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Modelling plant cell growth

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***Advanced article**

Abstract

Turgor, cellular hydrodynamics, mechanical properties of cell wall materials, and addition of materials to the cell wall are all important for plant cell growth. In order for a plant cell to grow, the cell wall must loosen and stretch, water must enter the cell, and turgor pressure must be able to drive drive expansion and provide mechanical support. During cell growth, the relative change in the water volume and the relative change in cell wall chamber volume are approximately equal. Mathematical equations for modelling plant cell growth are described to establish how cell volume and turgor can be calculated. Mathematical equations for ion transport are introduced to establish how cellular ion concentrations and osmotic pressure can be calculated. Combination of those equations formulates a method for modelling plant cell growth. Modelling of auxin dynamics, which play a key role in controlling cell expansion, is also described. One of the future challenges is to model the interplay between plant growth and auxin dynamics.

Key words

Plant growth; Mathematical modelling; Turgor; Cell wall; Cellular osmotic pressure; Ions; Ion transport; Modelling auxin dynamics.

Key concepts

- The plant cell is surrounded by the cell wall.
- In order for a plant cell to grow, the cell wall must loosen and lay down new material, water must enter the cell to provide the turgor pressure to drive expansion, and turgor pressure must be able to provide mechanical support.

- Turgor and cell volume are calculated using the mathematical equations, which describe how the relative change in the water volume and the relative change in cell wall chamber volume are approximately equal during the cell growth.
- Cellular ion concentrations and osmotic pressure are calculated using the equations that describe reversal potentials and voltage gating.
- The phytohormone auxin plays an essential role in many aspects of plant growth and development.
- Auxin concentration in the cells is a function of multiple factors including biosynthesis, degradation and conjugation, and transport.
- Modelling auxin dynamics needs to appropriately formulate the equations including auxin biosynthesis, degradation and transport.
- To model the role of auxin in plant cell growth, it is necessary to establish how auxin is related to the key factors for plant cell growth including turgor, cellular hydrodynamics, mechanical properties of cell wall materials, and addition of materials to the cell wall.

Introduction

Each plant cell is surrounded by a cell wall. An important role of the plant cell wall is to provide mechanical support. Turgor pressure pushing out on the cell wall, as well as the lignocellulosic properties of the wall itself, is required for mechanical support (Cosgrove 2005; 2016). Plant cell growth responds to the mechanical force exerted by the turgor pressure in the cell. In order for a plant cell to grow, the cell wall must loosen, water must enter the cell, and turgor pressure must be able to drive expansion and provide mechanical support. Moreover, the cell must add new materials to the wall to preserve its integrity. In addition, the mechanical property of the wall material determines how a cell wall expands. Therefore turgor, cellular hydrodynamics, mechanical properties of cell wall materials, and addition of materials to the cell wall are all critical processes for plant cell growth. **See also:** DOI: 10.1038/npg.els.0001671; DOI: 10.1002/9780470015902.a0001688.pub2; DOI: 10.1002/9780470015902.a0022336.

The phytohormone auxin plays an essential role in many aspects of plant growth and development (Vanneste and Friml 2009). It has been shown that plant growth is rapidly stimulated by auxin (Cleland 1984). Auxin-induced cell growth is related to how auxin acidifies the extracellular space to make cell walls more extensible (Cosgrove 2005). It has been shown that reduction of tissue rigidity by auxin is related to the demethyl-esterification of pectin in Arabidopsis (Braybrook and Peaucelle 2013). Since plant cell growth requires the regulation of cell wall biochemistry (Chebli and Geitmann 2017), understanding plant growth also therefore requires an understanding of auxin dynamics to establish how auxin is related to the key factors for plant cell growth including turgor, cellular hydrodynamics, mechanical properties of cell wall materials, and addition of materials to the growing wall. **See also:** DOI: 10.1002/9780470015902.a0020090.

