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REVIEW

## Advances in studies on the physiological and molecular regulation of barley tillering



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### Abstract

Tillering is a crucial trait closely associated with yield potential and environmental adaptation in cereal crops, regulated by the synergy of endogenous (genetic) and exogenous (environmental) factors. The physiological and molecular regulation of tillering has been intensively studied in rice and wheat. However, tillering research on barley is scarce. This review used the recent advances in bioinformatics to map all known and potential barley tiller development genes with their chromosomal genetic and physical positions. Many of them were mapped for the first time. We also discussed tillering regulation at genetic, physiological, and environmental levels. Moreover, we established a novel link between the genetic control of phytohormones and sugars with tillering. We provided evidence of how environmental cues and cropping systems help optimize the tiller number. This comprehensive review enhances the understanding of barley's physiological and genetic mechanisms controlling tillering and other developmental traits.

**Keywords:** barley, development, genetic regulation, phytohormone, tillering

## 1. Introduction

Barley (*Hordeum vulgare* L.) ranks as the world's fourth largest cereal crop in terms of planting area, only after

wheat, rice, and maize (<http://faostat.fao.org>). The Green Revolution, characterized by the introduction of semi-dwarfing genes into cereal crops, results in a dramatic increase in grain yield *via* increasing tiller and spike number per plant and, simultaneously, the reduction of plant height and lodging risk (Ye *et al.* 2019). Tillering, one of the major agronomic traits in cereal crops, is closely related to grain yield formation and stability (Dockter and Hansson 2015). Tillers are the lateral branches that grow from the main shoot or basal meristem of non-elongated internodes and produce their adventitious roots and spikes during their development (Beveridge and Kyojuka 2010).

The development of tillers is regulated by a complex

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network of multiple factors involved in genetics, physiology, and environment. Several mutants related to tillering have been identified in cereal crops, such as barley. Specifically, *many noded dwarf (mnd)* (Babb and Muehlbauer 2003) and *high number of tillers1 (hnt1)* (Ye et al. 2019) produce more tillers, while *uniculm2 (cul2)* (Okagaki et al. 2013) and *uniculme4 (cul4)* (Tavakol et al. 2015) have no tiller. Tillering is also influenced by many environmental factors, including water (Romina et al. 2014), nutrients (Tanaka and Nakano 2019), temperature (Wang et al. 2010), and light (Miralles and Richards 2000). Some tillers initiated in cereal crops at the vegetative stage, and only a few could grow into the shoots with spikes. Most tillers stopped development and died before the heading stage, becoming so-called non-productive tillers (Kebrom et al. 2013). These non-productive tillers compete with effective tillers for resources, such as light, nutrients, and water (Islam and Sedgley 1981). The effective regulation of tiller development is crucial to optimize the number of productive tillers (Xing and Zhang 2010). The proposed ideotype of cereal plants consists of fewer unproductive tillers (Jiao et al. 2010). In wheat, mutant *tiller inhibition (tin)* produced fewer tillers which could develop into larger spikes under water-limited conditions (Mitchell et al. 2013), revealing that the potential tiller number should be ideal, not too high or very low. The enhanced productivity of some cereal crops, followed by domestication, was complemented by fewer tillers, such as maize and foxtail millet (Doebley et al. 2006; Doust and Kellogg 2006). Particularly, the limitation of tiller development factors may lead to fewer tillers but higher productivity, e.g., *wealthy farmer's panicle (wfp)* in rice (Miura et al. 2010) and overexpression of a cytokinin dehydrogenase gene (*AtCKX1*) in the transgenic barley which resulted in more tillers but lower yield (Pospíšilová et al. 2016). However, a well-balanced number of tillers is the foremost requirement, as unproductive tillers waste nutrients (Jiao et al. 2010). Thus, elucidating the molecular and physiological mechanisms associated with tillering is significant for increasing crop productivity.

Considerable progress has been made in deciphering the genetic basis of tillering development in barley. However, there is a gap in the combined knowledge of genetic improvement, including genetics, genomics, and molecular physiology. It is important to compile and overview all new discoveries and gaps for an efficient breeding program. In the current review, we put steps forward for understanding tiller development and how genetics influence the process either separately or through interaction with other factors. We then discussed the molecular physiology, including hormonal and sugar regulation of tiller development, and highlighted the

potential of their manipulation to increase barley yield through regulating tillering development. As the first molecular evidence, the role of sugars in the development of lateral branches in barley was discussed because it acts as an important signal transducer and source of nutrients during tiller development. Moreover, we provided a brief account of the environmental influence of tiller development and its association with barley yield. Finally, we provided a perspective on the applications of recent advances in molecular physiology with functional genomics-based approaches for optimizing tillering and, thus, grain yield.

## 2. Tiller formation and development

Tillering is determined by the activity of shoot apical meristems (SAMs) and axillary meristems (AXMs). Shoot development occurs continuously throughout a plant's life in repeated stacked units called phytomers. In barley, a phytomer consists of upper and lower half-nodes separated by a portion of the stem, an internode. Leaf primordia develop on the upper half-node, and axillary buds (AXBs) and root initials on the lower half-node (Forster et al. 2007). Tillering in barley begins during germination, and new AXBs develop adjacent to the internode, covered by the leaf sheath of the previously formed phytomer (Fig. 1- ① ). Usually, two AXBs are already formed in mature embryos, the first being in the axil of the coleoptile (T0 AXB) and the second (T1 AXB) in the axil of the first leaf (Kirby and Appleyard 1981).

