# Genetics of Tillering in Rice and Barley

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## Abstract

Tillering, or the production of lateral branches (i.e., culms), is an important agronomic trait that determines shoot architecture and grain production in grasses. Shoot architecture is based on the actions of the apical and axillary meristems (AXMs). The shoot apical meristem (SAM) produces all aboveground organs, including AXMs, leaves, stems, and inflorescences. In grasses like rice (*Oryza sativa* L.) and barley (*Hordeum vulgare* L.), vegetative AXMs form in the leaf axil of lower leaves of the plant and produce tillers (branches). Tiller development is characterized by three stages, including (i) AXM initiation, (ii) bud development, and (iii) outgrowth of the axillary bud into a tiller. Each tiller has the potential to produce a seed-bearing inflorescence and, hence, increase yield. However, a balance between number and vigor of tillers is required, as unproductive tillers consume nutrients and can lead to a decreased grain production. Because of its agronomic and biological importance, tillering has been widely studied, and numerous works demonstrate that the control of AXM initiation, bud development, and tillering in the grasses is via a suite of genes, hormones, and environmental conditions. In this review, we describe the genes and hormones that control tillering in two key cereal crops, rice and barley. In addition, we discuss how the development of new genomics tools and approaches, coupled with the synteny between the rice and barley genomes, are accelerating the isolation of barley genes underlying tillering phenotypes.

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**At the global level**, the most important cereal crops are maize (*Zea mays* L.), rice, wheat (*Triticum aestivum* L.) and barley (*H. vulgare* spp. *vulgare*), with a total of 2.4 billion tons produced annually at a value of >446 billion

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Abbreviations: *als1*, *absent lower laterals1* gene; *ASP1*, *ABERRANT SPIKELET AND PANICLE1* gene; ATP, adenosine triphosphate; AXM, axillary meristem; BAPC/C, canaphase-promoting complex; *BLR*, *Arabidopsis BELLRINGER* transcription factor; BR, brassinosteroid; BSA, bulked segregant analysis; cDNA, complementary DNA; CK, cytokinins; *cul2*, *Uniculm2* gene; *cul4*, *uniculme4* gene; *ipa*, *ideal plant architecture1*; *int-b*, *intermedium-b* gene; *int-c*, *intermedium-c*; *D27*, *DWARF27* gene; *DLT*, *DWARF AND LOW-TILLERING* mutant allele; ERF, ethylene-responsive element-binding factor; *FZP*, *FRIZZY PANICLE* gene; GA, gibberellin; GA2oxs, C19- and C20-GA 2-oxidases; *gra-a*, *granum-a* gene mutation; GRAS, GIBBERELLIC-ACID INSENSITIVE, REPRESSOR of GAI and SCARECROW transcription factor; *grassy*, *grassy tillers* gene; GSK2, *GSK3/SHAGGY-like kinase*; *Hv20ox2*, a barley GA 20-oxidase gene; IAA, indole-3-acetic acid; *lnt1*, *low number of tillers1* gene; IPT, ISOPENTENYL TRANSFERASE; KNOX, *Arabidopsis* KNOTTED-like homeobox; LAS, *Arabidopsis* LATERAL SUPPRESSOR transcription factor; *LAX1*, *LAX PANICLE1* gene; LS, tomato LATERAL SUPPRESSOR transcription factor; *MIP1*, *MONOCULM1 Interacting Protein 1*; *mnd1*, *many noded dwarf1* gene; *mnd6*, *many noded dwarf6* gene; *MOC1*, *MONOCULM1* gene; MYA, million years ago; OsBZR1, transcription factor that regulates BR-responsive genes; *OsEATB*, *ERF protein associated with tillering and panicle branching*; PAT, polar auxin transport; PIN, PIN-FORMED protein; qSH1, a rice QTL for seed shattering on chromosome 1; QTL, quantitative trait locus; SAM, shoot apical meristem; *sdw1*, *semidwarf1* gene; SL, strigolactones; *sps*, *supershoot* mutant; STM, SHOOTMERISTEMLESS protein; *tad1*, *tillering and dwarf1* allelic mutant; *TB1*, *TEOSINTE BRANCHED1*; *te*, *tillering enhancer* allelic mutant; *tin*, *tiller inhibition* gene; *uzu*, *semibrachytic* mutant gene; WFP, WEALTHY FARMER'S PANICLE.

international dollars (FAOSTAT, 2012). All four of these crops are members of the Poaceae family. Much research to increase productivity, particularly of rice and wheat, is performed both by publicly funded plant breeding programs and by seed companies (Shiferaw et al., 2013). Meanwhile, the demand for cereal grains may double by 2050 (Tilman et al., 2011), which will require an average yield increase of 2.4% per year for the major cereals (Ray et al., 2012). To achieve this, multidisciplinary approaches are needed with genetic improvement playing a major role.