Modelling plant cell growth

Based on the mathematical equations developed by Lockard (1965) for modelling expansive growth of a cell with walls, Ortega and colleagues (Ortega 2010; Ortega and Welch 2013) developed the augmented growth equations by including a transpiration term that accounts for the water loss from the cell. The relative rate of change in water volume within the cell is described by equation 1.

$$\frac{dV_w}{V_w dt} = \frac{L_P A}{V_w}(\pi_i - \pi_o - P) - T_{loss} \qquad \text{(equation 1)}$$

Where V_w is the water volume, L_P is the relative cell wall hydraulic conductance, A is the wall area for water permeability. π_i and π_o are the cellular osmotic pressure and extracellular osmotic pressure, respectively. P is the turgor pressure relative to atmospheric pressure. T_{loss} is the relative rate of change in water volume lost via transpiration.

The relative rate of change in volume of the cell wall chamber is described by equation 2.

$$\frac{dV_{cwc}}{V_{cwc} dt} = \phi(P - P_c) + \frac{1}{\varepsilon}\frac{dP}{dt} \qquad \text{(equation 2)}$$

Where V_{cwc} is the cell wall chamber volume, ϕ is the irreversible cell wall extensibility, P_c is the critical turgor pressure, and ε is the volumetric elastic modulus.

During the growth of a plant cell, the relative change in the water volume, $\frac{dV_w}{V_w dt}$, and the relative change in cell wall chamber volume, $\frac{dV_{cwc}}{V_{cwc} dt}$, are approximately equal. Thus, the rate of change in turgor pressure is described by equation 3 if we consider no transpiration occurs (Ortega 2010).

$$\frac{dP}{dt} = \varepsilon(\frac{L_P A}{V}(\pi_i - \pi_o - P) - \phi(P - P_C)) \qquad \text{(equation 3)}$$

If we consider that major ions in plant cells are K^+, Cl^-, Ca^{2+} and H^+, cellular osmotic pressure is calculated as follows (Liu and Hussey 2014).

$$\pi_i = RT([Ca^{2+}]_i + [H^+]_i + [K^+]_i + [Cl^-]_i + [Osm]_i) \qquad \text{(equation 4)}$$

Where R is gas constant, T is temperature. $[Ca^{2+}]_i$, $[H^+]_i$, $[K^+]_i$ and $[Cl^-]_i$ are cellular concentrations of these ions. $[Osm]_i$ is the concentration of other cellular molecules that contribute to osmotic pressure in the cell.

Extracellular osmotic pressure is calculated as follows (Liu and Hussey 2014).

$$\pi_o = RT([Ca^{2+}]_o + [H^+]_o + [K^+]_o + [Cl^-]_o + [Osm]_o) \qquad \text{(equation 5)}$$

Where $[Ca^{2+}]_o$, $[H^+]_o$, $[K^+]_o$ and $[Cl^-]_o$ are concentrations of these ions in the extracellular space. $[Osm]_o$ is the concentration of other molecules that contribute to extracellular osmotic pressure.

Figure 1 summarises how turgor, cellular hydrodynamics, mechanical properties of cell wall materials, and addition of materials to the cell wall all work together to regulate plant cell growth. Equations 1-5 can be used to quantitatively calculate cell volume change during plant cell growth.

---Figure 1 here---

Modelling concentration changes of cellular ions

Modelling cellular osmotic pressure in equation 4 requires a calculation of the concentration of four cellular ions, $[Ca^{2+}]_i$, $[H^+]_i$, $[K^+]_i$ and $[Cl^-]_i$. This needs to incorporate the properties of ion transporters into the model (Gradmann 2001; Liu et al. 2010b; Liu and Hussey 2014).

The reversal potentials for the four major ions (potassium, proton, calcium, and chloride) are as follows.

$$\begin{aligned} E_K &= -V_{ref} \ln \frac{[K]_i}{[K]_o} \\ E_H &= -V_{ref} \ln \frac{[H]_i}{[H]_o} \\ E_{Ca} &= -\frac{V_{ref}}{2} \ln \frac{[Ca]_i}{[Ca]_o} \\ E_{Cl} &= V_{ref} \ln \frac{[Cl]_i}{[Cl]_o} \end{aligned} \qquad \text{(equation 6)}$$

Where $V_{ref} = \frac{RT}{F}$ and F is Faraday constant.

