

## eXtra Botany

### Special Issue Editorial

## Genetic encoding of complex traits

**Plants provide food for humans, directly or through their use as feed for animals. However, arable land is becoming scarce and resources, including water and fertilizers, are becoming depleted under the effects of global climate change and the growing human population. To ensure food security for future generations, new approaches to improve crop productivity based on fundamental knowledge are needed. This special issue describes progress in our understanding of four traits that may be important for the development of future crops.**

Plants sustain life on earth by converting light energy, water, and CO<sub>2</sub> into chemical energy and the building blocks of all organisms, including those that produce our food. However, a number of challenges threaten the production of sufficient food in the future, including loss of agricultural land, climate change, and the increasing human population. Furthermore, agriculture must address the United Nations Global Goals for Sustainable Development, in particular, the promotion of sustainable use of terrestrial ecosystems and ending hunger, achieving food security and improved nutrition, and promoting sustainable agriculture. To resolve the conflict between producing sufficient food for future generations and agricultural sustainability, it is necessary to develop innovative strategies for plant breeding and crop production. This is possible only through an increased fundamental understanding of how plants adapt to environmental conditions and constraints. The answers to these questions are encoded in the existing natural and artificially induced genetic variation that enables plant species and their associated microbes to colonize almost all terrestrial environments. However, many of the traits that are crucial for resource-efficient plant growth are complex, that is, they are encoded by multiple genes that interact with each other and with the environment. The contributions in this special issue address four such complex traits.

### Annual and perennial life history

Most perennial plants flower and reproduce repeatedly during their life cycle, whereas annuals reproduce only once. This

divergence in life history is associated with many related phenotypic differences. For example, perennials often reproduce clonally, reducing their dependence on seed production, while annuals usually produce high numbers of seeds (Albani and Coupland, 2010). In addition, perennials are able to return to vegetative development after flowering and typically produce more extensive root systems, making perennial plants successful in marginal soils while at the same time providing beneficial ecosystem services (Bandaru *et al.*, 2013). The mechanisms underlying flowering control are thus of utmost importance for the annual and perennial life history (Kiefer *et al.*, 2017). As reviewed by Coupland *et al.* (2021), the key player in the control of flowering initiation is the MADS-domain transcription factor FLOWERING LOCUS C (FLC). FLC represses a transcriptional network of flowering genes, and is itself inhibited by cold, thus underlying the process of vernalization. In perennial plants, FLC suppresses post-vernalization flowering in axillary branches and thus ensures their return to vegetative development (Lazaro *et al.*, 2018). The review of Coupland *et al.* (2021) in this issue focuses on the gene regulatory networks controlled by FLC and explains how they influence floral transition. A part of the regulatory network of flowering initiation is FLOWERING LOCUS T (FLT), a small protein that is synthesized in the leaves and translocated via the phloem to the shoot apical meristem to induce floral transition (Corbesier *et al.*, 2007). Since grain yield in cereals is dependent on the control of reproductive development, understanding the mechanisms of control of flowering may contribute to the identification of novel breeding targets. Therefore, Pieper *et al.* (2021) analysed the function of *HvFT4*, one of 12 *FT-like* genes from barley. Overexpression of *HvFT4* led to delayed flowering of barley, caused by delayed spikelet initiation, and was also associated with reduced numbers of spikes and grains per spike. These and other results led to the conclusion that *HvFT4* acts as a repressor of reproductive development in barley. Another piece of the jigsaw of control of reproductive development in barley is the identification of the photoperiod response gene *PHOTOPERIOD-H1* (*Ppd-H1*) as an integrator of photoperiod and drought stress signalling to modulate spike development (Gol *et al.*, 2021). While spring barley cultivars, which possess a mutation in the *Ppd-H1* gene,

were affected in their floral development by drought, this effect was lost in lines with the original wild barley *Ppd-H1* allele. Thus, the results demonstrated that in barley, *Ppd-H1* affects developmental plasticity in response to drought.

