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How can developmental biology help feed a growing population?

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ABSTRACT

Agriculture is challenged globally from a variety of fronts, including a steady increase in world population, changes in climate and a requirement to reduce fertiliser inputs. In the production of crops that are able to overcome these challenges, developmental biology can play a crucial role. The process of domesticating wild progenitors into edible crops is closely linked to modification of developmental processes, and the steps that are needed to face the current challenges will equally require developmental modifications. In this Spotlight, we describe the achievements by developmental biologists in identifying the genes responsible for domestication of some of the most important crops, and highlight that developmental biology is in a unique position to remain centre stage in improving crop performance to meet current and future demands. We propose that the explosive technological advances in sequencing, genome editing and advanced data processing provide an excellent opportunity for researchers to combine scientific disciplines and realise the continued potential of plants as the primary food source for generations to come.

KEY WORDS: Domestication, Gene function, Crop improvement, Model-to-crop translation, Plant development

Introduction

Plants form a vital component of the human diet, and the domestication of crops from their wild progenitor species has frequently involved modification of developmental traits such as shape, size and overall architecture to optimise yields, improve harvestability and make the food easier and more palatable to eat. These modifications have been driven by human selection and have formed the basis of an important relationship between humans and plants that has guided domestication of crops and the transition of humankind from a hunter-gatherer nomadic lifestyle to an agricultural-based society that formed the basis of modern civilisation. In recent years, advances in genomic technologies and our understanding of developmental processes have helped identify the genes and alleles that contributed to the emergence of modern crops from their progenitors. Research on crops has been complemented by studies using model plants, such as *Arabidopsis thaliana*. This has significantly advanced our understanding of the genes and molecular processes that determine the size and shape of multiple organs, as well as those that integrate environmental signals to regulate the vegetative-to-reproductive transition that is so important for fitness and seed productivity. Advances in our understanding of the genes that control development and the improved technological resources available to crop research means that we are well-poised to further modify developmental traits to

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boost crop productivity, which is vital given that yields of cereals need to significantly increase by 2050 to maintain food security for the world's growing population (Tilman et al., 2011; Fisher, et al., 2014; Hunter et al., 2017).

Domestication and breeding

During the Neolithic Revolution around 10,000 years ago, people began domesticating selected plant species and growing them in an agricultural setting. The most critical wild characters to overcome were associated with basic developmental processes. 'Taming' plants that had been under natural selection for their ability to succeed in the wild required the elimination of certain 'weedy' traits such as those linked with seed dispersal and plant architecture (Konishi et al., 2006; Gallavotti et al., 2004; Doebley et al., 1997). Studying the genetic basis of crop domestication is therefore largely equivalent to studying aspects of plant development. As a consequence, understanding the genetic and molecular mechanisms underlying developmental processes has massive potential to further improve the performance of today's major crops and point out routes for fast-track domestication of less developed crops.

For cereals including wheat, barley, rice and maize, naturally occurring varieties that were able to hold on to their seeds until harvest (dispersal-proof) provided a major advantage for early farmers. Phenotypic characterisation of dispersal-proof varieties revealed that they fail to develop abscission zones at the base of the seeds (between the pedicel and spikelet in cereals), thereby preventing the cell-separation process that is needed to shed the seeds (Konishi et al., 2006; Li et al., 2006; Hodge and Kellogg, 2016). Identifying the responsible gene(s) and studying the mechanism by which specification of the abscission zone cells has been altered is therefore a bona fide developmental biology problem. In addition to the fundamental understanding of cell-specification processes, such work may provide insight into yield loss in other crops. For example, seed dispersal remains a serious problem in more recently domesticated crops such as oilseed rape and soybean (Price et al., 1996; Tukamuhabwa et al., 2001).