The reversal potentials are used to establish current-voltage relationship (Gradmann 2001; Liu et al. 2010b; Liu and Hussey 2014). The current density due to the action of any transporter of the four ions can be described using two types of current-voltage relationship.

The first type of current-voltage relationship is an ohmic relationship.

$$I = g(V_m - E) \qquad \text{(equation 7)}$$

The second type of current-voltage relationship is a Goldman-Hodgkin-Katz constant-field relationship.

$$I = gV_m \frac{[c_i] - [c_o] e^{-\frac{zV}{V_{ref}}}}{1 - e^{-\frac{zV_m}{V_{ref}}}} \qquad \text{(equation 8)}$$

In equations 7 and 8, g is membrane conductance, V_m is membrane voltage, and E is reversal potential, as described by equations 6, z is the charge of an ion, $[c_i]$ and $[c_o]$ are the intracellular and extracellular ion concentrations, respectively.

Membrane voltage, V_m, is calculated using equation 9 (Gradmann 2001; Liu et al. 2010b; Liu and Hussey 2014),

$$C_m \frac{dV_m}{dt} = -\sum_{i=1}^{n} I_i \qquad \text{(equation 9)}$$

where C_m is membrane capacitance. The summation in equation 9 is the total of current due to ion movement through the cell membrane by the action of all transporters.

Ion movement through the cell membrane is controlled by voltage gating**.** The kinetics of voltage gating for different transporters can vary, depending on the mechanism by which voltage controls the action of those transporters (Gradmann 2001; Liu et al. 2010b; Liu and Hussey 2014). A simple mechanism for voltage gating is described by equation 10.

$$O \xleftrightarrow[k_{OC},k_{CO}]{} C \qquad \text{(equation 10)}$$

Where O and C are the completely open state and completely closed state, respectively. k_{OC} and k_{CO} are the rate constants that control the transition between the open state (O) and the closed (C) state, and they are functions of membrane voltage. k_{OC} and k_{CO} follow equation 11 (Gradmann 2001; Liu et al. 2010b; Liu and Hussey 2014).

$$\begin{aligned} k_{OC} &= k_{OC}^{0} e^{\delta_O \frac{V_m}{V_{ref}}} \\ k_{CO} &= k_{CO}^{0} e^{\delta_C \frac{V_m}{V_{ref}}} \end{aligned} \qquad \text{(equation 11)}$$

Where k_{OC}^{0} and k_{CO}^{0} are the rate constants at zero voltage, δ_O and δ_C are the voltage-sensitivity coefficients for the open state and closed state, respectively.

Thus, voltage gating can be described using equation 12 (Gradmann 2001; Liu et al. 2010b; Liu and Hussey 2014).

$$\begin{aligned} \frac{dP_O}{dt} &= -k_{OC}P_O + k_{CO}P_C \\ P_O + P_C &= 1 \end{aligned} \qquad \text{(equation 12)}$$

Where P_O and P_C are the probability for the transporter to be at the open and closed state, respectively.

A more complex mechanism for voltage gating is described by equation 13 (Gradmann 2001).

$$C_2 \xleftrightarrow[k_{C_2O},k_{OC_2}]{} O \xleftrightarrow[k_{OC_1},k_{C_1O}]{} C_1 \qquad \text{(equation 13)}$$

C_1 and C_2 are two different closed states. Voltage gating for this mechanism is described by equation 14.

$$\begin{aligned} &\frac{dP_O}{dt} = -(k_{OC_1} + k_{OC_2})P_O + k_{C_1O}P_{C_1} + k_{C_2O}P_{C_2} \\ &\frac{dP_{C_1}}{dt} = k_{OC_1}P_O - k_{C_1O}P_{C_1} \\ &P_O + P_{C_1} + P_{C_2} = 1. \end{aligned} \qquad \text{(equation 14)}$$

Where P_O, P_{C1} and P_{C2} are the probability for the transporter to be at the open state, the first closed state, and the second closed state, respectively.

