[1]
$\hat{P}_{ex}$ is the effective permeability by means of the PIN transporters. We have that $\hat{P}_{ex} = \frac{d_m}{\Delta t}$, where Δt is the time needed to cross the membrane. Say that the transport speed through the PIN transporter (in the membrane) is constant, c', then we have that $\Delta t = c' d_m$. We get that the $\hat{P}_{ex} = \frac{c}{c'}$ and so $\hat{P}_{ex}$ is not dependent on Δx.

It follows that

$$\begin{aligned} D &= \lim_{\Delta x \to 0} \frac{1}{2} (\hat{P}_s(1 - f_c) + \hat{P}_{ex} f_c)\Delta x \\ &= \lim_{\Delta x \to 0} \frac{1}{2} \left(C\frac{D_m}{c} + \hat{P}_{ex} f_c \Delta x \right) \\ &= C\frac{D_m}{2c} \end{aligned}$$

and

$$\begin{aligned} v &= \lim_{\Delta x \to 0} \frac{1}{2} \hat{P}_{ex} f_c \\ &= \frac{1}{2} P_{ex}. \end{aligned}$$

5 Steady State Analysis

The system of flux-coupled diffusion-convection equations for the cell array (see Section 4.2) is quite complicated to analyse dynamically. Instead we will determine the steady state solutions for diffusion within the cells and for diffusion and active transport within the cells. Then the number flux between adjacent cells is equal for every two adjacent cells. The number flux from the donor well into the stem and from the stem into the receiver well are also equal to this number flux between adjacent cells.
Recall that in our model we assume that there is no diffusion of auxin in radial transversal direction out of the transport channel.

5.1 Case of Intracellular Diffusion

We investigate the assumption of diffusion by examining the steady state solution of our model.
When the system is in steady state the number flux between adjacent cells and the number flux into the stem and out of the stem must be equal to each other. In the case of steady state we have

$$J := J_{0,1} = J_{i,i+1} = J_{N,N+1},$$

for all i.
Let $u_i^\star(x)$ be the steady state solution, then we get from (1), with l the cell length,

$$\begin{aligned}
J &= -PA\left(\frac{u_{i+1}^\star(0)}{A} - R\frac{u_i^\star(l)}{A}\right), \qquad i \in \{1, 2, \ldots, N-1\} \\
&= -P(u_{i+1}^\star(0) - Ru_i^\star(l)) \\
J &= -P_{in}A\left(\frac{u_1^\star(0)}{A} - R_{in}C_d\right) \\
&= -P_{in}(u_1^\star(0) - R_{in}AC_d) \\
J &= P_{out}R_{out}A\frac{u_N^\star(l)}{A} \\
&= P_{out}R_{out}u_N^\star(l) \qquad (9)
\end{aligned}$$

Within the cell the diffusion equation applies, so we know

$$\frac{\partial u_i}{\partial t} = D\frac{\partial^2 u}{\partial x^2},$$

where D is the effective diffusivity of auxin within the cells and thus

$$\frac{\partial^2 u_i^\star}{\partial x^2} = 0.$$

It follows that the steady state solution has the form

$$u_i^\star(x) = c_1 + c_2 x. \qquad (10)$$

It's easy to see that $c_1 = u_i^\star(0)$ and $c_2 = \frac{\partial u_i^\star}{\partial x}$. From Fick's first law of diffusion we know that the diffusive flux inside cell i equals $-D\frac{\partial u_i^\star}{\partial x}$. Since the system is in steady state it must hold that

$$J = -D\frac{\partial u_i^\star}{\partial x} = -Dc_2$$

and hence

$$c_2 = -\frac{J}{D}.$$

Substitution into (10) gives

$$u_i^\star(x) = u_i^\star(0) - \frac{J}{D}x$$

as the steady state solution for cell i.

From (9) we get that

$$\begin{aligned} u_1^\star(0) &= -\frac{J}{P_{in}} + R_{in}AC_d, \\ u_{i+1}^\star(0) &= -\frac{J}{P} + Ru_i^\star(l) \\ &= -\frac{J}{P} + R\left(u_i^\star(0) - \frac{Jl}{D}\right) \\ &= -J\left(\frac{1}{P} + R\frac{l}{D}\right) + Ru_i^\star(0). \end{aligned} \tag{11}$$

Let $x_i = u_i^\star(0)$ and let $x_1 = u_1^\star(0)$, then

$$\begin{aligned} x_{i+1} &= \alpha x_i + \beta, \\ x_1 &= \gamma, \end{aligned} \tag{12}$$

where $\alpha = R$, $\beta = -J\left(\frac{1}{P} + R\frac{l}{D}\right)$ and $\gamma = -\frac{J}{P_{in}} + R_{in}AC_d$.
From this follows:

$$\begin{aligned} x_2 &= \alpha\gamma + \beta \\ x_3 &= \alpha(\alpha\gamma + \beta) + \beta \\ &= \alpha^2\gamma + \alpha\beta + \beta \\ x_4 &= \alpha(\alpha^2\gamma + \alpha\beta + \beta) + \beta \\ &= \alpha^3\gamma + \alpha^2\beta + \alpha\beta + \beta \end{aligned}$$

Now it's easy to see that

$$\begin{aligned} x_n &= \alpha^{n-1}\gamma + \beta\left(\sum_{k=0}^{n-2}\alpha^k\right) \\ &= \begin{cases} \gamma + \beta(n-1), & \alpha = 1 \\ \alpha^{n-1}\gamma + \beta\frac{\alpha^{n-1}-1}{\alpha-1}, & \alpha \neq 1 \end{cases}. \end{aligned} \tag{13}$$

Replacing the x_n, α, γ and β gives

$$u_n^\star(0) \stackrel{R\neq 1}{=} R^{n-1}\left(-\frac{J}{P_{in}} + R_{in}AC_d\right) - J\left(\frac{1}{P} + R\frac{l}{D}\right)\frac{R^{n-1}-1}{R-1}. \qquad (14)$$

From (9) we get that

$$\begin{aligned} u_N^\star(l) &= \frac{J}{P_{out}R_{out}} - \frac{AC_r}{R_{out}} \\ &\stackrel{C_r=0}{=} \frac{J}{P_{out}R_{out}}, \\ u_N^\star(0) &= \frac{J}{P_{out}R_{out}} + \frac{Jl}{D} \\ &= J\left(\frac{1}{P_{out}R_{out}} + \frac{l}{D}\right). \end{aligned}$$

