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Understanding plant organ growth: a multidisciplinary field

Plant growth and development are complex, dynamic, and multifactorial events that need multiscale and multidisciplinary approaches to identify the different players involved in their regulation. In addition, growth is not only regulated by internal signals, but is also dependent on external cues, which implies the existence of a complex and interconnected network of regulators integrating all signals to drive and/or adapt growth. This virtual issue introduces active research and technical developments that are helping to build a holistic image of the regulation of plant organ growth, which is of high interest in view of the increasing need for plant-derived products.

In plants, final organ size is attained through the precise coordination of cell division, cell growth, patterning, and differentiation. How this final size is regulated is a challenging question since growth is a dynamic, complex process that therefore needs to be studied at different levels from the cell to the tissue, the organ, and the whole organism. In addition, growth is influenced by internal (genetic) and external (light, nutrient, water, pathogens, etc.) factors requiring complex and coordinated regulatory networks. For years, the model plant *Arabidopsis* has been studied to identify the essential players of growth control, with the transfer of some knowledge to crop species. Increasingly, scientists now directly use crops to study growth control mechanisms, which are often species specific.

Multiscale and multidisciplinary approaches to study plant organ growth

To assess the regulation of plant organ growth, a multidisciplinary approach that integrates genetics, physiology, imaging, computational modelling and physics is needed. Novel genes involved in the regulation of organ growth (Randall *et al.*, 2015; Van Leene *et al.*, 2016; Meng *et al.*, 2019) are often identified through traditional reverse and forward genetics, but the characterization of mutants and transgenic lines with altered organ size requires diligent phenotyping. In the past decade, numerous quantitative phenotyping methods and automated, high-throughput phenotyping platforms have been described (Fraas and Lüthen, 2015; Kuijken *et al.*, 2015; York, 2019). In particular, imaging-based phenotyping has been extensively developed in recent years to allow non-destructive and high-throughput quantitation of growth-related parameters (Fraas

and Lüthen, 2015). The phenotyping methods and imaging equipment are adapted to the organ studied (roots, leaves, or flowers) or the resolution (cell or whole organ) (Fraas and Lüthen, 2015; Kuijken *et al.*, 2015; Lee *et al.*, 2017; Youssef *et al.*, 2018). For example, a portable fluorescence spectroscopy imaging system allows the study of root architecture traits and distribution in the field (Wasson *et al.*, 2016). For the study of secondary growth, corresponding to the radial thickening of plant organs driven mainly by the vascular cambium, approaches relying on imaging and machine learning methods have been developed for precise quantification of growth at the cellular level and over time (Wunderling *et al.*, 2017).

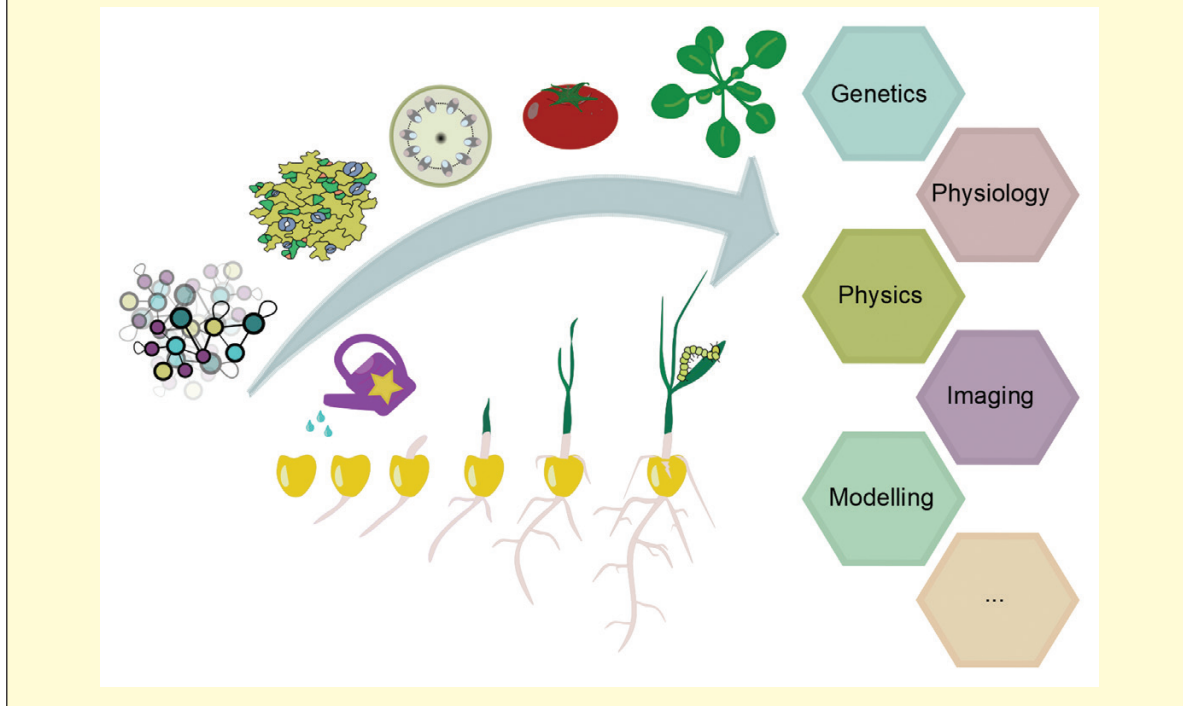
Automated and high-throughput phenotyping tools and platforms can also be used for large-scale assessment of growth-related traits of variants from diverse populations, with the aim of identifying polymorphisms responsible for growth variation (Atkinson *et al.*, 2015; Kuijken *et al.*, 2015; York and Lynch, 2015; Wu *et al.*, 2019). One such example employed high-throughput micro-CT-RGB imaging to quantify tillering traits during the early stages of growth in >200 rice accessions, allowing the identification, by genome-wide association, of several interesting loci associated with the phenotypic variation observed (Wu *et al.*, 2019).