Equations 6-14 can be used to calculate the concentration of four cellular ions, $[Ca^{2+}]_i$, $[H^+]_i$, $[K^+]_i$ and $[Cl^-]_i$ (Liu et al., 2010b; Liu and Hussey 2014). Thus, cellular osmotic pressure can be calculated using equation 4, and cell volume change during plant cell growth can be calculated using equations 1-3.

Modelling as a tool for elucidating the regulation of plant cell growth

Since turgor, cellular hydrodynamics, mechanical properties of cell walls, and addition of new materials to the cell wall all are required for plant cell growth, different models of plant cell growth may focus on different aspects and can lead to different conclusions.

Pollen tube growth is an excellent example for plant cell tip growth. There are two main models of pollen tube growth. The cell wall model considers that cell wall mechanical properties control growth (Winship et al. 2011) and the hydrodynamic model suggests that turgor controls growth (Zonia and Munnik 2011). For the cell wall model, it is suggested that the cell wall sets the pace for pollen tube growth. The main experimental evidence is that the stiffness of the cell wall is inversely correlated with growth rate, and that there are no rapid and large-scale turgor changes during growth (Winship et al.

2011). For the hydrodynamic model, hypertonicity and hypotonicity were shown to cause the pollen tube apical area to shrink and swell respectively, and these changes correspond to the doubling and halving of growth rate oscillatory periods respectively, compared to the oscillatory period of the isotonic growth condition (Winship et al. 2011; Zonia and Munnik 2011). Therefore, it was suggested that growth rate oscillations in pollen tube growth are regulated by hydrodynamics.

Hill et al. (2012) developed an osmotic model for pollen tube growth. Their model predicts that osmotic permeability is restricted to a constant area near the tip of a pollen tube. Importantly, their model shows that the turgor pressure has two opposing effects - "controlling the water entry; and controlling the area expansion of the tip wall polymers (pectin) which translates into new cell volume" (Hill et al., 2012). Kroeger et al. (2011) developed a model to investigate the relationship between growth rate and turgor. Their model shows that changes in the global turgor do not influence the average growth rate in a linear manner.

Liu et al. (2010b) developed a model to investigate the dynamics of four major ions (Ca^{2+}, K^+, Cl^-, H^+) in pollen tube growth. This model shows that tip and shank of a pollen tube forms an integrative system generating oscillations at the tip. Liu and Hussey (2014) developed a model that integrates the interplay of hydrodynamics, cell wall and ion dynamics. They have developed a method to dissect the regulation of hydrodynamics, cell wall and ion dynamics in pollen tube growth. Kato et al. (2010) developed a model that shows that vesicle trafficking can be directly correlated with the pollen tube growth rate. In addition, Rojas et al. (2010) developed a detailed model of cell wall mechanics that proposes a negative feedback between growth rate and vesicle secretion. Eggen et al. (2011) investigated the role of cell wall ageing in pollen tube growth. Yan et al. (2009) developed a model that investigates the role of calcium in participating in feedback regulation of the oscillating ROP1 Rho GTPase.

All these modelling efforts were aimed at elucidating pollen tube growth. Unsurprisingly, different models have focused on different aspects due to the complexity as described by equations 1-14. A future challenge is to integrate a wide range of biological data into a model that can make predictions for further experimental examination.

Modelling auxin dynamics

The phytohormone auxin plays an essential role in many aspects of plant growth and development (Vanneste and Friml 2009). It has been shown that plant growth is rapidly stimulated by auxin (Cleland 1984). Auxin-induced cell growth is related to how auxin acidifies the extracellular space of plant cells to make cell walls more extensible (Cosgrove 2005). Thus, modelling auxin dynamics is an important aspect for modelling plant growth. **See also:** DOI: 10.1002/9780470015902.a0023733.

Auxin concentration in the cells is a function of multiple factors including biosynthesis (Ljung 2013; Zhao 2014), degradation (Ljung 2013) and conjugation (Ludwig-Muller 2011), and transport. Importantly, auxin patterning in plant tissue with multiple cells such as Arabidopsis root is predominantly regulated by auxin transport proteins (Zazimalova et al. 2010).

