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Review

Tansley review

Of floral fortune: tinkering with the grain yield potential of cereal crops

Authors for correspondence:
Shun Sakuma
Tel: +81 857 31 5864
Email: ssakuma@tottori-u.ac.jp

Thorsten Schnurbusch
Tel: +49 39482 5341
Email: schnurbusch@ipk-gatersleben.de

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Shun Sakuma[1] and Thorsten Schnurbusch[2,3]

[1]Faculty of Agriculture, Tottori University, Tottori 680-8553, Japan; [2]Leibniz Institute of Plant Genetics and Crop Plant Research, Gatersleben 06466, Germany; [3]Faculty of Natural Sciences III, Institute of Agricultural and Nutritional Sciences, Martin Luther University Halle-Wittenberg, Halle, Germany

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Summary

Enhancing the yield potential and stability of small-grain cereals, such as wheat (*Triticum* sp.), rice (*Oryza sativa*), and barley (*Hordeum vulgare*), is a priority for global food security. Over the last several decades, plant breeders have increased grain yield mainly by increasing the number of grains produced in each inflorescence. This trait is determined by the number of spikelets per spike and the number of fertile florets per spikelet. Recent genetic and genomic advances in cereal grass species have identified the molecular determinants of grain number and facilitated the exchange of information across genera. In this review, we focus on the genetic basis of inflorescence architecture in Triticeae crops, highlighting recent insights that have helped to improve grain yield by, for example, reducing the preprogrammed abortion of floral organs. The accumulating information on inflorescence development can be harnessed to enhance grain yield by comparative trait reconstruction and rational design to boost the yield potential of grain crops.

I. Introduction

There are > 390 000 plant species on Earth, but just a few cultivated grass species serve as the main sources of human food. These cereal crops belonging to the grass family Poaceae, such as maize (*Zea mays*), wheat (*Triticum* sp.), rice (*Oryza sativa*), and barley (*Hordeum vulgare*), are staple foods worldwide. The estimated global production of these species was 2824 million tons in 2017 (FAOSTAT; http://www.fao.org/faostat). The world population is expected to reach 9 billion by 2050 and losses as a result of climate change may increase food price volatility (Godfray *et al.*, 2010; Tilman *et al.*, 2011). There are three possible approaches that could be used to meet the increasing demand for cereals and achieve sustainable productivity: expansion of arable lands, sustainable increases in cropping intensities (multiple cropping and shorter fallow periods), and yield enhancement as a result of the development of new varieties with improved yield potential. However, over the past two decades, the total area harvested for cereals is not expanding, and increasing cropping intensity remains challenging. Moreover, the rate of increase in total cereal

production and yield (production per unit area) has been moderate, except for maize (FAOSTAT).

Grain yield is a multifactorial trait determined by multiple quantitative trait loci (QTLs) that interact with each other and with the environment. Therefore, the genetics of grain yield has been investigated by dissecting it into its constituent components, such as grain number (GN) per unit area and grain size (mean grain weight). As these are multigene, quantitative traits, much effort is required to identify the underlying genes. One successful approach for such identification is to dissect the trait more precisely using near-isogenic lines or mutants. Improved reference genome sequences (Mascher *et al.*, 2017; Appels *et al.*, 2018) and expanding pan-genome projects in multiple species (Huang *et al.*, 2012; Hirsch *et al.*, 2014; Gordon *et al.*, 2017; Monat *et al.*, 2019) have enabled cost-effective genotyping and advanced identification of causal genes through sequencing alone. Recently, the existence of genome-wide genotype data for almost all barley accessions within the IPK gene bank in Gatersleben has allowed researchers to detect known and novel loci underlying agricultural traits (Mascher *et al.*, 2019; Milner *et al.*, 2019). However, the genetic basis of grain yield is still largely unknown, and the use of marker-assisted selection for grain yield remains limited in modern breeding. Recent studies have shown that grain yield is positively associated with GN per inflorescence, whereas the association with thousand-grain weight (TGW) is less profound in wheat (Fig. 1). Although there is a negative correlation between GN and TGW, GN has been a target of cereal breeders over the past century (Lynch *et al.*, 2017; Wurschum *et al.*, 2018; Voss-Fels *et al.*, 2019). Accordingly, this review focuses on genes that are responsible for inflorescence development and contribute to final GN in Triticeae crops. Meristem identity genes during initial reproductive stages are well described in maize and rice and are among the most important genetic factors determining GN of panicle-type inflorescences (Tanaka *et al.*, 2013; Kyozuka *et al.*, 2014; Zhang & Yuan, 2014; Whipple, 2017; Bommert & Whipple, 2018). In temperate cereals, such as wheat and barley, floret development and growth after the establishment of all reproductive organs is important for GN determination and yield. Therefore, we first clarify the structure of inflorescences and spikelets in cereal crops. Second, we review the genetic basis of inflorescence development and growth. Finally, we discuss how an understanding of the genes and molecular mechanisms that regulate floral development could contribute to enhancing grain yield.