From (14) we get that

$$u_N^\star(0) = R^{N-1}\left(-\frac{J}{P_{in}} + R_{in}AC_d\right) - J\left(\frac{1}{P} + R\frac{l}{D}\right)\frac{R^{N-1}-1}{R-1}.$$

It follows that

$$\begin{aligned} J\left(\frac{1}{P_{out}R_{out}} + \frac{l}{D}\right) &= R^{N-1}\left(-\frac{J}{P_{in}} + R_{in}AC_d\right) \\ &\quad -J\left(\frac{1}{P} + R\frac{l}{D}\right)\frac{R^{N-1}-1}{R-1}, \\ R^{N-1}R_{in}AC_d &= J\left(\frac{1}{P_{out}R_{out}} + \frac{l}{D} + \frac{R^{N-1}}{P_{in}}\right. \\ &\quad \left. + \left(\frac{1}{P} + R\frac{l}{D}\right)\frac{R^{N-1}-1}{R-1}\right). \end{aligned}$$

$$
\begin{aligned}
J &= R^{N-1}R_{in}AC_d \cdot \left[\frac{1}{P_{out}R_{out}} + \frac{l}{D} + \frac{R^{N-1}}{P_{in}} \right. \\
&\qquad \left. + \frac{1}{P}\frac{R^{N-1}-1}{R-1} + \frac{l}{D}\frac{R^N - R}{R-1}\right]^{-1} \\
&= R_{in}AC_d \cdot \left[\frac{1}{P_{out}R_{out}R^{N-1}} + \frac{l}{D}\frac{1}{R^{N-1}} + \frac{1}{P_{in}} \right. \\
&\qquad \left. + \frac{1}{P}\frac{1-\frac{1}{R^{N-1}}}{R-1} + \frac{l}{D}\frac{R-\frac{1}{R^{N-2}}}{R-1}\right]^{-1} \\
&= R_{in}AC_d\frac{D}{l} \cdot \left[\left(1 + \frac{\frac{D}{l}}{P_{out}R_{out}}\right)\frac{1}{R^{N-1}} + \frac{\frac{D}{l}}{P_{in}} \right. \\
&\qquad \left. + \frac{\frac{D}{l}}{P}\frac{1}{R-1}\left(1-\frac{1}{R^{N-1}}\right) + \frac{R}{R-1}\left(1-\frac{1}{R^{N-1}}\right)\right]^{-1} \\
&= R_{in}AC_d\frac{D}{l} \cdot \left[\left(1 + \frac{\frac{D}{l}}{P_{out}R_{out}}\right)\frac{1}{R^{N-1}} \right. \\
&\qquad \left. + \left(\frac{R}{R-1} + \frac{\frac{D}{l}}{P_{in}} + \frac{\frac{D}{l}}{P}\frac{1}{R-1}\right)\left(1-\frac{1}{R^{N-1}}\right) + \frac{\frac{D}{l}}{P_{in}}\frac{1}{R^{N-1}}\right]^{-1} \\
&= R_{in}AC_d\frac{D}{l} \cdot \left[\left(1 + \frac{\frac{D}{l}}{P_{out}R_{out}} + \frac{\frac{D}{l}}{P_{in}}\right)\frac{1}{R^{N-1}} \right. \\
&\qquad \left. + \left(\frac{R}{R-1} + \frac{\frac{D}{l}}{P_{in}} + \frac{\frac{D}{l}}{P}\frac{1}{R-1}\right)\left(1-\frac{1}{R^{N-1}}\right)\right]^{-1} \\
&\overset{N \text{ large}}{\approx} R_{in}AC_d\frac{D}{l}\left[\frac{R}{R-1} + \frac{\frac{D}{l}}{P_{in}} + \frac{\frac{D}{l}}{P}\frac{1}{R-1}\right]^{-1} \\
&= R_{in}AC_d\frac{D}{l}\left(1-\frac{1}{R}\right)\left[1 + \frac{\frac{D}{l}}{P_{in}}\left(1-\frac{1}{R}\right) + \frac{\frac{D}{l}}{P}\frac{1}{R}\right]^{-1}.
\end{aligned}
$$

Filling in our parameter values, putting $R = 100$, gives

$$J \approx 9 \times 10^{-18} \text{ mol/s, for } P_{in} = 1 \times 10^{-7} \text{ m/s}$$

and

$$J \approx 4 \times 10^{-17} \text{ mol/s, for } P_{in} = 7 \times 10^{-7} \text{ m/s.}$$

With experiments is measured that $J \approx 9 \times 10^{-18}$ mol/s (see Figure 2 on page 5). So for $P_{in} \sim 1 \times 10^{-7}$ m/s we get a value for J that fits the experimental results. In Section 5.4 and Appendix C equation (13) is further examined. We know that for $\alpha \gg 1$ the profile is likely to blow up for small n. In this case we have $\alpha = R \gg 1$ so we expect this profile to blow up, but maybe $\varepsilon = (\alpha - 1)\gamma + \beta$ is small enough.

Filling in our parameter values and taking $J = 9 \times 10^{-18}$ mol/s and $P_{in} = 1 \times 10^{-7}$ m/s gives

$$\begin{aligned} \alpha &= 100, \\ \beta &\approx -1 \times 10^{-9} \text{ mol/m}, \\ \gamma &= 1 \times 10^{-11} \text{ mol/m} \end{aligned}$$

and

$$\varepsilon \approx -1 \times 10^{-10} \text{ mol/m}.$$

Taking $J = 4 \times 10^{-17}$ mol/s and $P_{in} = 7 \times 10^{-7}$ m/s gives

$$\begin{aligned} \alpha &= 100, \\ \beta &= -5 \times 10^{-9} \text{ mol/m}, \\ \gamma &\approx 4 \times 10^{-11} \text{ mol/m} \end{aligned}$$

and

$$\varepsilon \approx -1 \times 10^{-10} \text{ mol/m}.$$

For both $P_{in} = 1 \times 10^{-7}$ m/s and $P_{in} = 7 \times 10^{-7}$ m/s we get $\varepsilon < 0$. Appendix C shows that for $\varepsilon < 0$ the profile doesn't relate to the experimental results. As mentioned, see Section 5.4 for further analysis.