Auxin concentration can display distinct patterns in plant tissue with multiple cells, such as the Arabidopsis root. Measuring auxin concentration reveals the presence of IAA concentration gradients within the Arabidopsis root tip with a distinct maximum in the organizing quiescent centre of the root apex (Petersson et al. 2009). Many auxin reporter gene expression studies, including DR5 (Ulmasov et al. 1997; Sabatini et al., 1999), DII-VENUS (Brunoud et al. 2012), and R2D2 (Liao et al. 2015) reporter data, also indicate the existence of auxin signalling gradients in the Arabidopsis root. In addition, computational modelling suggests that auxin transporters play key roles in forming auxin gradients (Band et al. 2014; Bennett et al. 2016; Grieneisen et al. 2007).

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The mass balance of auxin can be generally described using equation 15.

$$\frac{\partial[auxin]}{\partial t} = B_{auxin} - D_{auxin} + T_{auxin} \qquad \text{(equation 15)}$$

Where $[auxin]$ is auxin concentration; B_{auxin} is the rate for auxin biosynthesis; D_{auxin} is the rate for auxin degradation; and T_{auxin} is the rate for auxin transport.

Modelling auxin dynamics needs to appropriately formulate the equations for B_{auxin}, D_{auxin} and T_{auxin}. These equations can be very complex due to the multiple-level regulation of auxin biosynthesis and degradation, as well as due to passive transport by diffusion and active transport by the actions of auxin transporters (Liu et al. 2010a; 2013; Moore et al. 2015a; 2015b; 2017). Modelling auxin dynamics therefore needs careful consideration of these different aspects (Liu et al. 2010a; 2013; Moore et al. 2015a; 2015b; 2017). For example, each of the kinetics of auxin biosynthesis, degradation, and transport can be regulated by other hormones and the associated genes. Therefore, how to formulate kinetic equations for modelling auxin biosynthesis, degradation, and transport under the constraints of thermodynamic and kinetic principles should be carefully examined. How auxin moves through a complex spatial structure should also be carefully explored. **See also:** DOI: 10.1002/9780470015902.a0023733.

Perspectives for modelling the interplay between plant growth and auxin dynamics

The phytohormone auxin plays an essential role in many aspects of plant growth and development (Vanneste and Friml 2009), and so modelling plant growth requires an examinination of the dependence of plant growth on auxin dynamics. Cell growth and division can change cell volume, shape and number, leading to a complex spatial structur. Plant growth itself may affect auxin concentration and patterning, and so modelling auxin dynamics needs to consider the effects of plant growth on auxin dynamics. Figure 2 schematically describes the relationship between auxin dynamics and plant growth.

--- Figure 2 here---

Specifically, modelling the role of auxin in plant cell growth needs to establish how auxin is related to the key factors for plant cell growth including turgor, cellular hydrodynamics, mechanical properties of cell wall materials, and addition of materials to the cell wall. As indicated above, it has been shown that reduction of tissue rigidity by auxin is related to the demethyl-esterification of pectin in Arabidopsis (Braybrook and Peaucelle 2013). In equation 2, parameter ϕ is the irreversible cell wall extensibility. Linking auxin concentration or response with parameter ϕ in equation 2 via the demethyl-esterification of pectin could be possible to model how auxin affects growth by regulating cell wall extensibility. Moreover, experimental data showed that cell division of postembryonic plant organ follows certain rules (vonWangenheim et al. 2016) and that auxin can override a geometric division rule for some cells in root development (Yoshida et al. 2014). How auxin regulates cell division should also be further explored using mathematical modelling. Furthermore, since auxin can regulate both cell growth and division, mathematical modelling should try to develop an integrative view of how plant growth across multiple cells is regulated by auxin, by integrating plant cell growth as described by equations 1-14, with plant cell division. In principle, modelling the interplay between plant growth and auxin dynamics could adapt a range of modelling tools available for modelling different aspects of plant cells (Liu et al. 2010c; 2014; Liu and Hussey 2011).