Tiller development mainly consists of two phases: i) AXMs initiation and bud formation, as shown in Fig. 1- ① , and ii) bud growth into tiller (Fig. 1- ② ) (Schmitz and Theres 2005). Barley mutant *cul2* could not develop its axillary buds, having only one main culm with no-tillers due to losing the ability to initiate or maintain axillary buds (Babb and Muehlbauer 2003). In contrast, an increased number of tillers was observed in the *hnt1* mutant of barley with accelerated axillary bud initiation (Ye et al. 2019). On the other hand, bud growth fate is determined by a complex network of endogenous and environmental factors. The barley mutant of *low number of tillers1 (lnt1)* produces fewer tillers due to weak axillary bud growth and suppresses the formation of secondary tillers (Dabbert et al. 2010). The wheat mutant of *tin* and the rice mutant of *asp1* are also good examples of suppressed bud outgrowth (Domagalska and Leyser 2011; Yoshida et al. 2012).

During the seedling developmental phase, dozens of tiller buds are initiated, while few pass from the first tiller phase (bud initiation and formation) to the second phase of tiller development and growth. The first developed

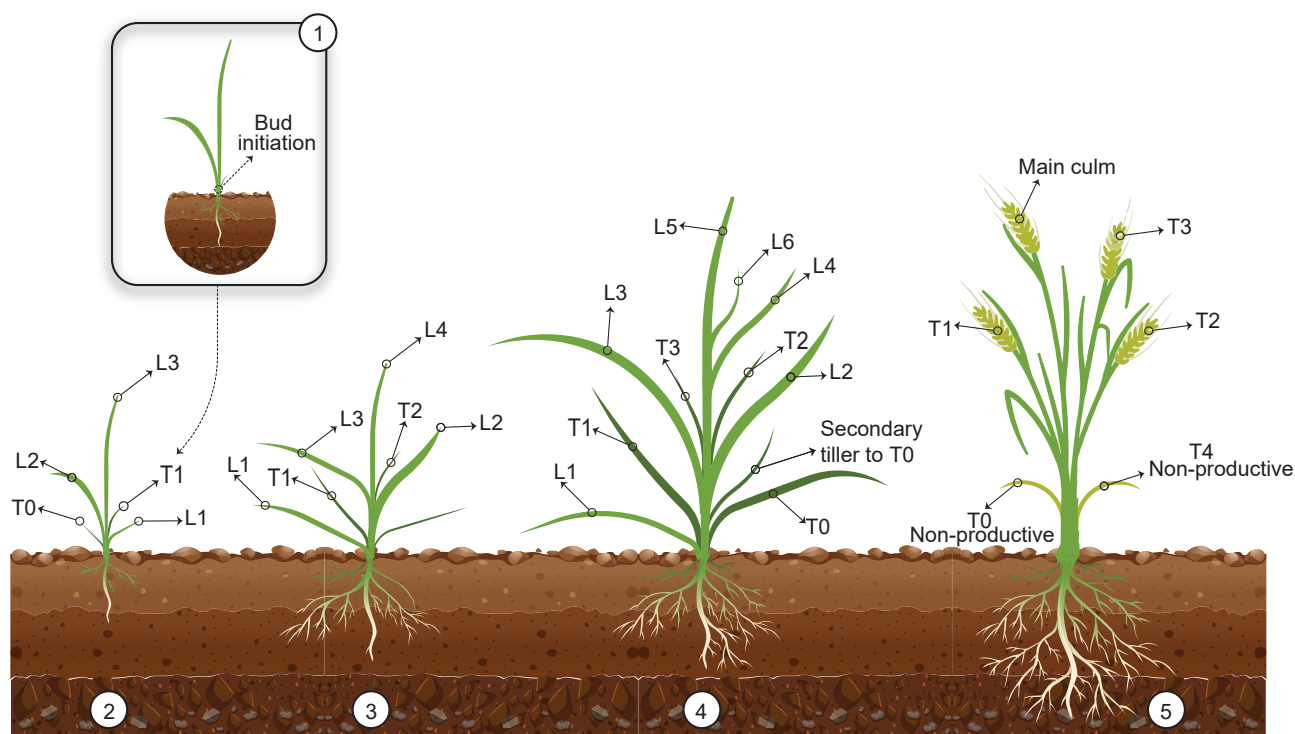
tiller is usually visible when seedlings have three leaves (Okagaki *et al.* 2018), and the initiation of reproductive growth indicates the end of tillering in grasses (Fig. 1). Plants can develop primary tillers which arise from axillary buds of the main culm (Fig. 1- ② -T1), and secondary tillers which arise out of leaf axils of primary tillers (Fig. 1- ③ -T2) (Kirby and Appleyard 1987). Some tillers will develop inflorescences called spikes, while other tillers fail to form spikes, becoming non-productive or vegetative tillers (Jones and Kirby 1977), as shown for T4 in the 5th part of Fig. 1. The proportion of tillers that develop into spikes depends on endogenous factors and environmental conditions (Okagaki *et al.* 2018).