5.2 Case of Intracellular Diffusion and Transport

We also take a look at a model with active transport within the cells. In *Chara* and *Nitella* cells their is evidence that such transport should exist because of the size of these cells, although its biochemical/-physical origins are unclear, [2, 9]. As we did before in the previous section we can determine the steady state solution. With active transport within cells we have the following governing equations:

$$\frac{\partial u_i}{\partial t} = D\frac{\partial^2 u_i}{\partial x^2} - v\frac{\partial u_i}{\partial x}$$

Here v is the transport velocity within the cells.
So for the steady state solution $u_i^\star$ it follows that

$$D\frac{\partial^2 u_i^\star}{\partial x^2} - v\frac{\partial u_i^\star}{\partial x} = 0$$

and hence our steady state solution has the form

$$u_i^\star(x) = c_1 + c_2 e^{\frac{v}{D}x}, \qquad v \neq 0. \tag{15}$$

The number flux at point x within cell i in the direction of increasing x is

$$-D\frac{\partial u_i^\star}{\partial x} + v u_i^\star(x).$$

Obviously in steady state the number fluxes between cells has to keep up with this flow in the cells. We get

$$\begin{aligned} J &= -D\frac{\partial u_i^\star}{\partial x} + v u_i^\star(x) \\ &= -D\left[c_2 \frac{v}{D} e^{\frac{v}{D}x}\right] + v\left(c_1 + c_2 e^{\frac{v}{D}x}\right) \\ &= -c_2 v e^{\frac{v}{D}x} + c_1 v + c_2 v e^{\frac{v}{D}x} \\ &= c_1 v. \end{aligned}$$

So

$$c_1 = \frac{J}{v}.$$

Substituting this in (15) gives

$$\begin{aligned} u_i^\star(x) &= \frac{J}{v} + c_2 e^{\frac{v}{D}x} \\ u_i^\star(0) &= \frac{J}{v} + c_2 \\ c_2 &= u_i^\star(0) - \frac{J}{v} \\ u_i^\star(x) &= \frac{J}{v} + \left(u_i^\star(0) - \frac{J}{v}\right) e^{\frac{v}{D}x} \\ &= \frac{J}{v}\left(1 - e^{\frac{v}{D}x}\right) + u_i^\star(0) e^{\frac{v}{D}x}. \end{aligned}$$

From (9) we get

$$\begin{aligned} u_1^\star(0) &= -\frac{J}{P_{in}} + R_{in} A C_d \\ u_{i+1}^\star(0) &= -\frac{J}{P} + R u_i^\star(l) \\ &= -\frac{J}{P} + R\left(\frac{J}{v}\left(1 - e^{\frac{v}{D}l}\right) + u_i^\star(0) e^{\frac{v}{D}l}\right) \\ &= -\frac{J}{P} + R\frac{J}{v}\left(1 - e^{\frac{v}{D}l}\right) + R e^{\frac{v}{D}l} u_i^\star(0). \end{aligned}$$

We have the same form as before, see (12), where now $\alpha = Re^{\frac{v}{D}l}$, $\beta = -\frac{J}{P} + R\frac{J}{v}\left(1 - e^{\frac{v}{D}l}\right)$ and $\gamma = -\frac{J}{P_{in}} + R_{in} A C_d$.
From (13) we get

$$u_N^\star(0) = R^{N-1} e^{(N-1)\frac{v}{D}l}\left(-\frac{J}{P_{in}} + R_{in} A C_d\right) + \left(-\frac{J}{P} + R\frac{J}{v}\left(1 - e^{\frac{v}{D}l}\right)\right)\frac{R^{N-1} e^{(N-1)\frac{v}{D}l} - 1}{R e^{\frac{v}{D}l} - 1}.$$

From (9) we also have

$$\begin{aligned} u_N^\star(l) &= \frac{J}{P_{out}R_{out}} \\ \frac{J}{v}\left(1-e^{\frac{v}{D}l}\right)+u_N^\star(0)e^{\frac{v}{D}l} &= \frac{J}{P_{out}R_{out}} \\ u_N^\star(0) &= \frac{J\left(\frac{1}{P_{out}R_{out}}-\frac{1}{v}\left(1-e^{\frac{v}{D}l}\right)\right)}{e^{\frac{v}{D}l}}. \end{aligned}$$

It follows that

$$\begin{aligned} \frac{J\left(\frac{1}{P_{out}R_{out}}-\frac{1}{v}\left(1-e^{\frac{v}{D}l}\right)\right)}{e^{\frac{v}{D}l}} &= R^{N-1}e^{(N-1)\frac{v}{D}l}\left(-\frac{J}{P_{in}}+R_{in}AC_d\right) \\ &\quad +\left(-\frac{J}{P}+R\frac{J}{v}(1-e^{\frac{v}{D}l})\right) \\ &\quad \cdot\frac{R^{N-1}e^{(N-1)\frac{v}{D}l}-1}{Re^{\frac{v}{D}l}-1} \\ z &= e^{\frac{v}{D}l} \\ \frac{J\left(\frac{1}{P_{out}R_{out}}-\frac{1}{v}(1-z)\right)}{z} &= R^{N-1}z^{N-1}\left(-\frac{J}{P_{in}}+R_{in}AC_d\right) \\ &\quad +\left(-\frac{J}{P}+R\frac{J}{v}(1-z)\right)\frac{R^{N-1}z^{N-1}-1}{Rz-1} \\ y &= Rz \\ \frac{J\left(\frac{1}{P_{out}R_{out}}-\frac{1}{v}\left(1-\frac{y}{R}\right)\right)}{\frac{y}{R}} &= y^{N-1}\left(-\frac{J}{P_{in}}+R_{in}AC_d\right) \\ &\quad +\left(-\frac{J}{P}+R\frac{J}{v}\left(1-\frac{y}{R}\right)\right)\frac{y^{N-1}-1}{y-1} \\ \frac{J\left(\frac{1}{P_{out}R_{out}}-\frac{1}{v}\left(1-\frac{y}{R}\right)\right)}{\frac{y^N}{R}} &= -\frac{J}{P_{in}}+R_{in}AC_d \\ &\quad +\left(-\frac{J}{P}+R\frac{J}{v}\left(1-\frac{y}{R}\right)\right)\frac{1-\frac{1}{y^{N-1}}}{y-1} \end{aligned}$$

