Modeling Strategies for Plant Survival, Growth and Reproduction

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Plants have developed effective strategies to cope with diverse environmental stresses during the course of their evolution. Recent advances in plant sciences have uncovered the dynamic yet co-ordinated regulation of stress responses and processes of growth, development and reproduction in plants. Thus integrated approaches that explore mutual adjustments of stress response and growth/reproductive machinery are necessary for in-depth understanding of plant strategies for propagation and survival under global environmental change.

Mathematical and computational models have been widely used in integrative approaches to study plants. For instance, models of crop growth have been widely used in agriculture (Yin and Struik 2010). Also, intermolecular interactions and gene regulation in hormone response pathways (Middleton et al. 2012), metabolism (Laisk et al. 2006) and the circadian clock (Locke et al. 2005) have been modeled in various plant systems to distinguish between competing hypotheses, to make new predictions and to design new experiments. In addition to these mechanistic models, evolutionary models that attempt to seek efficient strategies to increase the number of offspring in natural and fluctuating environments have long been used in ecology and evolutionary studies (Smith 1978). The integration of these two different types of models would offer great potential to understand the molecular regulatory bases of plant strategies for propagation and the evolutionary significance of why plants have evolved such molecular mechanisms.

In this Special Focus Issue, we introduce such integrated approaches with a special emphasis on mathematical and computational modeling. Papers range from circadian regulation of starch metabolism, and adjustment of timing of flowering in response to seasonal change in daylength, to transportation dynamics of essential micronutrients. Furthermore, these articles highlight how models help to untangle the non-intuitive relationships between local regulatory processes and global fitness as a measure of evolution.

Links Between the Circadian Clock, Carbon Metabolism and Timing of Flowering

Growth and maintenance processes requiring carbon must be maintained despite daily fluctuations in light and dark conditions. Buffering against daily fluctuations in the carbon supply is achieved through a diel turnover of starch. Carbon that is assimilated by photosynthesis during the day is partitioned between sucrose and starch; the sucrose is then used for immediate growth and maintenance, while the starch accumulates in leaves for storage until later demand at night (Caspar et al. 1985, Geiger and Servaites 1994, Gibon et al. 2004). Recent studies suggest that a bidirectional interplay between the circadian clock and carbon metabolism plays a key role in adjusting starch turnover to sustain growth under fluctuating environments (James et al. 2008, Graf et al. 2010, Dalchau et al. 2011, Haydon et al. 2013). Webb and Satake (2015) summarize recent new findings demonstrating the temporal organization of carbon metabolism, which in turn feeds back onto the circadian clock to regulate daily metabolism and growth. They show how these empirical findings are embedded in mathematical frameworks (Feugier and Satake 2013, Feugier and Satake 2014, Scialdone et al. 2013) to explore mechanisms underlying appropriate starch management under seasonal changes of daylength.

In addition to correct adjustment of starch turnover in response to seasonal changes of daylength, the circadian clock has an additional important output to regulate flowering timing by sensing changes in daylength. Flowering time in cereal crops directly influences grain productivity on which human societies depend. Nakamichi (2015) reviews the domestication history of major crop species and illustrates possible genetic modifications in the photoperiodic flowering pathway in long-day and short-day crops that allow spreading of crops to new habitats that are different from their geographic origins.

Regulation of Stomatal Opening by Vernalization and Photoperiodic Flowering Pathways