References

Band LR, Wells DM, Fozard JA, Ghetiu T, French AP, Pound MP, Wilson MH, Yu L, Li W, Hijazi HI et al. (2014) Systems analysis of auxin transport in the Arabidopsis root apex. Plant Cell **26**: 862–875.

Bennett T, Hines G, van Rongen M, Waldie T, Sawchuk MG, Scarpella E, Ljung K, Leyser O (2016) Connective auxin transport in the shoot facilitates communication between shoot apices. PLoS Biology **14**: e1002446.

Braybrook SA, Peaucelle A (2013) Mechano-chemical aspects of organ formation in Arabidopsis thaliana: the relationship between auxin and pectin. PLoS One **8**: e57813.

Brunoud G, Wells DM, Oliva M, Larrieu A, Mirabet V, Burrow AH, Beeckman T, Kepinski S, Traas J, Bennett MJ, Vernoux T (2012) A novel sensor to map auxin response and distribution at high spatio-temporal resolution. Nature **482**: 103–106.

Chebli Y, Geitmann A (2017) Cellular growth in plants requires regulation of cell wall biochemistry. Curr Opin Cell Biol. **44**: 28-35.

Cleland RE (1984) The Instron technique as a measure of immediate-past wall extensibility. Planta **160**: 514–520.

Cosgrove DJ (2005) Growth of the plant cell wall. Nature Reviews: Molecular Cell Biology **6**: 850–861.

Cosgrove DJ (2016) Plant cell wall extensibility: connecting plant cell growth with cell wall structure, mechanics, and the action of wall modifying enzymes. J Exp Bot **67**: 463–476.

Eggen E, de Keijser MN, Mulder BM (2011) Self-regulation in tip growth: the role of cell wall ageing. J Theor Biol **283**:c113-121.

Gradmann D (2001) Models for oscillations in plants. Aust J Plant Physiol **28**: 577–590.

Grieneisen VA, Xu J, Maree AFM, Hogeweg P, Scheres B (2007) Auxin transport is sufficient to generate a maximum and gradient guiding root growth. Nature **449**: 1008–1013.

Hill AE, Shachar-Hill B, Skepper JN, Powell J, Shachar-Hill Y (2012) An osmotic model of the growing pollen tube. PLoS One **7**: e36585.

Kato N, He H, Steger AP (2010) A systems model of vesicle trafficking in Arabidopsis pollen tubes. Plant Physiol **152**: 590-601.

Liao CY, Smet W, Brunoud G, Yoshida S, Vernoux T, Weijers D (2015) Reporters for sensitive and quantitative measurement of auxin response. Nature Methods **12**: 207–210.

Liu JL, Mehdi S, Topping J, Tarkowski P, Lindsey K (2010a) Modelling and experimental analysis of hormonal crosstalk in Arabidopsis. Molecular Systems Biology **6**: 373.

Liu J, Piette BMAG, Deeks MJ, Franklin-Tong VE, Hussey PJ (2010b) A compartmental model analysis of integrative and self-regulatory ion dynamics in pollen tube growth. PLoS One **5**: e13157.

Liu JL, Grieson CS, Webb AAR, Hussey PJ (2010c) Modelling dynamic plant cells. Current Opinion in Plant Biology **13**: 744–749.

Liu J, Hussey PJ (2011) Towards the creation of a systems tip growth model for a pollen tube. Plant Signal. Behav. **6**: 520–522.

Liu JL, Mehdi S, Topping J, Friml J, Lindsey K (2013) Interaction of PLS and PIN and hormonal crosstalk in Arabidopsis root development. Frontiers in Plant Science **4**: 75.

Liu J, Hussey PJ (2014) Dissecting the regulation of pollen tube growth by modeling the interplay of hydrodynamics, cell wall and ion dynamics. Front. Plant Sci. **5**: 392.

Liu J, Rowe J, Lindsey K (2014) Hormonal crosstalk for root development: a combined experimental and modeling perspective. Frontiers in Plant Science **5**: 116.