Compared with the genetic regulation of organ growth, relatively little is known about how mechanical forces regulate growth in plants. In their review, Echevin *et al.* discuss the recent advances and knowledge gaps regarding the role of biomechanics in the control of organ growth and morphogenesis (Echevin *et al.*, 2019). This manuscript is part of a collection of papers from the special issue 'Plant Biomechanics: Force, Form, and Function' that illustrates the importance of mechanics for the design of cells and tissues.

To unravel the contribution of the numerous processes involved in organ growth regulation and fully comprehend the complexity of the dynamics of growth, mathematical models are indispensable. Different types of models may be employed, such as purely genetic models probing relationships between molecular players, or models integrating molecular, physiological, and growth-related parameters at different scales. For example, to identify the key processes controlling grape berry growth, a functional-structural plant model was developed to simultaneously simulate berry growth and whole-plant carbon and water status (Zhu *et al.*, 2019). In addition, several mathematical models consider mechanics as a major driving force for growth and were developed to explain pollen tube growth or

Box 1. The study of plant growth needs multiscale and multidisciplinary approaches

Plant growth is a complex, dynamic, and multifactorial trait regulated by internal and external signals. The identification of the regulators of growth requires multiscale and multidisciplinary approaches.



the development of pavement cells and the shoot apical meristem (Smithers *et al.*, 2019).

Complex and organ-specific growth regulation at the molecular level

Many of the key players for the regulation of growth, identified through classical forward or reverse genetic approaches, influence growth at different stages of the plant life cycle or in different organs. Shoot and root meristems are made of pluripotent cells, are responsible for the production of lateral organs (primary root, leaves, and flowers), and are essential to model plant growth and architecture. Any perturbation in the formation and maintenance of meristems will therefore impact plant development. For example, in *Medicago truncatula*, disruption of HEADLESS, a homologue of Arabidopsis WUSCHEL, leads to disorganization and arrest of the shoot apical meristem and the formation of shorter leaves with altered shape (Meng *et al.*, 2019).

Studies mainly performed in Arabidopsis have identified numerous leaf growth regulators involved in various processes determining growth (González and Inzé, 2015), including cell division and the cell cycle (Blomme *et al.*, 2014), cell expansion, and also organelle development (Van Dingenen *et al.*, 2016). In Arabidopsis, GROWTH-REGULATING FACTOR (GRF) and GRF-INTERACTING FACTOR are key transcriptional regulators involved in leaf growth regulation, mainly acting to

control cell proliferation (Kim and Tsukaya, 2015). Leaf growth regulators have also been described in crops, such as in the *bigger organs (bio)* and *elephant-ear-like leaf 1 (ele)* pea mutants, which produce enlarged leaves (Li *et al.*, 2019).