II. Structure of cereal inflorescences

Grasses have diverse, complex inflorescence architectures and species-specific forms (Kellogg *et al.*, 2013) that resulted from adaptation and artificial selection throughout evolution and domestication. The grass inflorescence contains several grain-producing flowers called florets, which develop within specialized small branches, the spikelets ('little spikes'; Bonnett, 1966). The spikelet contains one or multiple florets enclosed by two glumes, and each floret can produce only one grain. Therefore, spikelet number, floret fertility, and their spatial arrangement are crucial for the final GN. Although leaves are produced in a distichous manner at angles of 180° in all cereals, spikelets are arranged in a spiral phyllotaxis in most of the branched inflorescences and are distichous in unbranched inflorescences (Kellogg *et al.*, 2013). A floret is always formed in an alternate phyllotaxy within a spikelet along a secondary axis, the rachilla. Table 1 summarizes the presence of branches, spikelets per node, florets per spikelet, and their spatial arrangements in the different cereals.

During the transition to the reproductive stage, the vegetative shoot apical meristem (SAM) is transformed into an inflorescence meristem (IM), which then produces branch meristems (BMs) in rice, sorghum (*Sorghum bicolor*), and maize (Tanaka *et al.*, 2013). In rice, the BM produces a spikelet meristem (SM), and each spikelet generates one floret. In maize and sorghum, BMs produce spikelet pair meristems (SPMs) and each SM produces two floret primordia. Therefore, the SM is considered determinate in these crop plants. Final spikelet number is determined by controlling the indeterminate BM phase in rice, sorghum, and maize (Table 1; Koppolu & Schnurbusch, 2019).

In Triticeae species such as barley, rye, and wheat, the IM directly produces SMs (Koppolu & Schnurbusch, 2019). The first visible reproductive structure in Triticeae plants is the double ridge stage, which appears as the upper 'spikelet ridge' and lower 'leaf ridge' in a distichous pattern (Fig. 2a; Kirby & Appleyard, 1981). The spikelet ridge constitutes a reproductive axillary meristem (AxM) that differentiates further into spikelet primordia including glumes, while the leaf ridge is suppressed during reproductive development. Although barley and rye IMs are indeterminate, the SM fate in barley and rye is similar to rice and maize, as only one and two florets are generated, respectively. The wheat IM has a determinate fate with a single terminal spikelet at the apical end of the inflorescence (Fig. 2b). The spikelets of wheat are indeterminate and usually produce eight to 12 florets (Fig. 2c); of these, three to

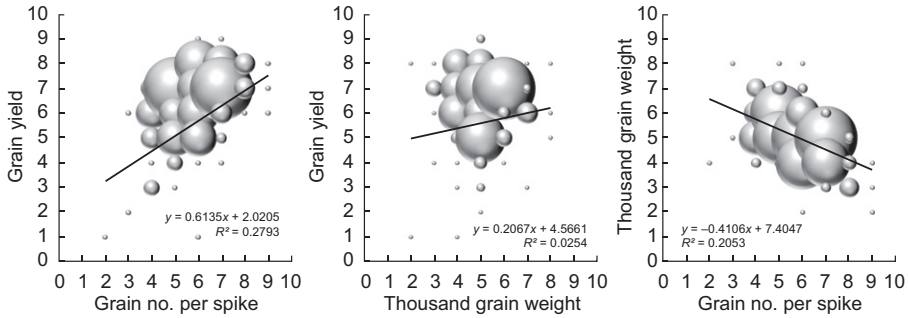

Fig. 1 Yield components in wheat. Each component is quantified as a score from 0 to 9. Data were obtained from 124 German winter wheat cultivars (2017; https://www.bundessortenamt.de/internet30/index.php?xml:id=20).

Table 1 Inflorescence architecture in cereals.

Species	Phyllotaxis	Branches	Pedicel	Terminal spikelet	No. of spikelets per node	No. of florets per spikelet	No. of grains per spikelet	References
Zea mays	Spiral	Yes	No	Yes	2	2	1	Bonnett (1966); Bommert *et al*. (2005)
Sorghum bicolor	Spiral	Yes	No	Yes	2	2	1	Brown *et al*. (2006)
Oryza sativa	Spiral	Yes	Yes	No	1	1	1	Bommert *et al*. (2005); Yoshida & Nagato (2011)
Avena sativa	Distichous	Yes	Yes	Yes	1	4–8	2–4	Bonnett (1966); Zimmer *et al*. (2019)
Triticum aestivum	Distichous	No	No	Yes	1	8–12	3–5	Bonnett (1966); Guo & Schnurbusch (2015)
Secale cereale	Distichous	No	No	No	1	2	1–2	Bonnett (1966)
Hordeum vulgare	Distichous	No	Noa	No	3	1	1	Bonnett (1966)

[1]Pedicels are not present in the central spikelet, but lateral spikelets are pediculated.

five become grain. Interestingly, the oat (*Avena sativa*) inflorescence (panicle) combines characteristics of rice and wheat inflorescences, with branches, a terminal spikelet, and indeterminate spikelets (Bonnett, 1966).