### 3. Genetic regulation of tiller development

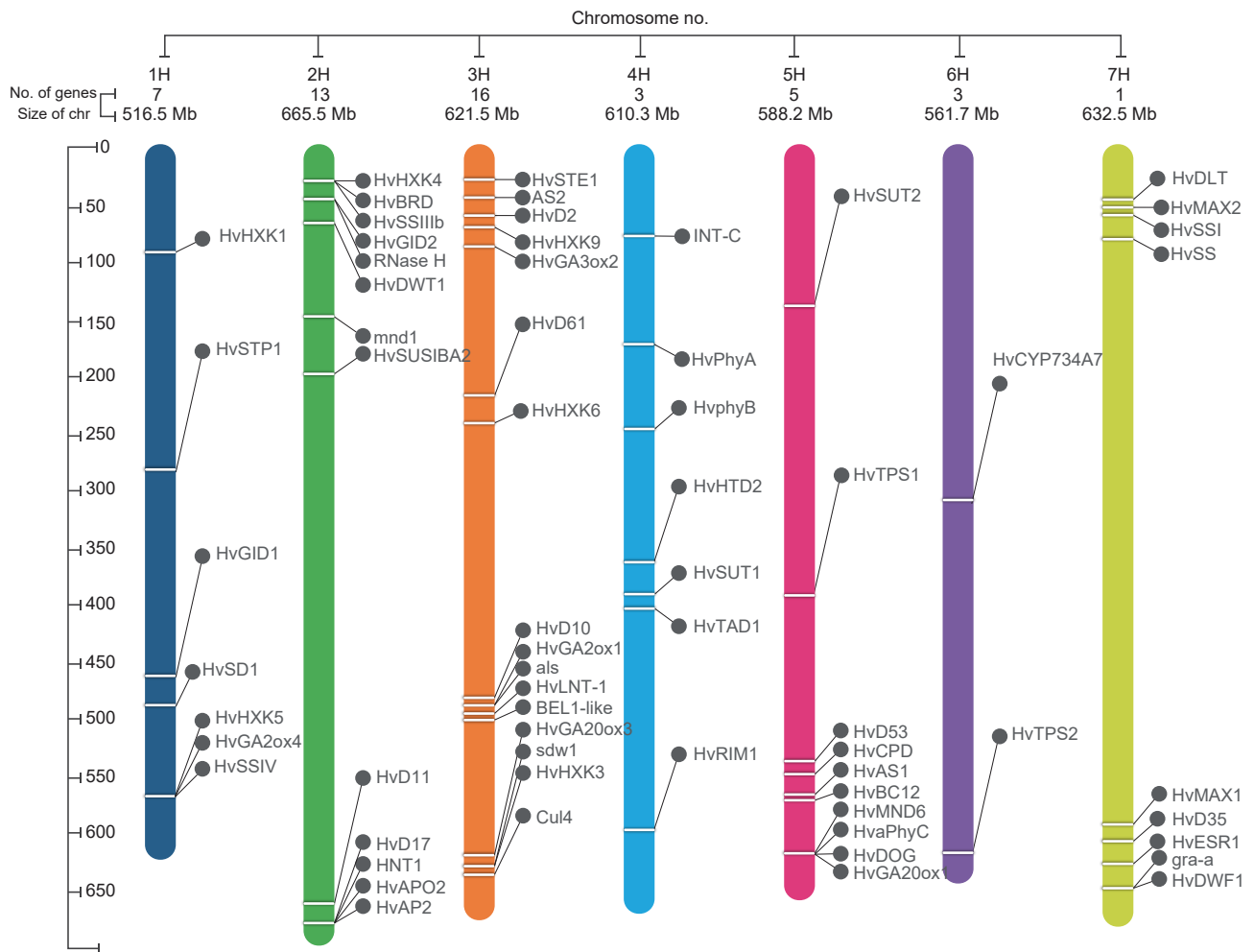
Tillering is a highly complex trait, and its genetic determinants have been well studied in rice and maize, while the relevant knowledge in barley is relatively limited (Hussien *et al.* 2014). The recent advancements in next-generation sequencing offer an excellent opportunity to identify and map causal mutations and genes that can be directly used in barley breeding programs. A number

of QTLs involved in the regulation of tillering have been mapped, and some of them have been cloned using a map-based cloning strategy. To illustrate the progress in molecular physiology and genetics regulating tiller development, we listed the known genes and mutants of barley tiller development (Fig. 2; Appendix A). The genetic and physical map of tiller developmental genes/mutants will support the understanding of molecular mechanisms underlying tiller development.

Based on phenotypic observations, tillering mutants of barley could be categorized into four classes: 1) *uniculm2* (*cul2*) mutants having only one culm with no developed tillers (Babb and Muehlbauer 2003), 2) mutants with fewer tillers, such as *Int1* (Dabbert *et al.* 2010), *absent lower laterals1* (*als1*) (Agharkar *et al.* 2007), and *uniculm4* (*cul4*) (Tavakol *et al.* 2015), 3) mutants with moderate tiller numbers, such as *intermedium-b* (*int-b*) and *semibrachytic* (*uzu*) (Babb and Muehlbauer 2003), and 4) mutants with higher tiller number, such as *hnt1* (Ye *et al.* 2019), *granum-a* (*gra-a*), *many noded dwarf1* (*mnd1*), *mnd6* and *Intermedium-c* (*Int-c*) (Babb and Muehlbauer 2003; Druka *et al.* 2011), *Grassy tillers* (*Grassy*) (Druka *et al.* 2011), *HvD14* (Marzec *et al.* 2016), *Many noded dwarf1/5* (*Mnd1/5*), *Many noded dwarf3* (*Mnd3*) (Franckowiak and



**Fig. 1** Architecture of barley plant with its developmental stages of tillers (Shaaf *et al.* 2019). ①, the first stage of tiller development: bud initiation, which can be seen after removal of the en-sheathing leaf. ②, the second stage of tiller development: bud outgrowth into tiller: T1; from leaf axil & T0; from coleoptile. ③&④, secondary tillers. ⑤, productive tillers, T1 and T2 with grain bearing spikelets and non-productive tillers; T0 and T4. T0, the tiller from coleoptile; T1, tiller from the first leaf of the main shoot; T2, tiller from the second leaf of the main shoot; T3, tiller from the third leaf of the main shoot; T4, the secondary tiller from the first tiller.