Flower development involves the conversion of the vegetative shoot apical meristem into an inflorescence meristem that then initiates floral meristems forming the floral organs, sepals, petals, stamen, and carpel. Initially, the proper development of floral organs requires the correct establishment of floral organ identity that involves different combinations of MADS-domain transcription factors (Sablowski, 2015; Callens *et al.*, 2018). Other transcription factors, such as the three closely related AP2 transcription factors, DORNROESCHEN, DORNROESCHEN-LIKE, and PUCHI, redundantly contribute to floral organ initiation and specification by controlling meristem identity (Chandler and Werr, 2017). After floral organ initiation, final size is determined by the number and size of cells forming the organ. In Arabidopsis, two genes involved in cell division regulation, *AINTEGUMENTA* and *CYCD3;1*, independently contribute to petal size control (Randall *et al.*, 2015). After pollination and ovule fertilization, fruit and seed development is initiated. In tomato, a model species for fleshy fruits, several genes regulating both cell division and cell expansion, and therefore influencing fruit growth and final size, have been described (Azzi *et al.*, 2015). MADS-box proteins also play a role in seed growth. In tomato, alteration of *SIMP3*, encoding an AGAMOUS MADS-box protein, leads to the modulation of seed size (Zhang *et al.*, 2019). In rice, an

ERF domain protein, FRIZZY PANICLE, plays an important role in the regulation of grain size since mutation of this gene causes the formation of smaller grains resulting from a reduction in cell number and cell size in the hulls (Ren *et al.*, 2018).

Phytohormones play major roles in plant growth, and the perturbation of hormone levels can result in changes to the growth and development of all organs. For example, gibberellins promote leaf growth, seed germination, and floral transitions, and mutants affected in gibberellin biosynthesis or signalling present growth alterations (Achard and Genschik, 2009). In sugarcane, alteration of *ScGAI*, an orthologue of DELLA protein genes that are well known growth repressors negatively regulated by gibberellin, affects culm and leaf growth (Garcia Tavares *et al.*, 2018). In roots, hormones, and especially auxin, play an essential role by controlling growth rate, branching, and lateral root formation (Pacifi *et al.*, 2015; Satbhai *et al.*, 2015; Abu-Abied *et al.*, 2018; Du and Scheres, 2018; Motte and Beeckman, 2019). Ethylene also affects primary root growth by regulating cell division and expansion, and is also a positive regulator of root hair development. Hu *et al.* (2018) have shown that *CSLD3*, a gene of the cellulose synthase-like D family, acts downstream of the ethylene signalling pathway for the control of root and root hair elongation.

Growth and environment

In contrast to animals, plants are sessile organisms, being anchored in the soil by their root system. Plants have therefore developed mechanisms allowing them to adapt their growth in response to environmental changes, such as fluctuations in temperature, light, water, or nutrient availability. Auxin is an essential integrator of these environmental cues, thereby regulating developmental growth (Mroue *et al.*, 2018).

Individual environmental stimuli have also been shown to affect organ growth in specific ways. In the leaf, persistent canopy shade leads to exit from cell proliferation that depends at least in part on the action of the HD-ZipII transcription factors ATHB12 and ATHB4 (Carabelli *et al.*, 2018). Root growth is influenced by external signals such as mineral nutrition and, in leaf cuttings of *Petunia hybrida*, it has been shown that iron and ammonium stimulate adventitious root formation (Hilo *et al.*, 2017). Water deficit also influences plant organ growth and development. During flowering, the abortion of reproductive organs in maize occurs as a result of mild water deficit due to interference with the hydraulic control of expansive growth (Turc and Tardieu, 2018). In rice, a reduction in seed yield and quality is caused by different mechanisms in high day or night temperatures, a phenomenon that depends on whether the variety is susceptible or tolerant to heat (Shi *et al.*, 2017).

Plant organ growth and crop yields

Organ growth regulation plays an important role in the future challenges that face us to meet the increasing demand for food, feed, and biofuels, for which agricultural yields must rise. Various strategies exist for improving crop yield, ranging

from translating findings from model organisms to crops, to studies directly performed in the target crop and often in agronomic field conditions. Simkin and collaborators review a number of studies that aim to improve photosynthetic carbon fixation through genetic engineering, thereby increasing the carbon source strength and providing increased carbohydrates for growth, and potentially increasing yield (Simkin *et al.*, 2019). An alternative approach is to improve the stress tolerance of crop species. For example, in transgenic wheat lines expressing a mutated version of the sunflower transcription factor HaHB4, increased yield and water use efficiency were observed, especially under conditions of water deficit (Araus *et al.*, 2019; González *et al.*, 2019). The modification of plant architecture is also a viable approach to improve crop yields. Wang and colleagues review the potential role of auxin biosynthesis, transport, and signalling proteins in altering root morphology, tiller and panicle architecture, and flower development to boost the yield of rice (Wang *et al.*, 2018).

We hope that this 'live' virtual issue on plant organ growth will further boost world-wide interest and research on the challenging biological problem of the regulation of growth. Understanding how organ size is controlled is of academic interest, but a better comprehension of this process can also contribute to the improvement of crop yield through genetic modification, gene editing, and advance breeding.

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