Advocating developmental biology

This article is part of Development's advocacy collection – a series of review articles which make compelling arguments for the field's importance. The series is split into two: one set of articles, including this one, addresses the question 'What are the big open questions in the field?' We would argue that there has never been a more exciting time to get involved in developmental biology: incredible new tools mean making fundamental problems are increasingly within reach. A complementary set of articles will ask 'What has developmental biology ever done for us?' Together, the articles will provide a collection of case studies looking backwards to the field's achievements and forwards to its potential, and a resource for students, educators, advocates and researchers alike. To see the full collection as it grows, go to http://dev.biologists.org/content/advocating-developmental-biology.

DEVELOPMENT

In addition to general domestication traits, several species-specific traits are also based on the manipulation of plant development. One example is the maize kernel (grain). In the wild progenitor of maize, teosinte (*Zea mays* ssp. *parviglumis*), the kernel is encased in a hardened tissue that functions to protect the developing offspring. However, the encasement makes it unsuitable as a food source, and maize domestication crucially relied on the liberation of the kernel so that it is exposed on the surface of the ear (Wang et al., 2005). Another example of species-specific trait modification comes from tomato, where the domesticated species *Solanum lycopersicum* produces fruits that are dramatically larger than the pea-sized fruits of its wild progenitor *S. pimpinellifollium* (Alpert et al., 1995; Frary et al., 2000). Third, the transition from the typically bushy architecture with many tillers and wide tiller angles of the wild rice progenitor, *Oryza rufipogon*, to the domesticated *O. sativa* (with optimal tiller angle and number) is considered one of the most important events in rice domestication (Jin et al., 2008).

Crop domestication was driven by farmers selecting seeds from the plants that performed best to use in the next generation, without any knowledge of genetics. The domestication of some of the major crops that we rely on today is considered to have been achieved around 4000-9000 years ago (Doebley et al., 2006), but additional improvements have still occurred through performance selection. In this way, step-wise improvements were achieved by selecting the highest-yielding plants as parents for the next generation. A major leap in wheat performance was achieved through traditional breeding in the 1950s via the adoption of semi-dwarf varieties by Norman Borlaug, who founded the CIMMYT crop research centre in Mexico. Semi-dwarfed wheat varieties display reduced lodging and contributed to yield increases by allowing more resources to contribute to grain development (reviewed by Khush, 2001) (Fig. 1). This led to what has been named the 'Green Revolution', credited to have saved ~1 billion people from starvation, for which Borlaug received the Nobel Peace Prize in 1970. The challenge for developmental biology has subsequently been to identify the genes underlying both the Domestication Syndrome (Hammer, 1984;

Olsen and Wendel, 2013) and the Green Revolution, and understand the molecular function of the proteins they encode.

The role of developmental biology

Developmental genetics has identified genes responsible for the domestication of several crops. Such findings are particularly impressive because they uncover crucial parts of human history, and also because they result from long-term projects in complex genetic backgrounds that teach us fundamental aspects of biology and gene function. For example, the qSH1 and SH4 genes were found to be responsible for preventing seed dispersal in domesticated rice (Konishi et al., 2006; Li et al., 2006). In the case of the qSH1 gene, which encodes a transcription factor that promotes seed abscission zone formation, the single base-pair mutation responsible for the dispersal phenotype is located in a cis-regulatory element 12 kb upstream. The effect of this polymorphism in domesticated rice is loss of qSH1 expression in the seed abscission zone, which leads to a defect in seed detachment (Konishi et al., 2006).

Another example is provided by maize, where the hardened tissue encapsulating the kernel is dependent on the *tga1* gene encoding an SBP-type transcription factor (Wang et al., 2005). A single amino acid substitution between teosinte and maize in the TGA1 protein is responsible for achieving the 'naked' kernel, which is an all-important domestication trait for maize (Wang et al., 2015). Both versions of the TGA1 protein are able to bind a GTAC motif; however, the maize-TGA1 protein forms dimers that are more stable than the teosinte-TGA1. This results in the maize-TGA1 transforming into a transcriptional repressor rather than an activator as in teosinte (Wang et al., 2015).