Domestication has shaped the inflorescence architecture of grain species (Doebley *et al*., 2006). The first critical event in domestication was the gain of the nonshattering trait, which resulted in plants that produced harvestable grain that remained attached to the stem, rather than falling to the ground. A few genes are responsible for this trait, as shown by the strong selection that occurred on these loci. For example, loss-of-function mutations of the *Non-brittle rachis 1* (*btr1*) genes underwent parallel selection during barley, einkorn wheat (*Triticum monococcum*), and emmer wheat (*Triticum turgidum*) domestication (Pourkheirandish *et al*., 2015, 2018; Avni *et al*., 2017). Mutations at regulatory sites of the *Shattering1* (*Sh1*) genes occurred in parallel during rice, sorghum, and maize domestication (Lin *et al*., 2012). Once nonshattering inflorescences were established, early farmers and breeders selected for variants with large inflorescences containing many/larger grains. In wheat and barley, this selection favored mutants that converted sterile florets into fertile florets (Komatsuda *et al*., 2007; Sakuma *et al*., 2019). By contrast, selection in rice favored more-branched inflorescences with more spikelets (Ashikari *et al*., 2005; Miura *et al*., 2010; Song *et al*., 2015). An improved understanding of the trajectory of changing inflorescence architecture could facilitate future crop improvement.

III. The genetic basis of floret development

1. Conversion of sterile to fertile florets

A common feature of cereal inflorescences is the presence of aborted or sterile florets and, as most grass species develop multiple florets per spikelet, this form is considered ancestral (Arber, 1934). For example, the lower floret of the maize ear is aborted and the pedicellate spikelet containing a single floret in sorghum panicles remains sterile. Similarly, the two laterally formed florets in two-rowed barley and several more distally formed florets in wheat and oat spikelets are usually destined not to develop. Moreover, rice developmental studies support the hypothesis that a three-floret spikelet was the original form of the genus *Oryza*, in which one pair of the sterile lemma is considered a remnant of two florets (Yoshida *et al*., 2009; Zhang *et al*., 2017).

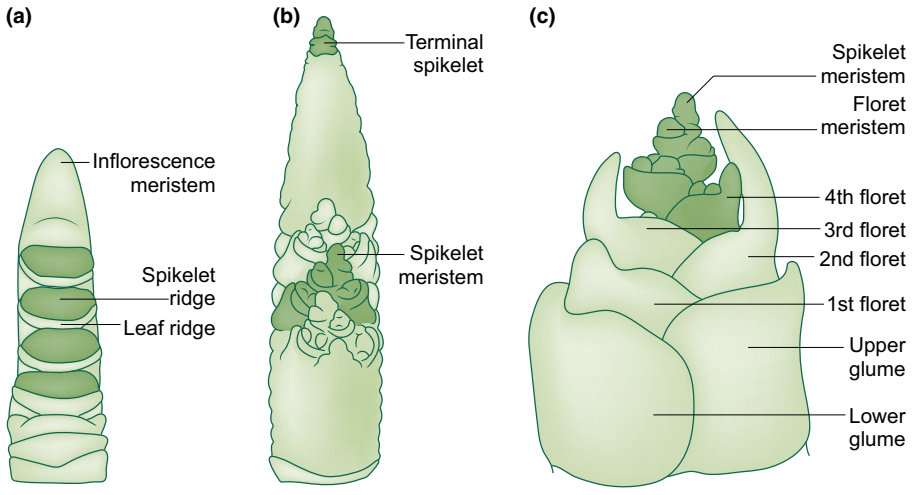

Fig. 2 Wheat inflorescence development. (a) At the double-ridge stage, the spikelet primordia (upper ridge) can be seen; this event is thus referred to as floral initiation. (b) At the terminal spikelet stage, the formation of the terminal spikelet determines the final number of spikelets per spike. (c) At the white anther stage (only one spikelet is shown), the spikelet meristem is still active and produces floret primordia. Schematics of meristem differentiation and organization in major grasses and respective inflorescence phenotypes are also summarized by Koppolu & Schnurbusch (2019).

The function of these preprogrammed sterile or aborted florets (in maize, sorghum, barley, wheat and oat) is unknown. Given their preservation in all wild species, sterile and aborted florets probably perform another role during survival in natural habitats, which compensates for the loss of reproductive potential. As agriculture usually favors productivity over survival strategies, understanding the genetic regulation of these floral abortion processes could be useful for improving floret fertility, thereby enhancing the final GN and productivity of cereal crops.