$$
\begin{aligned}
R_{in}AC_d &= J\left(\frac{1}{P_{in}} + \left(\frac{1}{P} - R\frac{1}{v}\left(1-\frac{y}{R}\right)\right)\frac{1-\frac{1}{y^{N-1}}}{y-1}\right. \\
&\quad \left. + \frac{\frac{1}{P_{out}R_{out}} - \frac{1}{v}\left(1-\frac{y}{R}\right)}{\frac{y^N}{R}}\right) \\
&= J\left(\frac{1}{P_{in}} - \frac{1}{v}\left(R-y-\frac{v}{P}\right)\frac{1-\frac{1}{y^{N-1}}}{y-1} + \frac{R}{y^N}\frac{1}{P_{out}R_{out}}\right. \\
&\quad \left. - \frac{\frac{R}{y^N} - \frac{1}{y^{N-1}}}{v}\right) \\
J &= R_{in}AC_d\left[\frac{1}{P_{in}} - \frac{1}{v}\left(R-y-\frac{v}{P}\right)\frac{1-\frac{1}{y^{N-1}}}{y-1} + \frac{R}{y^N}\frac{1}{P_{out}R_{out}}\right. \\
&\quad \left. - \frac{\frac{R}{y^N} - \frac{1}{y^{N-1}}}{v}\right]^{-1} \\
&\overset{N\text{large}}{\approx} R_{in}AC_d\left[\frac{1}{P_{in}} - \frac{1}{v}\left(R-y-\frac{v}{P}\right)\frac{1}{y-1}\right]^{-1} \\
&= R_{in}AC_d\left[\frac{1}{P_{in}} + \left(\frac{1}{P} - \frac{R}{v}(1-e^{\frac{v}{D}l})\right)\frac{1}{Re^{\frac{v}{D}l}-1}\right]^{-1}.
\end{aligned}
$$

Since the value for v is unknown we use $J = 9 \times 10^{-18}$ mol/s from the experimental results to determine a value for v. Filling in our parameter values gives

$$
\begin{aligned}
v &\approx 2 \times 10^{-7} \text{ m/s, for } P_{in} = 1 \times 10^{-7} \text{ m/s} \\
v &\approx -3 \times 10^{-6} \text{ m/s, for } P_{in} = 7 \times 10^{-7} \text{ m/s.}
\end{aligned}
$$

Since $v < 0$ for $P_{in} = 7 \times 10^{-}7$ m/s, only $P_{in} = 1 \times 10^{-7}$ m/s will be examined further.
Taking $J = 9 \times 10^{-18}$ mol/s and $v = 2,13903 \times 10^{-7}$ m/s we get

$$
\begin{aligned}
\alpha &= 100 \cdot e^{2\times 10^{-1}}, \\
\beta &\approx -1 \times 10^{-9} \text{ mol/m}, \\
\gamma &= 1 \times 10^{-11} \text{ mol/m}
\end{aligned}
$$

and

$$
\varepsilon \approx -7 \times 10^{-11} \text{ mol/m.}
$$

Note that J is dependent on v, so $v = 2,13903$ m/s is not the exact value to get $J = 9 \times 10^{-18}$ mol/s.
Again we have $\varepsilon < 0$ and Appendix C shows that the profile doesn't relate to the experimental results when $\varepsilon < 0$.

5.3 Case of Intracellular Mixing

Another possibility is the case of intracellular mixing. This case yields that the auxin is equally distributed within each cell when the system is in steady state. We get

$$u_i^\star(x) = u_i^\star(0).$$

From (9) we get that

$$\begin{aligned} u_1^\star(0) &= -\frac{J}{P_{in}} + R_{in}AC_d \\ u_{i+1}^\star(0) &= -\frac{J}{P} + Ru_i^\star(l) \\ &= -\frac{J}{P} + Ru_i^\star(0) \end{aligned}$$

Again we have the same form as in (12). As with diffusion we have $\alpha = R$ and $\gamma = -\frac{J}{P_{in}} + R_{in}AC_d$. In this case we have $\beta = -\frac{J}{P}$. From (13) we get

$$u_N^\star(0) = R^{N-1}\left(-\frac{J}{P_{in}} + R_{in}AC_d\right) - \frac{J}{P}\frac{R^{N-1}-1}{R-1}.$$

From (9) we also have

$$\begin{aligned} u_N^\star(l) &= \frac{J}{P_{out}R_{out}} \\ u_N^\star(0) &= \frac{J}{P_{out}R_{out}} \end{aligned}$$

It follows that

$$\begin{aligned} \frac{J}{P_{out}R_{out}} &= R^{N-1}\left(-\frac{J}{P_{in}} + R_{in}AC_d\right) - \frac{J}{P}\frac{R^{N-1}-1}{R-1} \\ R^{N-1}R_{in}AC_d &= J\left(\frac{1}{P_{out}R_{out}} + \frac{R^{N-1}}{P_{in}} + \frac{1}{P}\frac{R^{N-1}-1}{R-1}\right) \\ R_{in}AC_d &= J\left(\frac{1}{P_{out}R_{out}R^{N-1}} + \frac{1}{P_{in}} + \frac{1}{P}\frac{1-\frac{1}{R^{N-1}}}{R-1}\right) \\ J &= R_{in}AC_d \cdot \left[\left(\frac{1}{P_{out}R_{out}} + \frac{1}{P_{in}}\right)\frac{1}{R^{N-1}} + \left(\frac{1}{P_{in}} + \frac{1}{P}\frac{1}{R-1}\right)\left(1 - \frac{1}{R^{N-1}}\right)\right]^{-1} \\ &\overset{N \text{ large}}{\approx} R_{in}AC_d \cdot \left[\frac{1}{P_{in}} + \frac{1}{P}\frac{1}{R-1}\right]^{-1} \\ &> 0 \end{aligned}$$

Filling in our parameter values gives

$$J \approx 1 \times 10^{-17} \text{ mol/s, for } P_{in} = 1 \times 10^{-7} \text{ m/s}$$

and

$$J \approx 6 \times 10^{-17} \text{ mol/s, for } P_{in} = 7 \times 10^{-7} \text{ m/s.}$$