**Fig. 2** Chromosomal map of barley tillering related genes. Upside scale shows the name/number of chromosome, number of genes mapped on each chromosome and the size of chromosome in Mb. The white mark line indicates the physical location and the black bubble with black text is the name of specific gene.

Lundqvist 2002), and *many noded dwarf 4/6* (Mascher *et al.* 2014). Mutations are the primary source of genetic variations used to understand tiller development mechanisms. Therefore, uncovering the molecular genetics and physiology of the desirable and causative mutations have prospects for their utilization in breeding.

Studies have revealed the genetic and morphological characterization of certain tillering mutants. *Cul2* mutants, exhibiting only the main culm, are described as suppressing axillary buds (Babb and Muehlbauer 2003). *Lnt1*, *cul4*, and *als1* showed fewer tillers because axillary meristems cannot develop into primary tillers (Dabbert *et al.* 2009; Dabbert *et al.* 2010; Tavakol *et al.* 2015). Interestingly, when breeders crossed low tillering barley mutants with high tillering mutants, such as *als* or *cul2* with *gra-a* or *mnd1*, all hybrid plants produced a low tillering or unicum phenotype, suggesting epistatic behavior of low tillering to higher tillering mutants (Okagaki *et al.* 2013; Ye

*et al.* 2019). Like the rice SL mutants, the barley *HvD14* mutant showed a dwarf phenotype with high tillering (Marzec *et al.* 2016). The *uzu* gene encodes an ortholog of *BR11* in *Arabidopsis* and *D61* in rice, which is associated with tillering regulation (Babb and Muehlbauer 2003). *CUL4* encodes a BROAD COMPLEX, TRAMTRACK, BRIC-À-BRAC (BTB)-ankyrin domain-containing protein homologous to *Arabidopsis* BLADE-ON-PETIOLE 1 (BOP1) and BOP2, which regulates certain tiller processes, including outgrowth of tillers and development of secondary buds (Babb and Muehlbauer 2003).

*VRS1* encodes the homeodomain-leucine zipper class I (HD-ZIP1) transcription factor, which pleiotropically regulates tillering in barley by inhibiting bud outgrowth. It is found to be a homolog of *grassy tillers 1 (gt1)* in maize (Liller *et al.* 2015). *VRS5 (Int-C)* encodes a TEOSINTE BRANCHED 1/CYCLOIDEA/PCF1 (TCP) transcription factor, which is the homolog of TB1 in maize,

enhancing tiller number at the early development stage but suppressing bud outgrowth at the late development stage (Ramsay *et al.* 2011). *VRS4* is associated with trehalose-6-phosphate synthase (T6PS) and trehalose-6-phosphate phosphatase (T6PP), which are orthologues of maize *RAMOSA2*, encoding a LATERAL ORGAN BOUNDARIES (LOB) transcription factor promoting spikelet and floret determinacy (Koppolu *et al.* 2013). This suggests the potential roles of sugar pathways through T6PS and T6PP in determining plant stature developmental traits, including tillering (as discussed below). *JUBEL2* encodes a BEL-like homeodomain transcription factor, which is an ortholog of *Arabidopsis* BELLRINGER (BLR) and the low tillering mutant, *low number of tillers 1 (Int1)*, suggesting correspondence of *LNT1* to *JuBel2* (Müller *et al.* 2001). *ELI-A* encodes a conserved protein that may be a transposon. Although it has the ability to inhibit the *cul2* mutant phenotype, the single mutant with strong *eli-a* alleles produces fewer tillers, typically holding about half as many tillers as wild plants (Chatfield *et al.* 2000). High tillering phenotypes correspond with a mutation in *INT-C* and *MND*. *INT-C* is a member of *TB1* and an ortholog of the branching inhibitor of maize *TB1*, and loss-of-function mutants have a moderately high tillering phenotype (Ramsay *et al.* 2011). *MND* encodes a cytochrome P450 in the CYP78A family homologous to rice *PLASTOCHRON1 (PLA1)*, and *pla1* mutants have a similar phenotype to *mnd* ones (Le Bris *et al.* 1999). *Gra-a* produced more axillary buds (Schmitz and Theres 2005) and, similar to *mnd1*, showed excessive development of tillers and semi-dwarf phenotype (Druka *et al.* 2011). Comparatively differential expression of the genes in tillering mutants from those in non-mutants revealed that many up-regulated genes in low tillering mutants were involved in stress responses, such as the production of reactive oxygen species and calcium signaling, which are involved in organ development (Agharkar *et al.* 2007; Arend *et al.* 2009; Okagaki *et al.* 2013). Spike morphology in barley also affects tiller number, with two-rowed barley having higher tillers than six-rowed barley (Tucker 1977). In addition, the mutation in the barley row-type *VRS1* gene affected the tiller number pleiotropically (Liller *et al.* 2015). Genetic regulation of tiller development in barley revealed a significant variation in germplasm collection as well as the bi-parental population (Abeledo *et al.* 2004; Borràs *et al.* 2009). Taken together, we confirmed that these genes/mutants have a strong potential for improving barley grain yield by optimizing the productive tiller number. The molecular mechanism of the cross-talk between the genes regulating tiller development and spike development is still unexplored.

## 4. Physiological regulation of tiller development

### 4.1. Hormonal regulation

At present, auxin, strigolactones (SLs), cytokinins (CTKs), gibberellins (GAs), abscisic acid (ABA), and jasmonic acids (JAs) are reported to play essential roles in tiller development. Usually, the final phenotype of tiller development is a function of the interaction between a number of phytohormones.