Studies dealing with barley spike row type have substantially advanced our understanding of floret fertility. All *Hordeum* species display a determinate spikelet triplet (consisting of one central and two lateral spikelets) per rachis node, where each spikelet contains a single floret. The cultivated barley inflorescence can therefore be divided into two major spike forms, previously erroneously described as different species (Harlan, 1918): those with 'two-rowed' and 'six-rowed' spikes based on the fertility of their lateral spikelets (Fig. 3a). The six-rowed phenotype has been selected during domestication. Natural and induced mutants displaying various degrees of fertility in lateral florets have been investigated, and the underlying genes have been identified. The *Six-rowed spike 1* (*Vrs1*; *vrs* was historically derived from *vulgare* row-type spike) and *Vrs5* genes were identified among natural row-type variants of the cultivated barley gene pool. *Vrs1* encodes an HD-Zip I transcription factor and is predominantly expressed in the lateral florets, especially in the pistil, lemma, and palea, but also in the rachilla (Komatsuda *et al.*, 2007; Sakuma *et al.*, 2013). Loss-of-function mutations of *Vrs1* contribute to higher GN per spike through a complete conversion from sterile to fertile lateral florets. VRS1 specifically inhibits female organ development in the lateral florets of the two-rowed spikes, yet some two-rowed cultivars produce functional anthers that produce fertile pollen. The mechanism by which VRS1 induces female sterility remains unknown. A VRS1 homolog in persimmon (*Diospyros lotus*) functions as a sex determinant by regulating anther fertility (Akagi *et al.*, 2014).

Allelic variation at the barley *Vrs1* locus has been uncovered during the past decade. A single amino acid substitution (S184G) at the C-terminal region of VRS1 results in extreme suppression of lateral florets, a mutant phenotype called *deficiens* (Sakuma *et al.*, 2017). Cultivars carrying the gain-of-function *deficiens* allele produce enlarged grains with an increased TGW. The gain-of-function *deficiens* allele has been predominantly selected in Ethiopia, while the impaired or loss-of-function alleles producing the six-rowed spike phenotype have been selected independently several times (Komatsuda *et al.*, 2007; Saisho *et al.*, 2009; Casas *et al.*, 2018). Currently, the *deficiens* two-rowed types dominate UK winter barley grain production; hence, the area being used to grow spring barley is also increasing (Sakuma *et al.*, 2017). These trends are also observed in barley cultivation elsewhere in Europe, and *deficiens* types can be found in other important barley-growing regions, including the US. Furthermore, comprehensive resequencing of *Vrs1* among Spanish barley subpopulations revealed that the reversion from a nonfunctional six-rowed allele to a functional two-rowed allele (*Vrs1.b5*) occurred through a single nucleotide insertion (Casas *et al.*, 2018). These allelic variations indicate that *Vrs1* was a driving force for inflorescence form and row type during barley domestication.

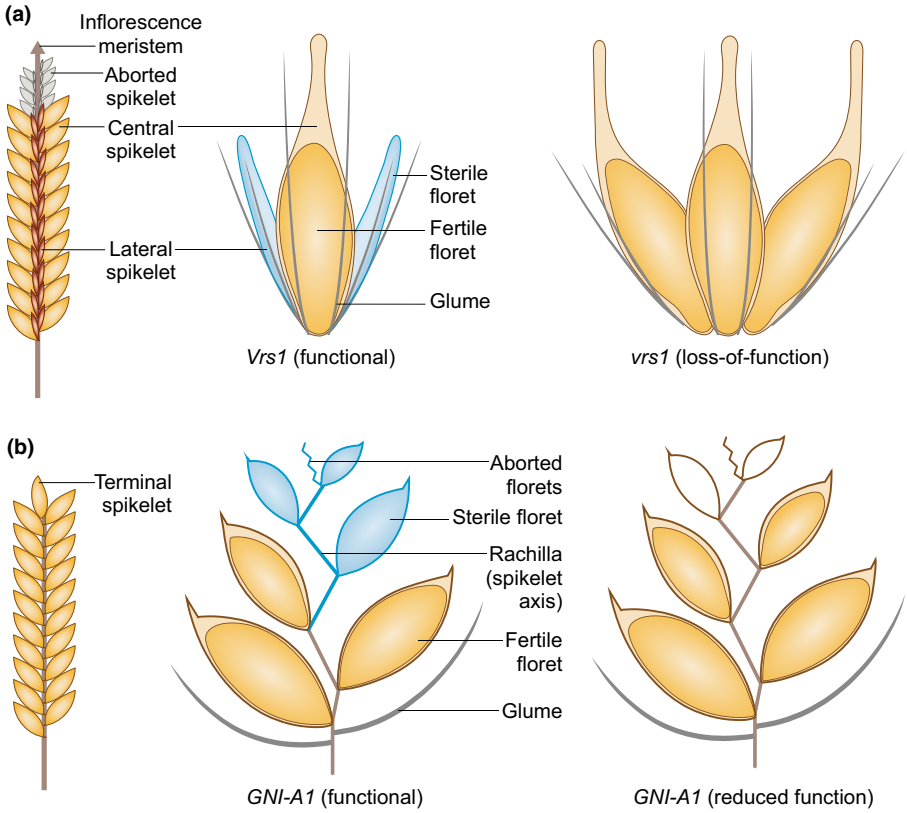

Fig. 3 Key genes for floret fertility in barley and wheat. (a) Structure of barley inflorescence showing two-rowed and six-rowed spikelets. *Vrs1* mRNA localizes in the lateral florets (blue). (b) Structure and fertility of wheat inflorescences and spikelets with functional and reduced-function alleles of *GNI-A1*. Blue florets indicate *GNI1* mRNA accumulation.