Ljung K (2013) Auxin metabolism and homeostasis during plant development. Development **140**: 943–950.

Lockhart JA (1965) An analysis of irreversible plant cell elongation J Theor. Biol. **8**: 264-275.

Ludwig-Müller J (2011) Auxin conjugates: their role for plant development and in the evolution of land plants. Journal of Experimental Botany **62**: 1757–1773.

Kroeger J, Zerzour R, Geitmann A (2011) Regulator or driving force? The role of turgor pressure in oscillatory plant cell growth. PLoS One **6**: e18549.

Moore S, Zhang X, Liu J, Lindsey K (2015a) Some fundamental aspects of modelling auxin patterning in the context of auxin-ethylene-cytokinin crosstalk. Plant Signaling and Behavior **10**: e1056424.

Moore S, Zhang X, Mudge A, Rowe JH, Topping JF, Liu J, Lindsey K (2015b) Spatiotemporal modelling of hormonal crosstalk explains the level and patterning of hormones and gene expression in Arabidopsis thaliana wildtype and mutant roots. New Phytologist **207**: 1110–1122.

Moore S, Liu J, Zhang X, Lindsey K (2017) A recovery principle provides insight into auxin pattern control in the Arabidopsis root. Scientific Reports **7**: 430004.

Ortega JKE (2010) Plant cell growth in tissue. Plant Physiology**154**:1244-1253.

Ortega JKE, Welch SWJ (2013) Mathematical models for expansive growth of cells with walls. Math Model Nat Phen **8**: 35–61.

Petersson SV, Johansson AI, Kowalczyk M, Makoveychuk A, Wang JY, Moritz T, Grebe M, Benfey PN, Sandberg G, Ljung K (2009) An auxin gradient and maximum in the Arabidopsis root apex shown by high-resolution cell-specific analysis of IAA distribution and synthesis. Plant Cell **21**: 1659–1668.

Rojas E, Hotton S, Dumais J (2011) Chemically mediated mechanical expansion of the pollen tube cell wall. Biophys J **101**:1844-1853.

Ulmasov T, Murfett J, Hagen G, Guilfoyle TJ (1997) Aux/IAA proteins repress expression of reporter genes containing natural and highly active synthetic auxin response elements. The Plant Cell **9**: 1963–1971.

Vanneste S, Friml J (2009) Auxin: A Trigger for Change in Plant Development. Cell **136**: 1005–1016.

vonWangenheim D, Fangerau J, Schmitz A, Smith RS, Leitte H, Stelzer EHK, Maizel A (2016) Rules and self-organizing properties of postembryonic plant organ cell Division Patterns. Curr. Biol. **26**: 439-449.

Winship LJ, Obermeyer G, Geitmann A, Hepler PK (2011) Pollen tubes and the physical world. Trends Plant Sci. **16**: 353–355.

Yan A, Xu G, Yang Z-B (2009) Calcium participates in feedback regulation of the oscillating ROP1 Rho GTPase in pollen tubes. Proc Natl Acad Sci USA **106**: 22002-22007.

Yoshida S, Barbier de Reuille P, Lane B, Bassel GW, Prusinkiewicz P, Smith RS, Weijers D (2014) Genetic control of plant development by overriding a geometric division rule. Developmental Cell **29**: 75–87.

Zazimalova E, Murphy AS, Yang H, Hoyerova K, Hosek P (2010) Auxin transporters—why so many? Cold Spring Harbor Perspectives in Biology **2**: a001552.

Zhao Y (2010) Auxin biosynthesis and its role in plant development. Ann Rev Plant Biol **61**:49-64.

Zonia L, Munnik T (2011) Understanding pollen tube growth: the hydrodynamic model versus the cell wall model. Trends Plant Sci. **16**: 347–352.

Further Reading

Taiz L, Zeiger E (2010) Plant Physiology, Fifth Edition. Sunderland, MA: Sinauer Associates.

Kariyan J, Konforti B, Wemmer D (2013) The molecules of life : physical and chemical principles. New York: Garland Science, Taylor & Francis Group.