**Auxin** Auxin is an important growth regulator that controls tiller development by regulating AXMs formation (Agusti and Greb 2013). It is actively synthesized in the shoot apex and indirectly suppresses the axillary bud outgrowth indirectly (Agusti and Greb 2013). The auxin transportation downwards from the shoot apex is termed polar transport (PAT). It is determined by auxin efflux carriers of the adenosine triphosphate (ATP)-binding cassette B and the PIN-FORMED (PIN) protein families present in xylem parenchyma (Petrášek and Friml 2009; Zazimalová *et al.* 2010). The mutation affecting auxin transport could result in various abnormalities, such as the inability to establish axillary meristems in inflorescences (Yoshida *et al.* 2012). Recently, a new mutant *hnt1* of barley was reported to have more tillers due to accelerated bud formation and initiation. It was suggested that HNT1 might regulate PAT-related genes (Ye *et al.* 2019). It was reported that BA1, a homolog of LAX1, controls AXM formation by regulating auxin transport (Gallavotti *et al.* 2004, 2008). BA1 acts downstream and is a direct target of the protein kinase BIF2, a PINOID ortholog important for PAT (Skirpan *et al.* 2008, 2009). *Arabidopsis max1* mutants showed increased axillary branching because of higher expression of PIN1 and auxin transport (Shinohara *et al.* 2013). For example, mutations in the genes that specify organ boundaries, like CUP-SHAPED COTYLEDON (CUC) genes in *Arabidopsis*, disturb PAT, resulting in reduced branching, loss of leaf serration, and abnormal inflorescences (Vroemen *et al.* 2003; Nikovics *et al.* 2006; Raman *et al.* 2008; Bilsborough *et al.* 2011). Vegetative and reproductive axillary meristem formation is also inhibited in three maize mutants with impaired PAT: *barren stalk 1 (ba1)*, *Barren inflorescence 1 (Bif1)*, and *bif2* (Mcsteen *et al.* 2007). Several lines of evidence from *Arabidopsis* and other species suggest that the diverse phenotypes resulting from reduced or ectopic expression of class 1 KNOX genes are attributed to an increased or decreased PAT, respectively (Shinohara *et al.* 2013). Auxin could down-regulate CTK levels by inhibiting the expression of IPT (*ISOPENTENYL TRANSFERASE*) genes, resulting in

suppressed AXM (Ferguson and Beveridge 2009). The exogenous application of auxin in barley plants inhibits tillering by suppressing bud formation (Woodward and Marshall 1988). However, the molecular mechanism for regulating barley tillering by auxin is still not completely clear.

**Cytokinins** Cytokinins are fundamental regulators of plant growth, including axillary bud activation and delay of senescence (Sakakibara 2006). In *Arabidopsis*, *supershoot (sps)* enhanced shoot propagation and AXM activity with CTK accumulation at bud initiation by suppressing a *SPS* gene (Tantikanjana et al. 2001). It was also reported that a particular *Arabidopsis* KNOTTED-like homeobox (KNOX) protein SHOOTMERISTEMLESS (STM) promoted the expression of (IPT7) ISOPENTENYL TRANSFERASE7 (Jasinski et al. 2005) and down-regulated gibberellin biosynthesis genes, resulting in low GA and high-CTK contents in the meristem. This may be crucial for maintaining meristematic activity (Jasinski et al. 2005). Transgenic rice plants overexpressing OsIPTs showed enhanced axillary bud activity by CTK overexpression (Sakamoto et al. 2006). In barley, the *HvCKX1* gene regulates the CTK status due to an enhanced cytokinin dehydrogenase activity that degrades CTK. *HvCKX1* knock-out mutants produced more tillers and grains than wild plants (Holubová et al. 2018), suggesting that the exploitation of CTK-regulating genes in barley may be profitable for optimizing the number of productive tillers.

**Strigolactones** SLs are recently reported to function as growth regulators by inhibiting AXB internode elongation (Gomez-Roldan et al. 2008). SLs may also induce the expression of transcription factors orthologous to maize *TB1*, rice *FINE CULM1 (FC1)*, and *Arabidopsis BRANCHED1*, which act downstream of strigolactones to inhibit internode elongation (Minakuchi et al. 2010). Five barley genes, *HvD14*, *HvD27*, *HvMAX1*, *HvCCD7*, and *HvCCD8*, are orthologous to genes in rice and *Arabidopsis* and involved in SLs' function of inhibiting tiller development (Wang et al. 2018). In *Arabidopsis*, SLs are synthesized in the roots upon expression of *MAX* genes and then transported to AXB (Gomez-Roldan et al. 2008). SLs interact with auxin in a dual-loop pathway to control axillary bud outgrowth, but the nature of this regulatory loop is still unresolved (Kebrom and Richards 2013). *Arabidopsis max1* mutants have increased axillary branching associated with overexpression of *PIN1* and enhanced auxin transport (Shinohara et al. 2013). The increased branching phenotype depends on the overexpression of *PIN1*, as *max1/pin1* double mutants exhibit fewer lateral branches (Bennett et al. 2006). In *Arabidopsis*, *max1* and *high tillering dwarf (htd)* in rice

showed enhanced shoot branching regulated by SLs (Zou et al. 2006). Future research should focus on the interactions of SLs and auxin to better understand the role of SLs' crosstalk with other phytohormones in affecting tiller development.