For $P_{in} = 1 \times 10^{-7}$ m/s we have a value for J that fits the experimental results. Filling in our parameter values and taking $J = 1 \times 10^{-17}$ mol/s and $P_{in} = 1 \times 10^{-7}$ m/s gives

$$\begin{aligned} \alpha &= 100 \\ \beta &\approx -3 \times 10^{-10} \text{ mol/m} \\ \gamma &= 0 \text{ mol/m} \end{aligned}$$

and

$$\varepsilon \approx -3 \times 10^{-10} \text{ mol/m.}$$

Taking $J = 6 \times 10^{-17}$ mol/s and $P_{in} = 7 \times 10^{-7}$ m/s gives

$$\begin{aligned} \alpha &= 100 \\ \beta &\approx -2 \times 10^{-9} \text{ mol/m} \\ \gamma &\approx 1 \times 10^{-11} \text{ mol/m} \end{aligned}$$

and

$$\varepsilon \approx -9 \times 10^{-11} \text{ mol/m.}$$

We get $\varepsilon < 0$ for both $P_{in} = 1 \times 10^{-7}$ m/s and $P_{in} = 7 \times 10^{-7}$ m/s. This doesn't relate to the experimental results.

5.4 Examining Exponential 'Blow-up' in Detail

From the previous sections it becomes clear that to assess the profile found with the experiments a more detailed analysis is needed than that exhibited in Appendix C. Such an analysis is also needed to be able to draw strong conclusions on the validity of the proposed models. In this section a less sensitive approach is used instead.
Recall that for intracellular diffusion and transport we have

$$\begin{aligned} \alpha &= Re^{\frac{l}{D}v}, \\ \beta &= -J\left(\frac{1}{P} - R\frac{1 - e^{\frac{l}{D}v}}{v}\right), \end{aligned}$$

and

$$\gamma = u_1^\star(0) = -\frac{J}{P_{in}} + R_{in}AC_d.$$

Define

$$\begin{aligned}\tilde{\beta} &:= \frac{\beta}{u_1^\star(0)} \\ &= \frac{-J\left(\frac{1}{P}-R\frac{1-e^{\frac{v}{D}l}}{v}\right)}{-\frac{J}{P_{in}}+R_{in}AC_d} \\ &= \frac{-\frac{P_{in}}{P}}{\frac{P_{in}R_{in}AC_d}{J}-1}\cdot\left[1-PR\frac{1-e^{\frac{v}{D}l}}{v}\right],\end{aligned}$$

then

$$\begin{aligned}\frac{u_n^\star(0)}{u_1^\star(0)} &= \begin{cases}\alpha^{n-1}+\tilde{\beta}\frac{\alpha^{n-1}-1}{\alpha-1}, & \alpha\neq 1\\ 1+\tilde{\beta}(n-1), & \alpha=1\end{cases} \\ &= \begin{cases}\alpha^{n-1}\left(1+\frac{\tilde{\beta}}{\alpha-1}\right)-\frac{\tilde{\beta}}{\alpha-1}, & \alpha\neq 1\\ 1+\tilde{\beta}(n-1), & \alpha=1\end{cases}.\end{aligned}$$

Recall

$$u_N^\star(l) = \left(u_N^\star(0)-\frac{J}{v}\right)e^{\frac{l}{D}v}+\frac{J}{v}$$

and define

$$\lambda := \frac{l}{D}v,$$

then

$$\begin{aligned}u_N^\star(l) &= \left(\alpha^{N-1}\left(u_1^\star(0)+\frac{\beta}{\alpha-1}\right)-\frac{\beta}{\alpha-1}-\frac{J}{v}\right)e^\lambda+\frac{J}{v} \\ &= e^\lambda\left(\alpha^{N-1}\left(u_1^\star(0)+\frac{\beta}{\alpha-1}\right)-\frac{\beta}{\alpha-1}\right)+\frac{J}{v}(1-e^\lambda)\end{aligned}$$

Recall

$$u_N^\star(l) = \frac{J}{P_{out}R_{out}}.$$

We get

$$\begin{aligned}\frac{J}{P_{out}R_{out}} &= e^\lambda\left(\alpha^{N-1}\left(u_1^\star(0)+\frac{\beta}{\alpha-1}\right)-\frac{\beta}{\alpha-1}\right)+\frac{J}{v}(1-e^\lambda) \\ J\left(\frac{1}{P_{out}R_{out}}-\frac{1-e^\lambda}{v}\right) &= e^\lambda\left(\alpha^{N-1}\left(u_1^\star(0)+\frac{\beta}{\alpha-1}\right)-\frac{\beta}{\alpha-1}\right)\end{aligned}$$

$$\begin{aligned}J\Bigg(\frac{1}{P_{out}R_{out}}-\frac{1-e^\lambda}{v}+e^\lambda\Bigg(\frac{\alpha^{N-1}}{\alpha-1}\left(\frac{1}{P}-R\frac{1-e\lambda}{v}\right)& \\ -\frac{1}{\alpha-1}\left(\frac{1}{P}-R\frac{1-e^\lambda}{v}\right)\Bigg)\Bigg) &= e^\lambda\alpha^{N-1}u_1^\star(0) \\ J\left(\frac{1}{P_{out}R_{out}}-\frac{1-e^\lambda}{v}+e^\lambda\left(\frac{\alpha^{N-1}-1}{\alpha-1}\left(\frac{1}{P}-R\frac{1-e^\lambda}{v}\right)\right)\right) &= e^\lambda\alpha^{N-1}u_1^\star(0)\end{aligned}$$

$$\frac{J}{u_1^\star(0)} = \frac{e^\lambda \alpha^{N-1}}{\frac{1}{P_{out}R_{out}} - \frac{1-e^\lambda}{v} + e^\lambda \left(\frac{\alpha^{N-1}-1}{\alpha-1} \left(\frac{1}{P} - R\frac{1-e^\lambda}{v} \right) \right)} \tag{16}$$

Then

$$\begin{aligned}
\tilde{\beta} &= \frac{\beta}{u_1^\star(0)} \\
&= \frac{-J\left(\frac{1}{P} - R\frac{1-e^\lambda}{v}\right)}{u_1^\star(0)} \\
&\overset{(16)}{=} -\frac{e^\lambda \alpha^{N-1}}{\frac{1}{P_{out}R_{out}} - \frac{1-e^\lambda}{v} + e^\lambda \left(\frac{\alpha^{N-1}-1}{\alpha-1} \left(\frac{1}{P} - R\frac{1-e^\lambda}{v} \right) \right)} \cdot \left(\frac{1}{P} - R\frac{1-e^\lambda}{v} \right).
\end{aligned}$$