## C<sub>4</sub> photosynthesis

C<sub>4</sub> photosynthesis is an evolutionary innovation that results in significantly greater plant productivity due to more efficient carbon fixation and consequently also better water and nitrogen use efficiency. It is a complex trait that, despite requiring anatomical, biochemical, and physiological adaptations, evolved independently more than 60 times during land plant evolution (Sage, 2017). However, the major staple crops, with the exception of maize, are C<sub>3</sub> plants, so engineering C<sub>4</sub> photosynthesis in these crops presents an attractive possibility to improve future crop yields (Schuler *et al.*, 2016). Although such engineering—for example, of C<sub>4</sub> rice—has been a long-standing goal, it still remains an enormous challenge to coordinately trigger alterations in plant metabolism and anatomy. Dissecting and understanding the genetic mechanisms underlying this complex trait are thus pre-requisites to exploit the C<sub>4</sub> photosynthetic machinery to enhance the photosynthetic efficiency and productivity of C<sub>3</sub> crops. A large number of tools and resources have been obtained within the past decade, including genome and transcriptome sequences from numerous C<sub>4</sub> species (reviewed in Schlüter and Weber, 2020), a metabolic model of C<sub>4</sub> photosynthesis (Bräutigam *et al.*, 2014), and mathematical models describing the evolution of C<sub>4</sub> photosynthesis (Heckmann *et al.*, 2013; Mallmann *et al.*, 2014; Blätke and Bräutigam, 2019). In addition, attention is starting to be given to other areas of C<sub>4</sub> biology, such as mineral nutrition (Jobe *et al.*, 2019). In this issue, Zamani-Nour *et al.* (2021) address another key issue for C<sub>4</sub> photosynthesis, namely metabolite transport. Overexpression of chloroplastic 2-oxaloacetate/malate transporter (OMT1), which plays an important role in C<sub>4</sub> plants, in rice unexpectedly led to large-scale alterations in metabolite accumulation, an imbalance between C and N metabolism, and a growth penalty. The phenotype could be reverted by overexpression of DiT2 transporter to export aspartate accumulated in the plastids. Thus, for engineering of the C<sub>4</sub> photosynthetic cycle, broader C and N metabolite fluxes need to be considered.

## Molecular mechanisms of plant–microflora interactions

Plants in their natural environment are in constant interaction with a wide range of microorganisms. These interactions can be beneficial, neutral, or detrimental for the plant, depending on the taxonomic composition of the microbiota as well as the environment (Bulgarelli *et al.*, 2013). Interactions between

plant roots and rhizosphere microbiota are, therefore, critical for plant fitness in natural environments as well as for agricultural crop yields. The past decade brought a great increase in understanding of the factors governing the composition of the plant microbiome and its benefits for plants (Haney *et al.*, 2015; Hiruma *et al.*, 2016; Muller *et al.*, 2016; Castrillo *et al.*, 2017; Finkel *et al.*, 2017; Jacoby and Kopriva, 2019). One of these factors is the glycans and glycoconjugates on the surface of the microbes, which are crucial for their recognition by plants. Wanke *et al.* (2021) review the role of these glycans in communication between plants and microbes. The focus of the review is the perception and recognition of the microbial extracellular glycans and their role in plant–microbe interactions. The leaf microbiome is the focus of a review by Chaudhry *et al.* (2021), which addresses the factors affecting the colonization of leaves and the microbe–microbe interactions within the leaf environment. The review discusses how microbial communities affect susceptibility to plant pathogens and vice versa, and the impact of pathogens and endophytes on leaf colonization. Particular attention is given to the plant immune system and its role in shaping the leaf microbiome.

## Role of metabolites in biotic interactions

Plants modulate the structure and function of microbial communities by exuding metabolites, which are an important carbon source for the growth of soil-borne microbes. But plants also produce a wide variety of secondary compounds, which play an active role in shaping the rhizosphere microbiome (Zhalnina *et al.*, 2018). Several metabolites have recently been shown to directly affect the composition or function of the microbial communities. In this issue, Jacoby *et al.* (2021) summarize current progress in the elucidation of the role of secondary metabolites in shaping the plant microbiome. A number of compounds, including coumarins, glucosinolates, benzoxazinoids, camalexin, and triterpenes, are discussed in detail, as are recent advances in methodologies that will be crucial for further dissecting the metabolic interdependence in the rhizosphere. One class of such secondary compounds, the glucosinolates, is the topic of a review by Mitreiter and Gigolashvili (2021). This review describes the molecular mechanisms of glucosinolate regulation, focusing on the integration of the glucosinolate transcriptional network with hormonal, environmental, and epigenetic factors. For the secondary metabolites to act in interaction with microbes, they need to be excreted from the cells. This transport, and particularly the G-family of ABC transporters, is reviewed by Gräfe and Schmitt (2021). The ABCG transporters are involved in various important processes, such as the response to pathogens, the formation of diffusion barriers, or the transport of phytohormones. However, the substrate specificity of many of these transporters is still unknown, and this review points out the importance of further research on these important transporters.

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