In the case of the Green Revolution traits in wheat, dominant mutations that stabilise members of the growth-repressing DELLA proteins, such as Rht-1, were found to cause the semi-dwarfing phenotype (Peng et al., 1999) (Fig. 1). In rice and barley, semi-dwarfed varieties were generated using loss-of-function alleles for enzymes with key roles in biosynthesis of gibberellin (GA) (e.g. *GA20oxidase* for *sd-1* and *sdw*-1) (Spielmeyer et al., 2002; Jia et al.,
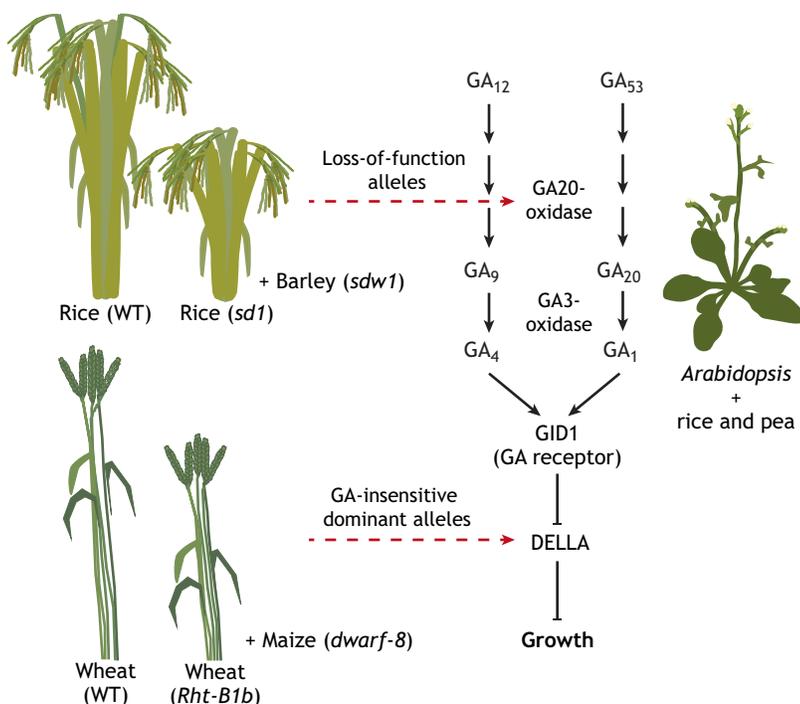

Fig. 1. Adoption of semi-dwarfed crop species in agriculture and elucidation of the gibberellin (GA)-dependent control of growth in model species. Semi-dwarfed wheat, rice and barley were central to the 'Green Revolution' of the 1960s/1970s, which involved the adoption of alleles that reduced stem growth and plant height. Subsequent analysis of the GA biosynthesis pathway and the regulation of growth by the DELLA protein in model species such as *Arabidopsis*, pea and rice identified the molecular basis of these dwarfing alleles used in crops. These include loss-of-function alleles for a key GA biosynthesis enzyme (GA20-oxidase) in rice and barley (*sd1* and *sdw1*), and dominant alleles of the *DELLA* gene in wheat and maize that encode a protein insensitive to GA treatment (e.g. *Rht-B1b*).

2011). The cloning and functional characterisation of the DELLA proteins as negative regulators of GA signalling was revealed in the model species, *Arabidopsis thaliana*, pea and rice (Peng et al., 1997; Dill et al., 2001); this fundamental work was important to facilitate the identification and molecular understanding of the dwarfing alleles in cereals, which included demonstration that a GA-insensitive DELLA protein underpins the *dwarf-8* locus of maize. Further molecular studies revealed that, in the absence of GA, DELLA proteins inhibit growth by preventing transcription factors like those of the basic helix-loop-helix (bHLH) family from binding and regulating their target genes (Feng et al., 2008). In contrast, when GA is present, it binds the GID1 receptor. This promotes GID1-DELLA interactions and thus relieves the bHLH transcription factors of repression. Upon GID1 interaction, DELLA proteins are ubiquitylated and subsequently degraded in the proteasome (Sun, 2008).