All wild *Hordeum* species possess a two-rowed spike having sterile lateral florets, except for *Hordeum bogdanii* Wilensky (Bothmer *et al.*, 1995). *H. bogdanii* is distributed in Central Asia, western Iran, Afghanistan, northern and western Pakistan, northern India, southern Siberia, Mongolia, and northern China. The lateral florets of *H. bogdanii* are usually well developed and set grains producing a six-rowed spike. Resequencing of *Vrs1* (accession no. AB711384) revealed some amino acid sequence variation, but why *H. bogdanii* produces fertile florets is unclear.

Vrs5 encodes a TCP transcription factor, which is an ortholog of the maize domestication gene *Teosinte Branched1* (*TB1*) (Doebley *et al.*, 1995; Ramsay *et al.*, 2011). Loss-of-function alleles of *Vrs5* promote lateral floret fertility and an increased number of tillers. During barley breeding, phenotypically opposing *Vrs5* alleles had been selected for in two-rowed (conferring smaller lateral florets) and six-rowed (conferring increased lateral floret fertility and grain size) spike types; interestingly, both *Vrs5* alleles exist in wild barley populations (Youssef *et al.*, 2017b). *Vrs5* alleles are rather modifiers of lateral floret size in cultivated forms because they always require a specific *Vrs1* (two- or six-rowed) allele to phenotypically enhance their full potential. The sorghum *multi seeded1* (*MSD1*) gene has also been identified as encoding a TCP transcription factor but is not an ortholog of *TB1* (Jiao *et al.*, 2018). The *msd1* mutant can produce normal grains from both sessile and pedicellate spikelets; the latter normally do not develop into viable florets and produce grains. Transcriptome analysis revealed that MSD1 upregulates biosynthetic enzymes involved in the synthesis of the plant hormone jasmonic acid (JA). Elevated JA concentrations might trigger programmed cell death which leads to the abortion of floral organ development in sorghum (Jiao *et al.*, 2018). This hypothesis is consistent with the effect of *tasselseed1* (*ts1*) on the fate of tassel spikelets (Acosta *et al.*, 2009). Maize tassel spikelets produce staminate florets because pistil primordia abort as a result of TS1-mediated programmed cell death. *Ts1* encodes a plastid-targeted lipoxygenase that catalyzes the first dedicated step in JA biosynthesis, which is the peroxidation of alpha-linolenic acid to (13*S*)-hydroperoxyoctadecatrienoic acid. Whether JA or any other hormone is involved in, for example, barley row-type determination and lateral floret abortion is not established, but hormonal effects represent an exciting topic for future research on improving floret fertility in cereal crops (Wang *et al.*, 2018).

Lateral floret fertility, at least in barley, appears to be a multigenic character beyond the effects of *Vrs1* and *Vrs5*. This is exemplified in the so-called *intermedium-spike* (*int*) forms of barley, of which natural (Youssef *et al.*, 2017b) and induced (Lundqvist, 2014) forms exist. These *int* types usually have enlarged lateral florets that vary with regard to awn development, fertility, and grain development, but also depending on environmental conditions, indicating that there is a gradual, quantitative transition from lateral floret abortion (*deficiens*, two-rowed) to complete fertility (six-rowed). From the induced barley six-rowed mutant populations, the mutants *vrs2*, *vrs3*, and *vrs4* have been described and the causal genes identified. *Vrs2* encodes a SHORT INTERNODES (SHI) transcription factor, which is involved in regulating floral organ patterning but similarly reproductive phase duration by controlling gibberellic acid homeostasis and floral progression (Youssef *et al.*, 2017a). The SHI family is also involved in regulating awn elongation and pistil shape, as evidenced by the *Short awn2* (*Lks2*) mutation in barley (Yuo *et al.*, 2012). *Vrs3* encodes a putative Jumonji C-type H3K9me2/3 histone demethylase, a regulator of chromatin state (Bull *et al.*, 2017; van Esse *et al.*, 2017). These studies reveal that combining a *vrs3* mutant allele with six-rowed *vrs1* and *vrs5* alleles leads to increased grain size in the lateral spikelets and greater grain uniformity (Bull *et al.*, 2017; Zwirek *et al.*, 2019). *Vrs4* encodes a LATERAL ORGAN BOUNDARY (LOB)-domain-containing transcription factor (Koppolu *et al.*, 2013). The gene is the barley ortholog of maize *ramosa2*, a regulator of inflorescence branching (Bortiri *et al.*, 2006). Transcript network analysis suggests that *Vrs3* and *Vrs4* suppress lateral floret fertility as upstream regulators of *Vrs1* (Koppolu *et al.*, 2013; Sakuma *et al.*, 2013; Zwirek *et al.*, 2019).