Put

$$\delta := \frac{1}{P} - R\frac{1-e^\lambda}{v},$$

then

$$\begin{aligned}
\frac{\tilde{\beta}}{\alpha-1} &= -\frac{e^\lambda \alpha^{N-1}\delta}{(\alpha-1)\left(\frac{1}{P_{out}R_{out}} - \frac{1-e^\lambda}{v}\right) + e^\lambda(\alpha^{N-1}-1)\delta} \\
&= -\frac{1}{\alpha^{-N+1}\frac{\alpha-1}{\delta}e^{-\lambda}\left(\frac{1}{P_{out}R_{out}} - \frac{1-e^\lambda}{v}\right) + 1 - \alpha^{-N+1}}
\end{aligned}$$

Recall

$$u_N^\star(0) = \alpha^{N-1}u_1^\star(0) - \beta\frac{\alpha^{N-1}-1}{\alpha-1}.$$

It follows that

$$\begin{aligned}
\frac{u_N^\star(0)}{u_1^\star(0)} &= \alpha^{N-1} + \tilde{\beta}\frac{\alpha^{N-1}-1}{\alpha-1} \\
&= \alpha^{N-1}\left(1 + \frac{\tilde{\beta}}{\alpha-1}\right) - \frac{\tilde{\beta}}{\alpha-1} \\
&= \alpha^{N-1}\left(\frac{\alpha^{-N+1}\frac{\alpha-1}{\delta}e^{-\lambda}\left(\frac{1}{P_{out}R_{out}} - \frac{1-e^\lambda}{v}\right) - \alpha^{-N+1}}{\alpha^{-N+1}\frac{\alpha-1}{\delta}e^{-\lambda}\left(\frac{1}{P_{out}R_{out}} - \frac{1-e^\lambda}{v}\right) + 1 - \alpha^{-N+1}}\right) - \frac{\tilde{\beta}}{\alpha-1} \\
&= \frac{\frac{\alpha-1}{\delta}e^{-\lambda}\left(\frac{1}{P_{out}R_{out}} - \frac{1-e^{-\lambda}}{v}\right) - 1}{\alpha^{-N+1}\frac{\alpha-1}{\delta}e^{-\lambda}\left(\frac{1}{P_{out}R_{out}} - \frac{1-e^\lambda}{v}\right) + 1 - \alpha^{-N+1}} - \frac{\tilde{\beta}}{\alpha-1} \\
&= \frac{\frac{\alpha-1}{\delta}e^{-\lambda}\left(\frac{1}{P_{out}R_{out}} - \frac{1-e^{-\lambda}}{v}\right)}{\alpha^{-N+1}\frac{\alpha-1}{\delta}e^{-\lambda}\left(\frac{1}{P_{out}R_{out}} - \frac{1-e^\lambda}{v}\right) + 1 - \alpha^{-N+1}}.
\end{aligned}$$

Define

$$\rho := \frac{\alpha - 1}{\delta} e^{-\lambda} \left(\frac{1}{P_{out} R_{out}} - \frac{1 - e^{-\lambda}}{v} \right),$$

then

$$\begin{aligned} \frac{u_N^\star(0)}{u_1^\star(0)} &= \frac{\rho}{\alpha^{-N+1}(\rho - 1) + 1} \\ &= \frac{\rho}{\frac{\rho - 1}{\alpha^{N-1}} + 1} \\ &\approx \rho. \end{aligned} \tag{17}$$

For $1 \leq n \leq N$ it holds that

$$\begin{aligned} \frac{u_n^\star(0)}{u_1^\star(0)} &= \frac{\alpha^{n-N}\rho - \alpha^{n-N} + 1}{\alpha^{-N+1}(\rho - 1) + 1} \\ &= \frac{\alpha^{n-N}(\rho - 1) + 1}{\frac{\rho - 1}{\alpha^{N-1}} + 1} \\ &\approx \alpha^{n-N}(\rho - 1) + 1. \end{aligned} \tag{18}$$

For the diffusive case, i.e. $v = 0$, we get

$$\begin{aligned} \rho &= \lim_{v \to 0} \frac{\alpha - 1}{\delta} e^{-\frac{l}{D} v} \left(\frac{1}{P_{out} R_{out}} - \frac{1 - e^{-\frac{l}{D} v}}{v} \right) \\ &= \frac{\alpha - 1}{\delta} \left(\frac{1}{P_{out} R_{out}} + \frac{l}{D} \right), \\ \delta &= \lim_{v \to 0} \frac{1}{P} - R \frac{1 - e^{\frac{l}{D} v}}{v} \\ &= \frac{1}{P} + R \frac{l}{D} \end{aligned}$$

and

$$\begin{aligned} \alpha &= \lim_{v \to 0} R e^{\frac{l}{D} v} \\ &= R. \end{aligned}$$

So for the diffusive case it follows that

$$\begin{aligned}
\rho &= \frac{R-1}{\frac{1}{P}+R\frac{l}{D}}\left(\frac{1}{P_{out}R_{out}}+\frac{l}{D}\right) \\
&= \frac{\frac{1}{P_{out}R_{out}}+\frac{l}{D}}{\frac{1}{P(R-1)}+\frac{R}{R-1}\frac{l}{D}} \\
&= \frac{\frac{D}{l\cdot P_{out}R_{out}}+1}{\frac{\frac{D}{l}}{P(R-1)}+\frac{R}{R-1}} \\
&= \frac{\frac{D}{l\cdot P_{out}R_{out}}+1}{\frac{\frac{D}{l}}{P(R-1)}+\frac{1}{R-1}+1} \\
&= \frac{\frac{D}{l\cdot P_{out}R_{out}}+1}{\frac{\frac{D}{l}+P}{P(R-1)}+1}.
\end{aligned}$$

With our parameter values, putting $R = 101$ we get

$$\rho \approx 40.$$

Also $\alpha = 101$ and $N = 160$, so

$$\alpha^{N-1} = 101^{159}.$$

This is big enough for (17) and (18) to be good approximations, so

$$u_N^\star \approx 40u_1^\star(0).$$

It also gives us the following profile:

$$\frac{u_n^\star(0)}{u_1^\star(0)} = 1 + \frac{\rho-1}{\alpha^{N-n}}$$

For the last cell we get $\rho = 40$.
For the second last we get $1 + \frac{\rho-1}{\alpha} = 1 + \frac{39}{101} \approx 1.386$.
For the third last we get $1 + \frac{\rho-1}{\alpha^2} = 1 + \frac{39}{10201} \approx 1.004$.
Note that in comparison with the last cell all the other values are close to 1. So this gives us a pretty flat profile with a very small peak at the very end.