The *TEOSINTE BRANCHED1* (*TB1*) gene was first identified in maize and epitomises the convergence of research investigating the genetic regulation of key domestication-related traits in crops and developmental research in model organisms (Doebley et al., 1995; Fig. 2). TB1 is known as *BRANCHED1* (*BRC1*) in *Arabidopsis*, pea and potato, *cycloidea* in snapdragon (*Antirrhinum majus*), *INTERMEDIUM-C* in barley, *TB1* in wheat and sorghum, and *fine culm* in rice (Luo et al., 1996; Doebley et al., 1997; Hubbard et al., 2002; Takeda et al., 2003; Aguilar-Martinez et al., 2007; Finlayson, 2007; Kebrom et al., 2010; Ramsay et al., 2011; Braun et al., 2012; Nicolas et al., 2015; Dixon et al., 2018). *TB1* was identified as a gene that contributed significantly to maize domestication by promoting the dominant growth of the main stem compared with side stems (a phenomenon known as apical dominance) in modern cultivars. It was subsequently revealed that increased expression of the *TB1* allele in modern cultivars suppresses branch outgrowth and alter floral architecture traits partly by activating expression of a gene encoding an ankyrin repeat domain protein (Doebley et al., 1997; Dong et al., 2017; Studer et al., 2017). This research coincided with the identification of the *TB1*-homologue, *cycloidea* (*CYC*) in *Antirrhinum*, which controls dorsoventral asymmetry, with loss-of-function alleles producing flowers that are radially symmetrical (Luo et al., 1996) (Fig. 2). In *Arabidopsis*, *BRC1* was shown to delay flowering of lateral branches by inhibiting the ability of FLOWERING LOCUS T (FT) protein to form part of the floral activation complex required to activate flowering within the shoot apical meristem (Niwa et al., 2013). These two developmental roles for *CYC* and *BRC1* discovered in model plants inspired the molecular dissection of the role for *TB1* in wheat, where its increased expression was found to promote formation of additional spikelets, with TB1 shown to interact with FT1 and delay the formation of spikelet meristems (Dixon et al., 2018) (Fig. 2). The conserved role of *TB1*-like genes in controlling floral architecture is further supported by *INT-C* contributing to the two-rowed versus six-rowed inflorescence architecture of barley, with the sixed-rowed phenotype being limited to domesticated barley (Ramsay et al., 2011) (Fig. 2). Moreover, *Tb1* in maize controls the formation of floral structures called cupules that contain spikelet pairs (Doebley et al., 1995) (Fig. 2). Taken together, these studies highlight the importance of a single developmental gene that has contributed significantly to ancient events of crop plant domestication, and how insights from modern research has provided clues about the developmental mechanisms that underpin the gene's contribution to key agricultural traits (Fig. 2).
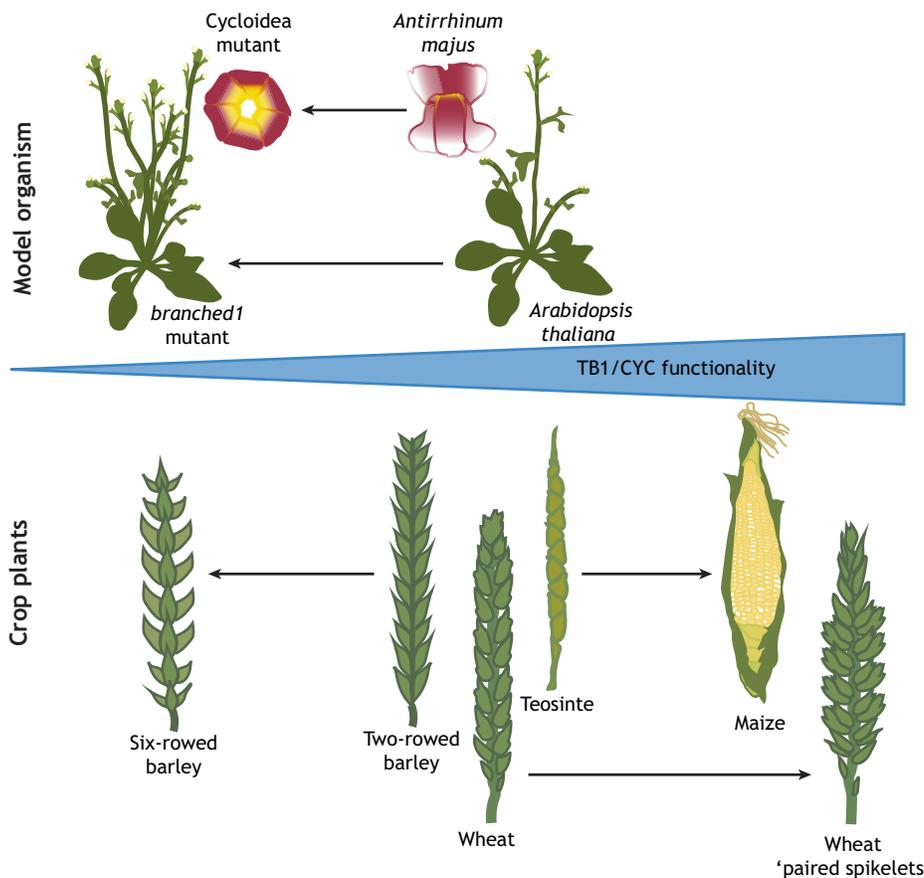