2. Unleashing apical floret abortion

During wheat spikelet development, a significant number of the more apical florets usually abort. This floret abortion accounts for *c.* 70% of potential grain loss in every spikelet (Guo & Schnurbusch, 2015). Recently, the *Grain Number Increase 1* (*GNI1*) gene was isolated in wheat (Sakuma *et al.*, 2019). *GNI1* is an ortholog of barley *Vrs1*. *GNI1* transcripts accumulate in the distal end of the spikelet, including the rachilla (Fig. 3b). The mRNA accumulation in the rachilla is common in barley and wheat, suggesting that its ancestral function is related to rachilla development. The spatial localization of the VRS1/GNI1 transcription factor might direct organ fate towards abortion. A single amino acid substitution (N105Y) in the homeodomain has been the target of selection during postdomestication in wheat. As a result, durum wheat and bread wheat have increased GN per spikelet (Fig. 3b). Transcriptome analysis of carriers of the impaired *GNI-A1* allele revealed that the mRNA for the *FLOWERING LOCUS T* (*FT*) homolog, *FT1*, encoding an inducer of flowering, accumulates only in developing spikelets. Further investigation is needed to better understand the functions of *FT1* during apical floret development in wheat.

Because the *Vrs1*/*GNI1* genes evolved from a Triticeae-specific gene duplication (Sakuma *et al.*, 2019), the paralogs (*Hox2*) are well conserved among grasses. However, the biological function of *Hox2* is largely unknown. Overexpression of *Hox2* in bread wheat produced plants with fewer spikelets and lower GN per inflorescence, suggesting an overall negative role in spike formation (Wang *et al.*, 2017). These studies indicate that gene duplication creates functional diversification and that mutations of paralogs have been a target of artificial selection.

From the recent finding that an increased number of fertile florets per spikelet can increase yield potential in wheat, rachilla growth and development are likely to become key traits of interest. Recently, loss-of-function mutations of the *Q* gene, which is a domestication gene for spike shape in wheat, have been reported (Debernardi *et al.*, 2017; Greenwood *et al.*, 2017). *Q* encodes an APETALA2 (AP2)-like transcription factor (Simons *et al.*, 2006). The loss-of-function mutants in tetraploid durum wheat showed a super-elongated rachilla with > 12 florets. However, these florets were almost completely sterile and did not produce grains, even

though the favorable *GNI1* allele was present (as almost all durum wheats carry the reduced-function allele of *GNI-A1*), suggesting that these loss-of-function alleles were too strong and weaker alleles should be identified and investigated for further improvement. Also, whether there is any interaction between GNI1 and Q remains unclear and should be investigated further.

Rachilla length is an important factor for spikelet development, thereby providing space for the number of fertile florets and the volumetric grain dimensions. The *sham ramification1* (*shr1*) and *shr2* mutants in tetraploid wheat produce spikelets with elongated rachilla between the second and third florets. The *shr1* and *shr2* mutations have been mapped on chromosomes 5AL and 2AS, respectively; however, the underlying genes have not yet been identified (Amagai *et al.*, 2014). Similarly, hexaploid *vavilovii* wheat shows elongated rachillae (Singh *et al.*, 1957). Loss of rachilla determinacy has also been observed in the barley *multiflorous2* (*mul2*) mutant, which shows a wheat-like rachilla extension, but surprisingly only in the lateral spikelets (Forster *et al.*, 2007). In the *mul2* mutant, rachillae of lateral spikelets can form up to three florets per spikelet, similar to wheat spikelets. However, the central spikelets remain determinate and produce only one floret per spikelet, implying that barley rachilla elongation/determinacy in central and lateral spikelets are genetically distinct. Therefore, converting typically determinate barley spikelets into indeterminate wheat-like spikelets might increase the yield potential of barley plants. In summary, elongated rachilla growth in combination with increased floret fertility represents a novel approach for improving the grain yield potential of cereal crops.

IV. Genes controlling spikelet number

1. Genetic regulation of spikelet initiation through timing and florigenic signals

The conversion of the SAM to the IM marks the onset of reproductive development, and its timing is crucial to crop yield (Gol *et al.*, 2017; Trevaskis, 2018). Temperature and photoperiod are the most important environmental signals influencing flowering, and both affect final spikelet number and GN. The flowering time is ultimately determined by homologs of Arabidopsis *FLOWERING LOCUS T* (*FT*), which are well conserved across flowering plants (Kardailsky *et al.*, 1999; Kobayashi *et al.*, 1999; Turck *et al.*, 2008). In rice, *Heading date 3a* (*Hd3a*), a rice *FT* homolog, has been identified as a floral inducer under short-day conditions (Kojima *et al.*, 2002). The Hd3a protein is transported from the leaf phloem to shoot apical cells, where it interacts with 14-3-3 proteins and OsFD1, a bZIP transcription factor, to form a florigen activation complex that activates the floral identity gene *APETALA1* (Abe *et al.*, 2005; Tamaki *et al.*, 2007; Taoka *et al.*, 2011). The Hd3a protein also accumulates in axillary meristems to promote shoot branching through florigen activation complex formation (Tsuji *et al.*, 2015).