6 Discussion and Conclusions

This thesis examined the transport of auxin in *Arabidopsis thaliana*. The starting point was the article of G.J. Mitchison, [8]. This article suggested that there was simple diffusion within cells as only form of transport within the cells of *Arabidopsis*. There was some reasonable doubt whether this is true or not.
In this thesis there is some support. The value found for the flux of auxin between adjacent cells, assuming simple diffusion, corresponds to the value measured with experiments done in the Plant BioDynamics Laboratory in Leiden. However in other cases this value also corresponds to the experiments.
Assuming simple diffusion also gave us a reasonably good match with the profile of the distribution of auxin within the stem. Other cases in this thesis are not examined and it can be that something other than simple diffusion gives a match as well as this one.
The formula for the profile as used in Appendix C should be used carefully or not at all in further investigation. The approach in Section 5.4 is recommended to be used instead.

A Parameter values

Meaning	Parameter	Value
Permeability	P	4×10^{-8} m/s
Permeability		
at the donor end of the stem	P_{in}	$1 \times 10^{-7} - 7 \times 10^{-7}$ m/s
Length of the stem	L	16×10^{-3} m
Length of a cell	l	1×10^{-4} m
Total number of cells in the stem	N	$L/l = 160$
Cross section surface of all the		
transport channels together	A	1×10^{-8} m^2
Volume of the cell	V	$Al = 1 \times 10^{-12}$ m^3
Concentration of auxin		
in the donor well	C_d	1×10^{-4} mol/m^3
Concentration of auxin		
in the receiver well	C_r	0 mol/m^3
Accumulation ratio	R	3 - 400
Accumulation ratio		
at the donor end of the stem	R_{in}	100
Accumulation ratio		
times permeability		
at the receiver end of the stem	$P_{out}R_{out}$	2×10^{-8}
Effective diffusivity of auxin		
within the cells	D	1×10^{-10} m^2/s

In literature is found that for the diffusion of IAAH through the cell membrane is $\sim 5 \times 10^{-7}$ m/s. Taking into account a pH-value of 4-5 in the apoplast between donor well and first transporter cell we estimate a lower effective permeability with a lower bound for P_{in} of 1×10^{-7} m/s. It may be that there are still functioning AUX-transporters in this part of the membrane increasing P_{in}, [4, 6].

B Matlab Simulation

B.1 Parameters.m

```
L=16*10^-3; % length of the stem in m
N=160; % number of cells
l=L/N; % length of cells in m
d=25*10^-6; % diameter cell in m
fu=0.15; % fraction non-vacuole
fa=0.5; % fraction auxin in anion form in apoplast
fc=0.97; % fraction auxin in anion form in cell (cytoplasm)
fd=0.97; % fraction auxin in anion form in donor well
Cd=1*10^-4; % concentration donor well (mol/m^3)
Cr=0; % concentration receiver well
Ps=5*10^-7; % permeability for diffusion protonated form
Pex=5*10^-6*fc; % transporters
P=Ps*(1-fc)/2; % permeability
Pin=Ps*(1-fd)/2; %
Pout=Ps*(1-fc)/2; %
A=pi*(d/2)^2; % cross surface between cells in m^2
V=A*l*fu; % volume cell in m^3
R=1+Pex*fc/(Ps*(1-fc)); % accumulation ratio
Rin=1+Pex*fd/(Ps*(1-fd));
Rout=1+Pex*fc/(Ps*(1-fc));
N=round(N); % rounding N to an integer value

D=10^-10; % diffusion constant auxin in cell in m^2/s
Pr=2.4*10^-8; % Pout*Rout
```

B.2 conc.m

```
function dy = conc(t,y,P,Pin,Pout,A,V,R,Rin,Rout,Cd,Cr,N)
dy = zeros(N,1);
dy(1) = (-Pin*A*(y(1)-Rin*Cd)+P*A*(y(2)-R*y(1)))/V;
for i=2:N-1
    dy(i) = (-P*A*(y(i)-R*y(i-1))+P*A*(y(i+1)-R*y(i)))/V;
end
dy(N) = (-P*A*(y(N)-R*y(N-1))+Pout*A*(Cr-Rout*y(N)))/V;
```

B.3 Auxplot.m

```
[T,Y] = ode45(@(t,y)conc(t,y,P,Pin,Pout,A,V,R,Rin,Rout,Cd,Cr,N),[0 10^5],zeros(N,1));
X = zeros(N,1);
for i = 1:N
    X(i) = i;
end
YT = Y';
hold off
bar(X,YT(:,21)) % The integer in this line is the value for t+1
```

C Examining equation (13)

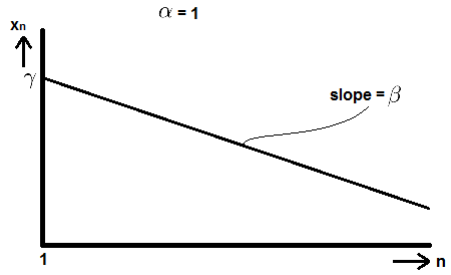
Now we examine the profile of x_n (as a function of n) for different α, β and γ in

$$x_n = \begin{cases} \gamma + \beta(n-1), & \alpha = 1 \\ \alpha^{n-1}\gamma + \beta\frac{\alpha^{n-1}-1}{\alpha-1}, & \alpha \neq 1 \end{cases} . \tag{19}$$

We know that $\alpha, \gamma > 0$ and $\beta < 0$. Considering we don't want x_n to blow up fast we can distinguish between $\alpha = 1$ and $\alpha > 1$. $\alpha < 1$ is not relevant because we need an increase in the profile of x_n.
When $\alpha = 1$ we get

$$x_n = \gamma + (n-1)\beta,$$

so the profile of x_n is a straight line with a slope of β starting at γ. Concentrations of auxin will be negative if n is large enough.