Fig. 2. Complementary genetic analysis of *TEOSINTE BRANCHED1/CYCLOIDEA* function in model and crop species to explain key developmental traits. Analysis of key developmental traits, including shoot branching, floral symmetry and inflorescence architecture, in model (e.g. *Arabidopsis thaliana*, *Antirrhinum majus*, pea) and crop species (e.g. maize, barley, wheat, rice) has identified a key role for the gene *TEOSINTE BRANCHED1/CYCLOIDEA* (*TB1/CYC*). *TB1/CYC* alleles have been identified to modify shoot and floral architecture traits by altering gene expression or the functionality of the encoded protein, as highlighted by the width of the blue triangle. Examples of model species are shown above the triangle and crop species below. Not all of the trait differences represented by the illustrations are driven by allele diversity for *TB1*.

Fundamental understanding of developmental processes guides crop improvement

Developmental biology in crop plants is not just about revealing the history of domestication: knowledge about gene function in both model and crop species is pointing the way to improve specific traits. In the 1980s, *Arabidopsis* became the favourite model system for flowering plants and was the first plant genome to be sequenced (Arabidopsis Genome Initiative, 2000). Work in *Arabidopsis* has led to an unprecedented wealth of knowledge on plant development. Although some aspects of plant development are shared only between *Arabidopsis* and its closest relatives, other processes are widely conserved across the plant kingdom (for example gibberellin signalling and the function of DELLA proteins described above) and *Arabidopsis* can therefore guide improvements in crop performance. Such model-to-crop approaches have particular potential between *Arabidopsis* and the evolutionarily closely related Brassica crops such as oilseed rape, cabbage and broccoli (Beilstein et al., 2010). Knowledge of tissue specification in the *Arabidopsis* fruit, for example, is a powerful example of the model-to-crop approach. The *Arabidopsis* seed pod opens and disperses its seeds in a process known as pod shatter, similar to oilseed rape (Spence et al., 1996). It has been estimated that losses in oilseed rape due to pod shatter range from 11-25% depending on the weather around the time of harvest (Price et al., 1996). In addition to the significant yield loss [∼£100-150 million in the UK in 2017 (DEFRA, 2018)], the seeds that drop to the ground may germinate in following years and contaminate successive crops in the rotation cycle.