The exchange of transcription factors in the florigen activation complex allows the promotion of processes other than flowering. For example, the potato FT homolog *Solanum tuberosum* SELF PRUNING 6A (StSP6A) forms a tuberigen activation complex with 14-3-3 and FD-like protein (StFDL1a/1b), which is not the closest FD homolog of potato (StFD) (Navarro *et al.*, 2011). Similarly, poplar (*Populus tremula* × *tremuloides*) FT2 promotes vegetative growth and inhibits bud set through the formation of a florigen activation complex containing the FD-like protein PtFDL1 (Tylewicz *et al.*, 2015).

In barley and wheat, which are long-day flowering plants, the expression of *VERNALIZATION3* (*VRN3*), a homolog of *FT*, is induced by the *Photoperiod-1* (*Ppd-1*) (Gauley & Boden, 2019). *Ppd-1* is a member of the pseudo-response regulator (PRR) gene family, whose protein products contain CCT (CONSTANS, CONSTANS-like, TIMING OF CAB1) and pseudo-receiver domains (Turner *et al.*, 2005). Characterization of the 'paired spikelet' phenotype in wheat revealed that the *Ppd-1* allele, which confers early flowering, inhibits paired spikelet formation by promoting the expression of *FT1* (Boden *et al.*, 2015). The 'paired spikelet' phenotype is characterized by the formation of two spikelets which share one rachis node in a dorsal-to-ventral fashion, rather resembling a piggyback situation. Furthermore, wheat *TB1* (ortholog of *Vrs5*) is also involved in paired spikelet development through interaction with FT1 (Dixon *et al.*, 2018b). Increased dosage of wheat *TB1* promotes paired spikelet formation and delays inflorescence growth and development by reducing expression of the meristem identity gene *VRN1*, which encodes a MADS-box transcription factor. The photoperiod-insensitive alleles of *Ppd-1* reduce the number of spikelets per inflorescence as a result of a shortened duration of spikelet developmental stages (Guo *et al.*, 2018; Ochagavia *et al.*, 2018). Furthermore, loss of function of the *FT-B1* homoeolog increases the spikelet and tiller number when grown at lower temperatures (Dixon *et al.*, 2018a). These findings support a pleiotropic function of *FT* beyond flowering, and thus further investigations might open up a new avenue towards improving inflorescence form.

2. Modulation of spikelet meristem identity genes

Most high-grain-yield cultivars in rice have a higher IM activity and produce relatively more branches than lower-yield cultivars. Higher activity of *OsSPL14*, which encodes a SQUAMOSA promoter binding transcription factor, promotes panicle branching and higher grain yield (Jiao *et al.*, 2010; Miura *et al.*, 2010). *Grain number 1a* (*Gn1a*) was also identified from a mutation found among high-yielding cultivars (Ashikari *et al.*, 2005). *Gn1a* encodes a cytokinin oxidase/dehydrogenase, and reduced *Gn1a* function produces larger panicles with increased branch numbers. The rice zinc finger protein DROUGHT AND SALT TOLERANCE (DST) enhances grain production by controlling *Gn1a* expression (Li *et al.*, 2013). Loss-of-function mutations of *ABERRANT PANICLE ORGANIZATION1* (*APO1*), *APO2*, and *ABERRANT SPIKELET AND PANICLE1* (*ASP1*) result in a less branched inflorescence owing to the precocious specification of the spikelet meristem identity (Ikeda *et al.*, 2005; Ikeda-Kawakatsu *et al.*, 2009, 2012; Yoshida *et al.*, 2012). These results suggest that these genes maintain branch meristem identity and delay the

transition to spikelet meristem identity, providing more opportunities for grain production.

In barley and wheat inflorescences, branch formation is actively suppressed; this decreases the grain yield potential of barley and wheat, compared with rice and maize. Studies using branched-spike mutants in barley (*compositum2* (*com2*)) and wheat (*branched head*^{t}*-A1* (*bh*^{t}*-A1*)) led to the identification of the AP2/ETHYLENE RESPONSIVE FACTOR (AP2/ERF) transcription factor, which is the ortholog of rice *FRIZZY PANICLE* (*FZP*) and maize *BRANCHED SILKLESS1* (*BD1*). A missense mutation (L96P) at the *bh*^{t}*-A1* gene in tetraploid 'Miracle-Wheat' produces branch-like structures with more spikelets and grains per spike (Poursarebani *et al.*, 2015). The mutant allele was introgressed into an elite durum wheat to develop near-isogenic lines with increased spikelet number and GN per spike without reduction of grain size; however, the 'branching' phenotype was lost in this genetic background (Wolde *et al.*, 2019). Noncanonical or extra spikelet formation in this germplasm is anatomically slightly different from the previously mentioned 'paired spikelets'. For the *bh*^{t}*-A1* derived germplasm these extra or secondary spikelets also share one rachis node with the primary spikelets but are usually in a ventral-to-ventral orientation to each other. Although there are clear anatomical differences among different noncanonical spikelet types, collectively, all of these 'additional or extra spikelets' are often subsumed as 'supernumerary spikelets'. For example, in hexaploid wheat, nonsense mutations in the *WFZP-A* and *WFZP-D* homoeologs enable the formation of supernumerary spikelets, producing a so-called multi-row spike, which shows a combination of spikelet arrangements along the spike (Dobrovolskaya *et al.*, 2015).