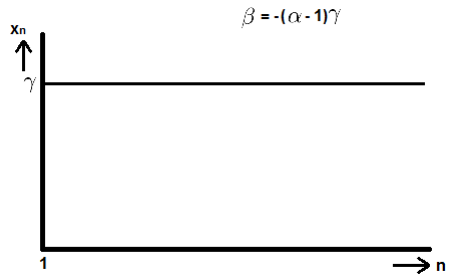
When $\alpha > 1$ and $\beta = 0$ we get that the profile is exponentially increasing, but $\beta < 0$, so β can cancel out the increase. When we have β such that $x_2 = x_1 = \gamma$, we get from (19) that

$$\begin{aligned} \gamma &= \alpha\gamma + \beta \\ \beta &= -(\alpha-1)\gamma. \end{aligned}$$

When we substitute this back into (19) we get

$$\begin{aligned} x_n &= \alpha^{n-1}\gamma - (\alpha-1)\gamma\frac{\alpha^{n-1}-1}{\alpha-1} \\ &= \alpha^{n-1}\gamma - \left(\alpha^{n-1}-1\right)\gamma \\ &= \gamma. \end{aligned}$$

So when $\alpha > 1$ and $\beta = -(\alpha-1)\gamma$ we get that the profile of x_n is constant.



Take $\beta = -(\alpha-1)\gamma + \varepsilon$, where $\varepsilon \neq 0$, and let $\alpha > 1$, then we get from (19) that

$$\begin{aligned} x_n &= \alpha^{n-1}\gamma - ((\alpha-1)\gamma - \varepsilon)\,\frac{\alpha^{n-1}-1}{\alpha-1} \\ &= \alpha^{n-1}\gamma - (\alpha-1)\gamma\frac{\alpha^{n-1}-1}{\alpha-1} + \varepsilon\frac{\alpha^{n-1}-1}{\alpha-1} \\ &= \gamma + \varepsilon\frac{\alpha^{n-1}-1}{\alpha-1}. \end{aligned}$$

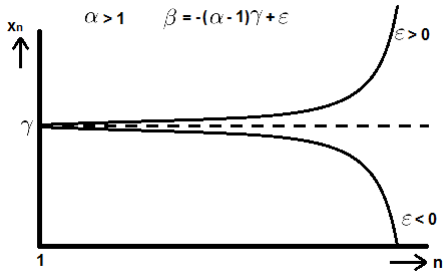
Define

$$x(\nu) := \gamma + \varepsilon\frac{\alpha^{\nu}}{\alpha-1}, \quad \nu > 0$$

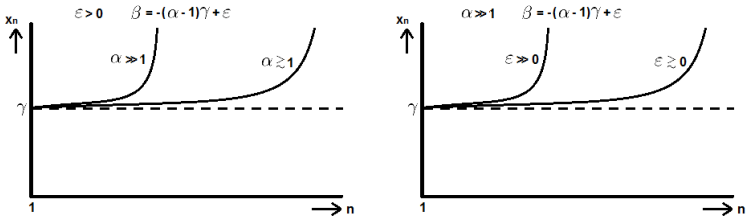
where $\nu = n-1$ is a continuous variable. Looking at the first and second derivative of $x(\nu)$,

$$\begin{aligned} \frac{dx}{d\nu} &= \varepsilon\frac{\alpha^{\nu}\log(\alpha)}{\alpha-1} \\ \frac{d^2x}{d\nu^2} &= \varepsilon\frac{\alpha^{\nu}\log^2(\alpha)}{\alpha-1}, \end{aligned}$$

we see that for $\alpha > 1$ the sign of the first and second derivative is that of ε. So when $\alpha > 1$ and $\varepsilon > 0$ we get that $x(\nu)$ has an increasing and convex exponential profile. when $\alpha > 1$ and $\varepsilon < 0$ we get that $x(\nu)$ has a decreasing and concave exponential profile.



In the case of $\varepsilon > 0$ we have a profile that relates to the experimental results. In the first derivative of $x(\nu)$ we can see that the slope is determined by α and ε. When $\alpha \gtrsim 1$ the profile will blow op when ν is large enough. When $\alpha \gg 1$ the profile will blow up for small ν. When ε increase, the slope of $x(\nu)$ increases. So when $\varepsilon \gtrsim 0$ it can compensate a blow up that could appear when $\alpha \gg 1$.



References

[1] Theo Blom, *Transport and Accumulation of Alkaloids in Plant Cells*, PhD thesis Rijksuniversiteit Leiden, pp. 42, 1991.

[2] Kees Boot, Kees Libbenga, Sander Hille, Remko Offringa and Bert van Duijn, *Polar Auxin Transport: an Early Invention*, Journal of Experimental Botany, Vol. 63, No. 11, pp. 4213-4218, 2012.

[3] A. Chavarria-Krauser and M. Ptashnyk, *Homogenization of Long Range Auxin Transport in Plant Tissue*, Nonlinear Analysis: Real World Applications, Vol. 11, No. 6, pp. 4524-4532, 2010.

[4] A. Delbarre, P. Muller, V. Imhoff and J. Guern, *Comparison of Mechanisms Controlling Uptake and Accumulation of 2,4-dichlorophenoxy Acetic Acid, Naphthalene-1-acetic Acid, and Indole-3-acetic Acid in Suspension-cultured Tobacco Cells*, Plante, Vol. 198, No. 4, pp. 532-541, 1996.

[5] E.M. Kramer, *A Mathematical Model of Pattern Formation in the Vascular Cambium of Trees*, Journal of Theoretical Biology, Vol. 216, No. 2, pp. 147-158, 2002.

[6] E.M. Kramer, *How Far Can a Molecule of Weak Acid Travel in the Apoplast or Xylem?*, Plant Physiology, Vol. 141, No. 4, pp. 1233-1236, 2006.

[7] Ottoline Leyser, *Auxin*, Current Biology, Vol. 11, No. 18, pp. R728, 2001.

[8] G.J. Mitchison, *The Dynamics of Auxin Transport*, Proc. R. Soc. Lond. B, No. 209, pp. 489-511, 1980.

[9] J.A. Raven, *Polar Auxin Transport in Relation to Long-distance Transport of Nutrients in the Charales*, Journal of Experimental Botany, Vol. 64, No. 1, pp. 1-9, 2013.