**Gibberellins (GAs)** GA has been reported to play a role in internode elongation in grasses. Bioactive GA is deactivated by an enzyme encoded by the *GA2ox1* gene. The deactivation of GA probably prevents GA from reaching nodes under the shoot apex and results in the inhibition of internode elongation (Sakamoto et al. 2001). It was observed that overexpression of *GA2ox* produced more tillers, suggesting that the increase in bioactive GA and less *GA2ox1* activity inhibits tillering and permits internode elongation in rice (Lo et al. 2008). More tillers were observed in the GA-responsive mutant of turfgrass (Agharkar et al. 2007). In rice, *MOC1 (MONOCULM1)*, a tillering regulator, is guarded by belting with the DELLA protein of *SLR1 (SLENDER RICE1)*. GA has a role in the degradation of *SLR1*, resulting in stem elongation and reduced tiller number (Liao et al. 2019). In barley, the *LNT1 (LOW NUMBER OF TILLERS1)* gene encodes *JUBEL2*, which is a homolog to the KNOX protein regulating *GA2ox*, as reported in maize (Dabbert et al. 2009). The expression of *GA2ox1* in the *lnt1* barley mutant should be investigated to elucidate the regulation of tiller development by GAs.

**Abscisic acid (ABA)** Previous studies indicated that ABA inhibits bud outgrowth, as shown after exogenous ABA treatment in *Arabidopsis* (Chatfield et al. 2000). The possibility that ABA may control tiller development has been widely explored. Functional connections exist between the biosynthetic pathways of ABA and other phytohormones, such as SLs. The effect of this connection on tillering has been proved in barley (Wang et al. 2018). In barley, two transgenic lines accumulating ABA as a result of RNAi-mediated down-regulation of HvABA 8'-hydroxylase 1 and 3 were developed. LC-MS/MS analysis confirmed higher ABA levels in stem base tissues in these transgenic lines. Both lines showed enhanced tiller formation and lower expression levels of *HvD27*, *HvMAX1*, *HvCCD7*, and *HvCCD8*, indicating that ABA suppresses SL biosynthesis, leading to enhanced tiller formation (Wang et al. 2018). Recently, a study has also shown that ABA-related gene expression increased in bud-containing tissues of *Arabidopsis* under low red light to far-red light exposure, which led to a general reduction in branch number. This study suggests that a high red light to far-red light exposure could inhibit the ABA effect (González-Grandío et al. 2013). Endogenous ABA exerts a direct effect on regulating axillary bud outgrowth in intact *Arabidopsis*, acting as a general inhibitor (Yao and

Finlayson 2015). The biosynthetic pathways of ABA and SLs appear to be connected, but so far, the mechanism has not been well explored.

**Jasmonic acid (JA)** JA is one of the emerging endogenous growth regulators affecting many developmental processes in plants. It was previously known as a growth inhibitor but is now identified as a signal transducer related to stress responses. For example, JA may affect nutrient uptake and sugar transportation, leading to stress tolerance (Ruan *et al.* 2019). The very first investigation of JA's role in tillering in grass species was reported in sorghum, where it was shown that exogenous application of JA promoted in situ bud growth (Liu and Finlayson 2019). The ERF109 transcription factor regulates auxin transport-related genes (Xu *et al.* 2020), and the sorghum homolog of ERF109 associated with JA GO terms was strongly induced by leaf removal (Liu and Finlayson 2019). Based on the results obtained in a study on sorghum, there is a possibility that JA application on buds induces ERF109, resulting in overexpression of the auxin transport-related genes, thus leading to bud growth acceleration (Liu and Finlayson 2019). It would be interesting to investigate the JA-auxin interaction at the molecular level to elucidate JA's role in bud regulation related to tiller development.

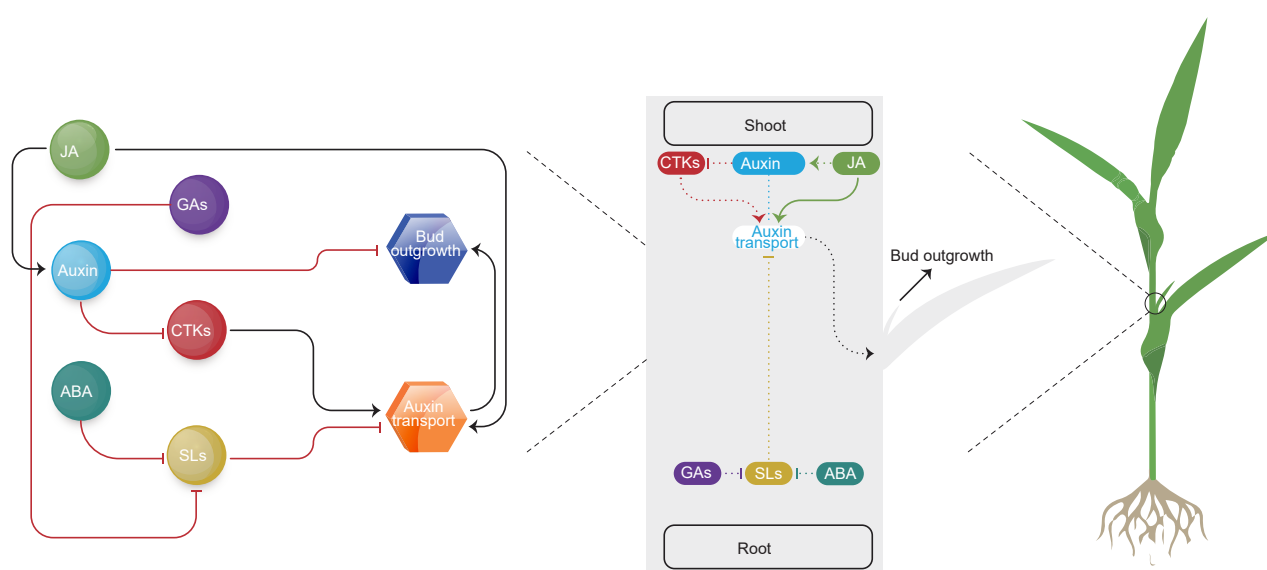
#### 4.2. Cross-talk of phytohormones in regulating tiller development