Murray JD (2003) Mathematical biology: I: Introduction. Springer-Verlag Berlin Herdelberg.

Murray JD (2003) Mathematical biology: II: Spatial models and biomedical applications. Springer-Verlag Berlin Herdelberg.

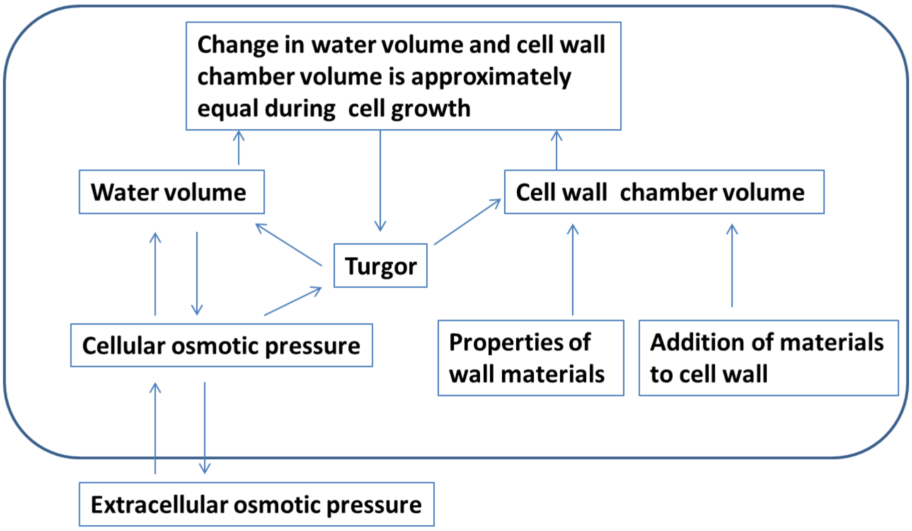

Figure 1. A schematic description about modelling plant cell growth. This figure shows how the key factors including water volume, cell wall chamber volume, turgor, cell wall properties, addition of materials to cell wall, as well as cellular and extracellular osmotic pressure are related during cell growth. Equations 1-14 in the text establish how these factors are quantitatively connected with each other during cell growth.

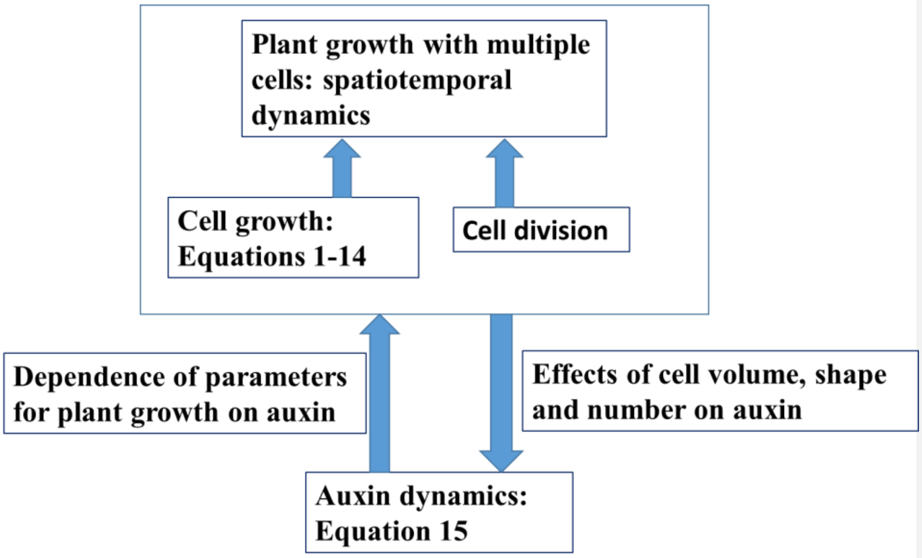

Figure 2. A schematic description about modelling the interplay between plant growth and auxin dynamics. This figure shows how equations 1-14 can be coupled with equation 15.