Crop productivity is greatly influenced by the efficiency of photosynthesis. One of the factors that regulate photosynthetic efficiency is stomatal aperture, which controls CO2 uptake (Wang et al. 2014). Plants regulate stomatal aperture in response to various environmental signals such as atmospheric CO2 concentration and light intensity. Previous studies revealed that phototropins (plant blue-light receptor kinases) mediate stomatal opening via activation of plasma membrane...
H^+-ATPase, which creates inside-negative electrical potential across the plasma membrane and drives K^+ uptake through voltage-gated inward-rectifying K^+ channels. Furthermore, FLOWERING LOCUS T (FT), known also as florigen, and photoperiodic components in guard cells positively affect stomatal opening in Arabidopsis thaliana (Kinoshita et al. 2001, Kinoshita et al. 2011, Ando et al. 2013). Kimura et al. (2015) addressed a new mechanism by which the vernalization and photoperiodic flowering pathways control stomatal opening in A. thaliana. They reveal that the vernalization signaling pathway regulates stomatal opening through the FLOWERING LOCUS C transcriptional repressor and its target genes, FT and SUPPRESSOR OF OVEREXPRESSION OF CO1 (SOC1). Furthermore, SOC1 is likely to regulate stomatal opening via transcriptional regulation of several genes involved in stomatal opening, such as those encoding plasma membrane H^+-ATPases in guard cells. The development of a detailed mechanistic model of guard cell ion transport and relevant systems was recently achieved (Buckley and Mott 2013). Such collaboration between experimental and modeling studies should promote our understanding of complex signaling mechanisms controlling stomatal aperture for future studies.

### Transportation Systems of Nutrients and Their Impact on Grain Yield

Nutrients are major determinants of plant growth and productivity in nature and agriculture. Recently, increasing numbers of mineral transporters localized to the plasma membrane in plant root cells have been identified (Barberon and Geldner 2014). Furthermore, the polar localization of some of these transporters has been identified thanks to the discovery of the polarly localized silicic acid transporters Lsi1 and Lsi2 in rice roots (Ma et al. 2006, Ma et al. 2007). In Arabidopsis, a similar localized polarity was found for the boric acid transporters NIP5;1 and BOR1/BOR2 (Takano et al. 2010). In this issue, Shimotohno et al. (2015) applied the previously developed mathematical model of auxin transportation (Grieneisen et al. 2014). Furthermore, the polar localization of some of these transporters has been identified thanks to the discovery of the polarly localized silicic acid transporters Lsi1 and Lsi2 in rice roots (Ma et al. 2006, Ma et al. 2007). In Arabidopsis, a similar localized polarity was found for the boric acid transporters NIP5;1 and BOR1/BOR2 (Takano et al. 2010). In this issue, Shimotohno et al. (2015) applied the previously developed mathematical model of auxin transportation (Grieneisen et al. 2007) to boron transport in roots, and compared the simulation outputs with the experimental data for boron distribution using laser ablation-inductivity coupled plasma-mass spectrometry (LA-ICP-MS). They suggested that roots of A. thaliana have two functional domains with different physiological roles in terms of boron transport and boron utilization. In another root study, Sakurai et al. (2015) developed a mathematical model of the silicon (Si) transport system in rice, and assimilated the actual data for silicon concentration in the xylem sap into their mathematical model. They suggested that the double-layered structure of the Casparian strip in rice roots plays an important role in efficient Si uptake. They also demonstrated that of the various combinations, the arrangement of Lsi1 and Lsi2 found in wild-type rice roots is the most efficient for Si uptake.

Another essential nutrient for growth is photosynthetically derived sucrose. Sucrose is transported from source leaves to sinks via phloem. Fluxes of sucrose solution in phloem have been modeled based on the pressure–flow hypothesis in which solution flux between sink and source is determined by their hydrostatic pressure difference (Münch 1930). A number of mechanistic models of phloem transport based on the pressure–flow hypothesis have been proposed (Dewar 1993, Minchin et al. 1993, Thompson and Holbrook 2003, Hölttä et al. 2006). Seki et al. (2015) advanced these models by considering a complex phloem network in rice panicles, and used this model to determine the optimal shape of panicles that would allow high grain yield. Such mathematical models should be useful for designing theoretical crop ideotypes for high grain yield before any yield improvement breeding experiments are actually performed.

We hope that this Special Focus Issue will provide readers with a useful overview of the field of plant modelling and inspire new ideas and directions for future investigations into plant survival, growth and reproductive strategies.

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### References


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