Seed dispersal is facilitated by the formation of specific tissues. The valves (or seed pod walls) are connected to a central replum via the so-called valve margin cells. The valve margin tissue will break down late in development to mediate the detachment of valves from the replum and release of the mature seeds (Spence et al., 1996). Components controlling the formation of the specific pod tissues in *Arabidopsis* have been identified and described, revealing a fascinating developmental mechanism involving a tight network of genetic and hormonal interactions (Ferrándiz et al., 2000; Liljegren et al., 2004; Dinneny et al., 2005; Sorefan et al., 2009; Arnaud et al., 2010). Specifically, it has been demonstrated that valve-margin identity genes are actively repressed in both the valves and the replum, restricting their activity to the strips of cells that form at the valve-replum border (Dinneny et al., 2005). It has since been demonstrated that this mechanism is conserved in Brassica species (Østergaard et al., 2006; Girin et al., 2010), and this advance has now been translated into oilseed rape and demonstrated to reduce pod shatter (Braatz et al., 2018), providing potentially the clearest model-to-crop example reported to date.

While *Arabidopsis* has proved a particularly excellent model for Brassica crops, it has also led to the elucidation of mechanisms potentially translatable to a wide range of crops. For example, analysis of the molecular pathways controlling *Arabidopsis* meristem maintenance has benefited research in tomato, maize and rice, and developmental traits influencing flower number and plant architecture. Seminal research in *Arabidopsis* identified a negative-feedback loop involving WUSCHEL (WUS) and CLAVATA3 (CLV3) that coordinates stem cell proliferation with differentiation; subsequently, receptors and signalling components that relay the CLV3-derived signal at the cell membrane to the nucleus to reduce expression of *WUS* were identified (Brand et al., 2000; Schoof et al., 2000, reviewed by Somssich et al., 2016). Genes that encode components of this negative-feedback loop have subsequently been identified in rice, tomato and maize, with mutant alleles found to affect kernel row numbers of the maize ear and meristem size and floral organ number in tomato and rice (Suzaki et al., 2004; Bommert et al., 2005, 2013a,b; Xu et al., 2015). However, that the route of information between *Arabidopsis* and other plants is not a one-way street. Work in maize recently identified the leucin-rich-repeat receptor, FASCIATED EAR3 (FEA3), that provides feedback from organ primordia to control the stem cell niche in plants (Je et al., 2016). This activity had previously been hypothesised, but not demonstrated.

Another example where pioneering research in *Arabidopsis* has provided general information on plant development is the identification of components of the photoperiod-dependent floral induction pathways (Imaizumi and Kay, 2006). This knowledge inspired the optimisation of floral-activating gene activity in the leaf and the meristem of tomato to increase fruit production (Park et al., 2014; Lemmon et al., 2016), and also explained how extending the duration of meristem maturation increased spikelet and floret numbers in wheat and rice (Yoshida et al., 2013; Boden et al., 2015). With the improved sequence information and genetic resources that are now available in crop species, it is likely that discoveries from model plant research will drive further improvements in productivity and performance.

Brachypodium distachyon is emerging as a strong model system for grass crops in the Pooideae subfamily that includes wheat, barley, rye and oats (Scholthof et al., 2018). In terms of developmental biology, recent advances in *Brachypodium* root development are allowing comparative studies between monocot and dicot species, revealing both genetic and hormonal differences (Pacheco-Villalobos and Hardtke, 2012; Pacheco-Villalobos et al., 2016; Kim and Dolan, 2016; van der Schuren et al., 2018). Moreover, studying root development in *Brachypodium* will likely provide leads on how to improve root architecture of grass crops. Given that *Brachypodium* is a wild grass, it will be interesting to compare its root development with Pooideae crop species; one might identify traits lost during domestication but that may provide an advantage if reintroduced to crop plants today.

Whereas some model organisms function as testbeds for crops growing in fields, other species serve both as important crops and powerful model systems with which to study biological processes. Maize, rice and barley provide particularly strong examples of this. Maize, with its century-long tradition of mutant characterisation and development of genetic resources, will continue to be a powerful species for studying fundamental aspects of plant development and gene regulation (Hake and Ross-Ibarra, 2015). Indeed, maize was the model system that Barbara McClintock used to reveal the existence of transposable elements (McClintock, 1950), which later earned her the Nobel Prize, and to this day maize continues to further our understanding of epigenetic control of gene expression.