3. The power of using weak alleles to improve grain yields

Recently, several studies have revealed that weak and mild alleles have the potential to improve agricultural traits. In rice, a QTL for culm strength, *STRONG CULM2* (*SCM2*), was identified, and the causal mutation was found to be a 9.5 kb insertion upstream of *APO1*, a gene previously reported to control panicle structure (Ookawa *et al.*, 2010). In addition, *Small Grain and Dense Panicle 7* (*SGDP7*) and *CONTROL OF SECONDARY BRANCH 1* (*COS1*) are identical to *FZP* (Bai *et al.*, 2017; Huang *et al.*, 2018). The causal mutations of *SGDP7* and *COS1* are an 18 bp insertion *c.* 5.3 kb upstream of *FZP* and a 4 bp deletion *c.* 2.7 kb upstream of *FZP*, respectively. In the case of *COS1*, the mutation occurred during rice domestication and is already fixed in cultivars. In *SGDP7*, the mutation is found in restricted regions and subspecies after domestication and is not yet being used in breeding. In maize, a weak allele of *fea2-1328* with a single amino acid change in the leucine-rich repeat domain leads to increased inflorescence meristem size and kernel row number but normal ear length and kernel arrangement (Bommert *et al.*, 2013). In wheat and barley, AP2 homologs (*Q* and *Cly1*) play an important role in spike shape and architecture. The mutations in the microRNA172 binding sites, leading only to diminished transcript suppression, are associated with increased spike density and cleistogamous flowers (Nair *et al.*, 2009; Houston *et al.*, 2013; Debernardi *et al.*, 2017).

V. Future perspectives

In recent decades, emerging research has advanced our understanding of the genetic basis of inflorescence development in cereals. Cloning of important genes controlling grain yield-related traits was mainly achieved by positional cloning, often requiring immense effort and time. Moreover, these efforts were based on characterizing classical mutants or natural variation with large phenotypic effects. These mutants often display extreme phenotypes; therefore, fine-tuning of the traits is required. Several studies have found that relatively weak alleles, such as subtle amino acid changes and mutations in regulatory elements, have been selected during domestication or postdomestication: for example, *GNI-A1* and *bh*^{t}*-A1* in tetraploid wheat, *Vrs1.t* (*deficiens*) in barley, and *FZP* (*SGDP7/COS1*) in rice. This information, in combination with trait reconstruction derived from closely related grass species (e.g. for rachilla extension or inflorescence branching), hints that this could be a promising future direction for research. This approach was exemplified in an investigation of leaf shape in the brassica species Arabidopsis and *Cardamine hirsuta*. In this case, shape diversity (i.e. reconstruction of key features of Cardamine leaf morphology in Arabidopsis) was achieved through the distinct effects of only two homeobox genes affecting leaf growth (Kierzkowski *et al.*, 2019). Thus, a more profound understanding of inflorescence growth and development in closely related species belonging to the so-called 'secondary' or 'tertiary gene pool' of cereal crops seems likely to become critical for altering crop yield potentials through comparative trait reconstruction.

Recent studies have also demonstrated that the key regulators of inflorescence shape are functioning during species-specific developmental stages. In rice and maize, SM identity genes acting during early developmental stages are central regulators of inflorescence architecture, whereas in barley and wheat, the late developmental stages appear to be important for spikelet and floret development. In wheat, more than half of the grain yield potential is wasted during the floret abortion process. The identification of the *GNI1* gene might thus be a starting point for understanding floret fertility in wheat. Identifying the downstream target and/or interaction partner of *GNI1* will provide new insights into further improving grain yield. One urgent task is to investigate the relationship with *FT* genes. Interestingly, *FT1* homoeologs are highly expressed in the developing spikes, but their function remains elusive (Sakuma *et al.*, 2019). Another aspect that should be investigated is the tradeoff between GN and grain size. In the case of barley, the six-rowed spike produces more but smaller grains compared with the two-rowed spike (Liller *et al.*, 2015).

Multiple genomics platforms are now established, including for large and complex cereal crop genomes. If the existing genetic materials are not yet sufficient to address specific questions and purposes, traditional induced mutation approaches or genome modification approaches (e.g. CRISPR/Cas technology) are now available in cereal crops (Kumlehn *et al.*, 2018). Therefore, we expect an acceleration in the rate of identification of causal genes responsible for important agricultural traits. A greater understanding of the genes controlling these traits might enable us to design new crops. Rice researchers have successfully demonstrated the effectiveness of

rational design for higher yield and quality traits (Zeng *et al.*, 2017). However, rational design approaches are not yet possible in wheat and barley. Further isolation of the genes related to grain yield potential is needed to improve the temperate cereal crops.

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ORCID

Shun Sakuma https://orcid.org/0000-0003-1622-5346
Thorsten Schnurbusch https://orcid.org/0000-0002-5267-0677

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