It is well-documented that phytohormones interact in a complex network to regulate tiller formation. The

individual and the cumulative effect of different interacting phytohormones on tillering were shown in Fig. 3. For phytohormonal cross-talk in tiller development, the major and direct roles are played by CTKs and auxin. CTKs promote tillering by boosting the auxin transport that enhances the bud outgrowth, while auxin inhibits CTKs, which lowers or stops the auxin transport, resulting in auxin accumulation and bud dormancy. The other phytohormones play indirect roles in regulating tiller development by inhibiting or promoting auxin transporters (or other phytohormones), resulting in low or high tillering phenotypes, respectively. SLs and JAs are the most recently identified phytohormones playing their roles in shoot branching. Previous studies revealed that SLs inhibited bud outgrowth by blocking the auxin transport, while JA had an inhibitory effect on SLs and promoted the auxin transport, resulting in enhanced tiller development. Likewise, ABA and GAs inhibit the SLs, which indirectly stimulates bud outgrowth.

#### 4.3. Regulation of tiller development by sugars

In addition to their metabolic roles, sugars can also act as a mediator in many important developmental processes of plants. Sugars are an energy provider and resource of carbon for protein synthesis. Sucrose functions as a signal to control growth and differentiation with its related products, glucose and fructose (Ruan 2012; Lunn *et al.* 2014). Very few studies discussed the role of sugars in tiller development from a developmental and physiological viewpoint or showed the genetic regulation of sugar



**Fig. 3** Summary of hormonal cross-talk and their relationship in regulation of tillering. The arrow-shaped lines indicate the promoting effect and T-shaped arrows indicate the inhibitory effect of phytohormones. SLs, strigolactones; CTKs, cytokinins; GAs, gibberellins; ABA, abscisic acid; JA, jasmonic acid.

content and composition and its role in tiller development in cereals. This section emphasizes the role of sugars in regulating tiller development in barley.

In shoot branching, sugar is crucial for enhancing bud outgrowth. During the development of lateral branches, sugars seem to play a signaling role, notable through trehalose 6-phosphate, interacting with phytohormones. In wheat, the tin mutant showed a lower tiller number with low sucrose levels in the inhibited buds due to the down-regulation of sucrose inducible genes (Kebrom *et al.* 2012). Likewise, the defoliation causing bud inhibition was found to be associated with the up-regulation of sucrose starvation and down-regulation of sucrose-inducing genes in dormant buds of sorghum (Kebrom and Mullet 2015), suggesting that the outgrowth may be dependent on the overall status of plant sugar. Recently, the molecular mechanism of regulation of shoot branching by sucrose has been reported in *Arabidopsis* and rice (Zafar *et al.* 2020; Fichtner *et al.* 2021). In barley, some reports shed light on the role of sugar-related genes, specially *HEXOKINASE (HXK)*, *SUCROSE TRANSPORTER (SUC)*, and trehalose 6-phosphate (Tre6P) for regulating shoot branching (Barbier *et al.* 2021; Fichtner *et al.* 2021). Three sugar-related QTLs (*HvSUT1*, *HvHXK9*, and *HvHXK6*) associated with *HEXOKINASE* and *SUCROSE TRANSPORTER* genes were found to be related to the regulation of tillering in barley (Alqudah *et al.* 2016). Although the role of sugar in the regulation of shoot branching has been highlighted in very recent reports to our knowledge, no prior study has been conducted in barley to explore the role of sugars and the molecular mechanisms in the regulation of shoot branching (Fichtner and Lunn 2021). Therefore, we mapped around 20 sugar-related genes in barley for the first time. Among them, *HEXOKINASE*- and Tre6P-related genes are strongly supported by recent studies (Barbier *et al.* 2021), ultimately offering an opportunity to understand their molecular basis. These findings raise the importance of sugar-related genes in affecting most plastic traits, including tillering in grasses. Thus, it can be concluded that further investigations should be conducted at the molecular level on the regulation of tillers by sugars.

## 5. Regulation of tiller development by the environment-responding genes and agronomic factors

Tillering is also influenced by many environmental factors, including temperature, photoperiod, water, and nutrient availability (Skinner and Simmons 1993; Miralles and Richards 2000; Romina *et al.* 2014). With respect to global warming, changing phenological properties