The success of the Green Revolution is largely attributed to the adoption of semi-dwarfed wheat cultivars, which were developed using a random mutation that repressed stem growth. Today, we know the identity and function of the gene based on fundamental research and it is likely that if the semi-dwarfed mutant had not been identified, scientists and breeders would have predicted the effect of such a mutation based on current knowledge and brought about the Green Revolution decades later (Fig. 1). Fortunately, Borlaug's adoption of this dwarfing allele came early enough to save billions from starvation, but knowledge obtained on gene function and developmental aspects may still lead to second- and third-generation Green Revolutions that are important to address threats of food shortage in the immediate future (Box 1).

Box 1. Development as an emerging trend for crop improvement: a personal case study by Scott Boden

As a child growing up in the warm and dry climate of southern Australia, I was reminded frequently of the negative impact that extreme weather conditions and drought can have on crop production and the livelihood of farmers. As my interest in science developed at school and university, I was inspired by the potential improvements that could be secured through advanced understanding of the biology that underpins a plant's response to its environment, and the number of grains that form on a plant. I have since followed this inspiration to build a group studying genes that regulate development of grain-producing flowers in wheat, and how flowering is influenced by temperature, with the hope of developing superior yielding cultivars that are resilient to a changing climate.

Wheat has a large and complex hexaploid genome that contains two to three copies of each gene, and so has not been a tractable organism with which to perform genetic-based developmental studies. However, with the recent release of an annotated genome and sequenced mutant resources, wheat is becoming more of a 'model' species (Krasileva et al., 2017; IWGSC, 2018). We, and other groups, are now identifying genes that contribute to the number and arrangement of flowers that form on an inflorescence, and our ability to fast-track gene discovery and understand the biology that controls flower development is assisted greatly by work that has come from model species, including *Arabidopsis*, pea, rice, maize, tomato and barley (Boden et al., 2015; Poursarebani et al., 2015; Dobrovolskaya et al., 2015; Greenwood et al., 2017; Debernardi et al., 2017; Dixon et al., 2018). Studies using these models have identified multiple genes and molecular processes that regulate inflorescence development, including those involved in hormone and sugar metabolism, micro-RNA-mediated regulation of floral-promoting transcription factors, and maintenance of meristem size and maturation. These insights are being used to reveal the molecular basis of historical wheat mutants with altered forms of inflorescences, including those with more flowers – simultaneously, analysis in wheat is advancing our understanding of how gene function and activity contributes to diverse forms of inflorescence architecture.

Now is an exciting time to be involved in plant developmental biology, as the availability of genome sequences, mutant resources and gene editing techniques expands our ability to test how gene function can be modified to increase crop productivity – groups that have used this approach in tomato, rice and maize inspire my research in wheat (Jiao et al., 2010; Miura et al., 2010; Park et al., 2014; Soyk et al., 2017). Moving forward, combined analysis of reproductive development in models and crops promises to uncover genes and molecular pathways that contribute to the remarkable diversity of floral structures displayed by plants, which will provide the key to unlock the step-changes in yield that are required for the world's growing population.

Looking forward: technologies to translate knowledge on plant development to improve crops

The advantages of models over crops as systems of choice to elucidate gene function typically include small organism size, short generation time, genetic resources, sequenced genomes and transformability. However, some of these advantages are no longer restricted to model species as technology develops. While *Arabidopsis*, *Brachypodium* and other model systems still have much to offer, the resources that are becoming available in complex crops is truly impressive. Efforts such as gene cloning and mutant production, which recently might have required over 10 years of work, is now feasible and realistic even within a 4-year PhD. This is due to the technical revolution in molecular biology and particularly large-scale sequencing in the last 5-10 years. Whereas crop breeding formerly involved genetic mapping of specific traits and tracking their segregation in breeding programmes via marker-assisted selection, modern sequencing technology allows for relatively fast identification of the relevant genetic variation

responsible for the trait. This is even possible for crops with particularly large and complex genomes, such as wheat, for which a reference genome sequence was recently published (International Wheat Genome Sequencing Consortium, 2018).

