Quantitative predictions on auxin transport

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A manifold of leaf vein patterns shows conserved properties.

Conserved structures:
- central midvein towards the petiole
- secondary veins spanning the leaf blade
- higher order veins reticulating the spacing
Auxin and its efflux carrier build patterning mechanism

**Plant hormone auxin**
- Auxin is produced in leaves and transported towards the stem.
- Defective auxin transport results in disrupted veins → auxin induces vascular differentiation.


**Efflux carrier PIN**
- PIN membrane bound channel protein.
- PIN knock out leads to undirected auxin transport.
- PIN yields directed auxin transport in mammalian and yeast cells.


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Quantitative predictions on auxin transport.
In a string of cells auxin waves can be excited

In vitro experiment

- strand of cells cut from plant
- apply source of auxin to one cell
- auxin wave travels down the cells
- radioactively labeled auxin becomes diluted
- observe spatial auxin distribution at different time steps
- velocity of $\approx \mu m/sec$

Goldsmith Plant Phys. (1967)
1. Deduction of a microscopic model
   - Auxin dynamics
   - Efflux carrier dynamics

2. Theoretical analysis and prediction of observables
   - Nonlinear analysis
   - Analytic calculation of auxin amplitude
   - Analytic calculation of auxin amplitude

3. Experimental setup to measure transport dynamics

4. Conclusion & Outlook
Auxin needs efflux carriers to exit cell

\[
\dot{A}(n) = s_A - d_A A(n) - \frac{e_A}{\ell} [J(n) - J(n-1)], \quad J(n) = A(n)P_r(n) - A(n+1)P_l(n+1)
\]

**Dynamics of the weak acid auxin**

- protonated auxin follows concentration gradient into cell
- gets ionized at pH7 of cytoplasm, auxin is trapped
- efflux facilitated by carrier \(P_r, P_l\) with efficiency \(e_A\)
- extracellular diffusion suppressed by small interspace
- fast synthesis \(s_A\) and degradation \(d_A\) in cells
Efflux carrier mediate a self-enhancing flow of auxin

\[ \dot{P}_r(n) = -d_P P_r(n) + [P_{tot} - P_r(n) - P_l(n)][s_P + g_P J^2(n) \theta(J(n))] \]

**Cycling of membrane bound PIN efflux carrier**

- PIN proteins are membrane bound
- efflux carrier cycle between endosomes and cell membrane \( s_P, d_P \)
- auxin flux yields enhanced attachment \( g_P \)
- directed transport due to self-enhancing flow of auxin
- efflux carrier production too slow for wave \( v \approx \mu m/sec \)
Parameters are sensitive to environmental conditions

Full microscopic model

Varying parameters
auxin metabolism and transport affected by
- light
- temperature
- wind

Rescaling
- normalize concentrations $a = A/A_{eq}$, $A_{eq} = s_A/d_A$ and $P_r = P_r/P_{tot}$
- transport efficiency $e_A$ fastest time scale, others estimated slower
- measure time and rates in slowest estimated time-scale $d_P$

Questions

- What is the underlying nonlinear mechanism resulting in wave formation?
- How do parameters control wave properties?
- Are quantitative predictions possible?
Auxin traffic jam builds up wave

Auxin is piled up by yet undirected efflux carriers

- fast transport efficiency rate
- bottle neck due to slow directed attachment rate of efflux carriers

Microscopic equations

\[ \dot{a}(n) = d_A(1 - a(n)) - \left( e_A P_{\text{tot}}/\ell \right) [J(n) - J(n - 1)] \]

\[ \dot{p}_r(n) = -p_r(n) + [1 - p_r(n) - p_l(n)] \left[ s_P + g_P P_{\text{tot}}^2 A_{\text{eq}}^2 J^2(n) \Theta(J(n)) \right] \]

\[ \dot{p}_l(n) = -p_l(n) + [1 - p_r(n) - p_l(n)] \left[ s_C + g_P P_{\text{tot}}^2 A_{\text{eq}}^2 J^2(n - 1) \Theta \right] \]

\[ J(n) = a(n)p_r(n) - a(n + 1)p_l(n + 1) \]
Excitability of a bistable system due to advection

Reaction-advection system

\[ \dot{a} = g(a, p_r) + \tilde{g}(a, p_r, \nabla a, \nabla p_r) \]

\[ \dot{p}_r = f(a, p_r) + \tilde{f}(a, p_r, \nabla a, \nabla p_r) \]
Excitability of a bistable system due to advection

**Reaction-advection system**

\[
\begin{align*}
\dot{a} &= g(a, p_r) + \tilde{g}(a, p_r, \nabla a, \nabla p_r) \\
\dot{p}_r &= f(a, p_r) + \tilde{f}(a, p_r, \nabla a, \nabla p_r)
\end{align*}
\]

**A wave developing**

- bistable system
- excitation triggers wave
- advection drives system past second fixed point
- relaxation back
Excitability of a bistable system due to advection

Reaction-advection system

\[
\dot{a} = g(a, p_r) + \tilde{g}(a, p_r, \nabla a, \nabla p_r)
\]

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A wave developing

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Quantitative predictions on auxin transport
Theoretical predictions explain microscopic model

Varying transport efficiency

- higher transport efficiency leads to more auxin accumulation

Change of carrier attachment

- attachment rate
- sets $P_{r, eq} \rightarrow$ auxin is faster moved away

Change in enhanced attachment

- higher directed attachment $\rightarrow$ auxin is faster moved away

$$A_{max}^2 = \frac{2(dP + 2sp)}{gPP_{tot}^2} \left( 1 + \sqrt{1 + \frac{e_A^2P_{tot}^2(dP + sp)^2}{\ell dP^2sp^2}} \left[ 1 + \sin(\phi/3) - \frac{\cos(\phi/3)}{\sqrt{3}} \right]\right), \phi = \arctan \left(-\sqrt{\frac{1}{4} \frac{e_A^4P_{tot}^4(dP + sp)^4}{\ell^4dP^4sp^4}}\right)$$
Theoretical predictions explain microscopic model

Varying transport efficiency

- Higher transport efficiency leads to more auxin accumulation.

Change of carrier attachment

- Attachment rate sets \( P_{r,eq} \) → auxin is faster moved away.

Change in enhanced attachment

- Higher directed attachment → auxin is faster moved away.

\[
A_{\text{max}}^2 \propto \frac{e_A P_{\text{tot}}}{\ell d_P} \frac{1}{g_P P_{\text{tot}}^2 A_{\text{eq}}^2} \frac{(1+s_P d_P)(1+2s_P d_P)}{s_P d_P} \quad \nu \propto e_A P_{\text{tot}}
\]
Measure auxin amplitude in experiment

**Experimental setup**

![Experimental setup diagram]

**Observing an auxin wave**

- quantify radioactively labeled or deuterated auxin
- GFP-labeled carriers mark position of wave front
- avoid boundary layer effects $>100$ cells
- vary transport parameters by external stimuli (wind, light) or by use of mutants

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Conclusion

Unveil nonlinear mechanism behind auxin wave
- found bistable system that is driven excitable due to advection terms
- analyzed influence of parameters on wave properties

Quantitative predictions
- able to solve dynamics analytically and make quantitative forecasts
- hope to inspired experiments to test predictions
Stationary flow pattern in two dimensions

- by what mechanism do 2D patterns arise
- how do 2D patterns depend on the parameters and form
- how may plants regulate 2D patterns
Thanks goes to ...

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