may be an efficient method for planting cereal crops, especially winter barley and wheat. Tillering was inhibited by high temperature, substantial vernalization, and less photoperiod sensitivity (Wang *et al.* 2010). Tiller production in barley was shown to be significantly affected by the genes in response to the environment, such as vernalization genes *VERNALIZATION-H1 (Vrn-H1)* and *Vrn-H2* and the photoperiod response gene *Ppd-H1* (Von Korff *et al.* 2006; Wang *et al.* 2010). Photoperiod affects tiller number by altering the duration of the vegetative growth. Barley genotypes carrying the photoperiod-sensitive *Ppd-H1* allele had high expression levels of *Vrn-H3* (Campoli *et al.* 2012). Alqudah *et al.* (2016) reported that the barley accessions carrying the reduced photoperiod sensitivity (*Ppd-H1*) allele produced much more productive and non-productive tillers per plant than the accessions sensitive to photoperiod. In addition, the genes associated with barley flowering time, including *Ppd-H1*, *Sdw1*, *Vrn-H1*, and *Vrn-H3* exerted pleiotropic effects on plant development, including tillering (Wiegmann *et al.* 2019). These pleiotropic effects were found to be strongly regulated by the response to environmental factors, such as day length and temperature (Herzig *et al.* 2018; Wiegmann *et al.* 2019). A number of quantitative trait loci (QTLs) that control tillering have been described in wheat (Naruoka *et al.* 2011; Yang *et al.* 2013; Xie *et al.* 2016). In a study on the tillering traits, a number of QTLs were identified under the short day and artificially vernalized conditions, where the Ppd genes were active, and the QTLs were located on chromosomes 6B (QTLs 45, 48) and 4B (QTL 29), respectively (Giunta *et al.* 2018). Flowering-associated genes may influence wheat tiller number. Overexpression of *TaZIM-A1* caused delayed heading and increased effective tiller number by regulating TaFT and *VERNALIZATION1 (VRN1)* expression (Liu *et al.* 2019). The photoperiod-sensitivity gene *Ppd-1* influences tiller number in wheat (Dyck *et al.* 2004). The later-heading *vrn-A1* allele was associated with more tillers per plant in a wheat cultivar Cappelle-Desprez (Kato *et al.* 2000).

It may be suggested that the wild barley germplasm can improve plant development to boost grain yield. Several agronomic factors or agricultural management practices also influence tillering and productive tillers. For example, the cropping pattern can affect tillering, as cereal crops deplete nutrients from the soil, lowering the number of productive tillers in the next crop. There is a higher number of productive wheat tillers in a wheat–rice cropping pattern compared to a wheat–sunflower cropping pattern (Nawab *et al.* 2011). Cereal crops are exhaustive compared to legumes that facilitate the soil with nitrogen (N) and phosphorus (P) (Stagnari *et al.*



2017). In addition, a higher barley yield was observed when grown in a crop rotation, including legumes, rather than in a continuous barley crop sequence (Jones and Singh 2000). Water availability also regulates tillering, as water-limited conditions result in fewer tiller formations (Chaturvedi *et al.* 1981). Improvements in soil moisture through mulch application reduced the number of non-productive tillers and increased rice yield (Jabran *et al.* 2015). Excessive evaporation resulting in drought stress reduces the number of productive tillers in wheat and maize (Balwinder-Singh *et al.* 2016; Zhang *et al.* 2017). Nutrient management is also an important factor affecting tillering (Bakht *et al.* 2010). Although N and P are essential nutrients with regard to tillering in grasses, potassium (K) also plays a role in tiller regulation, such as increasing the tiller number in rice (Bahmaniar and Ranjbar 2007). Planting density or seeding rate also influences the morphology and number of tillers, with an increased number of non-productive tillers at higher planting densities in barley (Kirby and Faris 1972). Similarly, a low tiller number was reported with dense seeding of spring wheat (Otteson *et al.* 2008). In short, the influence of environmental and agronomic factors on tillering and productive tillers have been intensively studied, but the precise roles of all these factors are still not fully described. It is suggested that some integrated experiments be conducted to understand the mechanisms of these factors toward the regulation of tiller initiation and development.

## 6. Conclusion and perspective

Tillering is a major yield determinant in cereal crops and is controlled by different endogenous and environmental factors. The misregulation of developmental genes may affect various physiological processes, resulting in higher or lower tiller numbers. Tiller development involves bud initiation and outgrowth. The bud initiation is severely inhibited in the *uniculm2* mutant with zero tillers. The mutants related to bud outgrowth are mainly determined by *Int1*, *als1*, and *cul4*; the candidate gene of *als1* has not yet been identified. LNT1 encodes a JuBel2 homeodomain transcription factor, and *cul4* encodes BOP-like BTB-ankyrin protein, which plays crucial roles in a weak bud outgrowth of tillers. The mutants *gra-a*, *grassy*, *mnd1*, *mnd3*, *mnd5*, *aps1*, and *int-m* enhance tiller production, whereas *cst1*, *int-b*, and *cul2* inhibit tillering in barley.

However, the candidate genes for these mutants are yet to be identified. Some candidate genes of mutants that increase tiller production have been identified, e.g., *HNT1*, *INT-C*, *HvD14*, *MND6*, and *UZU1*, which encode

proteins to regulate tillering in barley. SDW1 regulates the biosynthesis of GA phytohormone and enhances tiller production. Few genetic studies have targeted and functionally characterized tillering genes in barley. Further investigations and functional validation of tillering genes are necessary for exploring more-natural tillering-enhancing alleles for crop breeding. Here, we provide an essential foundation for uncovering the biological functions of sugar-related genes, suggesting that sugar-regulated genes potentially regulate tillering in barley and, most likely, other temperate cereals such as wheat. Targeting such genes by genome editing approaches such as an efficient CRISPR/Cas9 system to produce heritable and desirable alleles is expected to accelerate crop breeding significantly. Abiotic stresses, such as extreme temperature, drought, and phosphorus depletion, inhibit the growth of lateral branches in barley, while nitrogen availability and photoperiod insensitivity promote barley tillering. Breeders prefer to select the lines with low non-productive tillering and high-productive tillers (carrying spikes) to increase grain yield. It is also critical to explore the tillering-enhancing alleles to maximize grain yield. A deep understanding of tillering as affected by genetic and agronomic factors will broaden our knowledge of biological processes and may allow breeders to better control and optimize tillering. Future studies should focus on the regulatory roles of phytohormones and their molecular interaction to define tillering and yield formation in barley and other cereal crops.

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## Declaration of competing interest

The authors declare that they have no conflict of interest.

**Appendix** associated with this paper is available on <http://www.ChinaAgriSci.com/V2/En/appendix.htm>

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