An additional major game changer for advancing knowledge of gene function in crops is CRISPR technology. Whereas mutant production has traditionally been achieved on a random basis using chemicals or irradiation, CRISPR/Cas9 facilitates targeted gene editing in any transformable species for which sequence information is available (Doudna and Charpentier, 2014; Lawrenson et al., 2015). This technology provides a step-change in crop improvement, facilitating the introduction of genetic changes in a highly controlled manner.

This could, for example, accelerate the production of crops that can grow with less nutritional input or are better suited to grow in a changing environment. It is hard to imagine a better opportunity to maintain or even increase crop production in a sustainable manner alongside a pressing need to protect the environment by changing current agricultural practices. The exploitation of available technologies requires scientists to advocate the potential they bring to address societal and climatic threats alongside potential risks. However, technologies such as gene editing are particularly susceptible to public perception and legislation (Court of Justice of the European Union, 2018). Given the current environmental and population-size challenges, it is therefore more important than perhaps ever before that politicians make their decisions based on solid scientific facts by taking the advice of experts, and not be influenced by opinions based on unrealistic and emotionally driven views on agricultural practices.

There is no doubt that the massive development in technology and sequence data will attract more researchers to carry out studies directly in crop species. Genome sequencing, CRISPR technology and the possibility of reducing generation time of annual crops via an optimised light regime (a technology known as 'speed-breeding'; Watson et al., 2018) provides a fertile environment for achieving the next Green Revolutions.

Finally, it is important to realise that plants growing in the field are exposed to a wide range of environmental factors that are not experienced in the growth room or glass house under highly controlled conditions and which will affect the development of the plants. Stress-response experiments carried out in controlled environments are therefore not predictors of how plants respond to environmental challenges that they experience in the field. Understanding how plants develop under different and highly complex conditions will therefore become necessary to predict how they will perform in diverse climates. In order to achieve this, we envision that interactions between developmental biologists and scientists from traditionally distant disciplines will become increasingly important. One example is the acquisition and analysis of large-scale image data from field-based phenotyping platforms (Shakoor et al., 2017). In addition to plant geneticists, such experiments will depend on scientists with training in mathematics and experience in analysing large datasets. Likewise, different environmental conditions may affect development via changes in the metabolome of the plant and/or lead to stress-induced developmental defects. Cross-discipline alliances will be important in the future to address questions in these areas.

Concluding remarks

The history of humans is one of obtaining knowledge and using that knowledge to improve our quality of life. A high quality of life is closely linked to having access to sufficient amounts of nutritious

food, and throughout history efforts have been focused on improving methods to maximise food production. Indeed, insufficient food supply and associated increase in food prices invariably lead to societal instability and unrest (Lago et al., 2011 preprint; Jones et al., 2017).

Comparing modern-day crops with their wild ancestors provides a powerful illustration as to the massive challenge humans at the beginning of the Neolithic Revolution were faced with when beginning to cultivate plants for food production. For example, wheat looked similar to (and in fact was) wild grass and the ears of teosinte were small and insignificant compared with the delectable appearance of corn ears today. The first farmers selected the best performers based on evidence. Humans today are facing the triple challenge of having to feed an ever-increasing population while dealing with a more unpredictable climate and environmental issues surrounding unsustainable agronomical practices.

The only thing that separates us from people of the Neolithic Revolution is the knowledge we have acquired over many generations. If we are to overcome the serious challenges to food security in the future, it is pivotal that we are able to use the knowledge and technology we have at hand, and that we connect with our ancestors in basing our decisions on evidence and hard facts. Drastic measures will need to be employed and there is no doubt that plant development in combination and collaboration with other disciplines, will continue to be a crucial factor.

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