Tillering is a key component of yield for major cereals such as wheat, rice, barley, and rye (*Secale cereale* L.) (Sakamoto and Matsuoka, 2004; Sreenivasulu and Schnurbusch, 2012). In grasses, tillers are side branches (i.e., culms) that grow at the ground level from nodes of nonelongated internodes, determining the overall shoot architecture of the plant and affecting important agronomical features like competition with weeds, herbicide treatment, spacing, and the ease of harvesting (Donald, 1968; Seavers and Wright, 1999). Although sharing some key steps in their development, tillers differ from lateral branches in eudicots in that they can produce adventitious roots and grow independently from the main plant shoot.

While the molecular mechanisms controlling branching in dicots have been widely investigated (Wang and Li, 2008; Domagalska and Leyser, 2011), they are not thought to be completely conserved with tiller development in monocots, particularly in the cross-talk among hormonal pathways and other genetic networks (Kebrom et al., 2013). For instance, *TEOSINTE BRANCHED1* (*TB1*)-like genes in dicots and monocots are known to work downstream of strigolactones (SL). But while the mRNA level of *TB1*-like genes in *Arabidopsis* and pea (*Pisum sativum* L.) was down-regulated by SL, experimental evidence showed no transcriptional regulation for *FC1/OsTB1* by SL in rice (Aguilar-Martínez et al., 2007; Minakuchi et al., 2010; Kebrom et al., 2013). Another example is offered by the rice gene *MONOCULM1* (*MOC1*) and its orthologs in *Arabidopsis* and tomato (*Solanum lycopersicum* L.). Although they are all required for AXM initiation during the vegetative phase, *MOC1* plays additional functions in bud outgrowth and control of plant height (Li et al., 2003). There are also examples of the genes identified in eudicots that have not been identified to date in monocots, such as the reduced-branching mutations in the *REGULATOR OF AXILLARY MERISTEMS1*, *2*, *3* and *BLIND* genes of *Arabidopsis* and tomato (Schmitz et al., 2002; Keller et al., 2006; Müller et al., 2006). These examples illustrate the importance of identifying and characterizing the genes involved in the control of tillering in cereals.

Tiller development is regulated by a complex network of genetic, hormonal, and environmental factors, making tillering a highly plastic trait that allows wild cereals to adapt to different environmental conditions. It is also a major target for manipulation of plant architecture in breeding programs (Kebrom et al., 2013). Tillers can develop inflorescences and contribute to grain yield, but tillers that grow late in the season will not produce any grain and will lower the overall harvest index (Sakamoto and Matsuoka, 2004; Mäkelä and Muurinen, 2011), indicating that a balance between number and vigour of tillers is required. A model plant with reduced height, low number of unproductive tillers, higher number of grains, and erect leaves has been proposed as the ideotype for cereal breeding (Donald 1968; Khush, 2001). Indeed, reduced tillering accompanied increased productivity in the domestication of maize (Doebley et al., 2006). Cereal varieties grown before the Green Revolution were responding to N fertilizer by profuse tillering and stem elongation, thus increasing biomass. Ideotype breeding led to shorter plants with more productive tillers and improved response to N, and increased harvest index to 0.5 (Khush, 2003). In rice, this ideotype is associated with certain alleles of the *wealthy farmer's panicle* (*wfp*)/*ideal plant architecture1* (*ipa1*) locus, which confer low tillering coupled with desired inflorescence features resulting in higher yield (Jiao et al., 2010; Miura et al., 2010). Reduced tillering has also been associated with improved kernel weight under terminal water deficit environments in wheat near-isogenic lines carrying the *tiller inhibition* (*tin*) gene (Atsmon and Jacobs, 1977; Kebrom and Richards, 2013; Mitchell et al., 2013).

In addition to being important crops, barley and rice are genetic model systems for the Poaceae family (Izawa and Shimamoto, 1996). Rice has a small genome (~430 Mb) with a high degree of chromosomal synteny with other major cereal crops (Bolot et al., 2009). Barley, with its diploid genome, represents another convenient model, particularly for Triticeae crops which share high genomic colinearity, providing a basis for genetic and genomic analyses in polyploid wheats (Bennetzen and Freeling, 1997; Hayes et al., 2003; Kumlehn and Hensel, 2009).

The conservation of synteny and integration of genomic tools among small grain cereals, particularly rice, barley, and wheat, allows the transfer of knowledge among these major crops. In the following sections, we will summarize progress in the identification and characterization of genes, hormones, and developmental pathways underlying tillering in rice and barley. Additionally, we highlight the emergence of new genomics resources and high-throughput technologies that are revolutionizing genetic studies in these cereal species, often by leveraging the high degree of colinearity that their genomes exhibit.

## Tiller Development in Rice and Barley

Plant development is a continual process of organogenesis involving the activity of meristems, pluripotent stem cell populations present in different parts of the plant. Shoot architecture is ultimately determined by the activity and determinacy of the SAM and AXMs (Wang and Li, 2008). Tiller development in grasses comprises three main stages: (i) establishment of an AXM marked by formation of stem cell population in the leaf axil, (ii) production of leaf

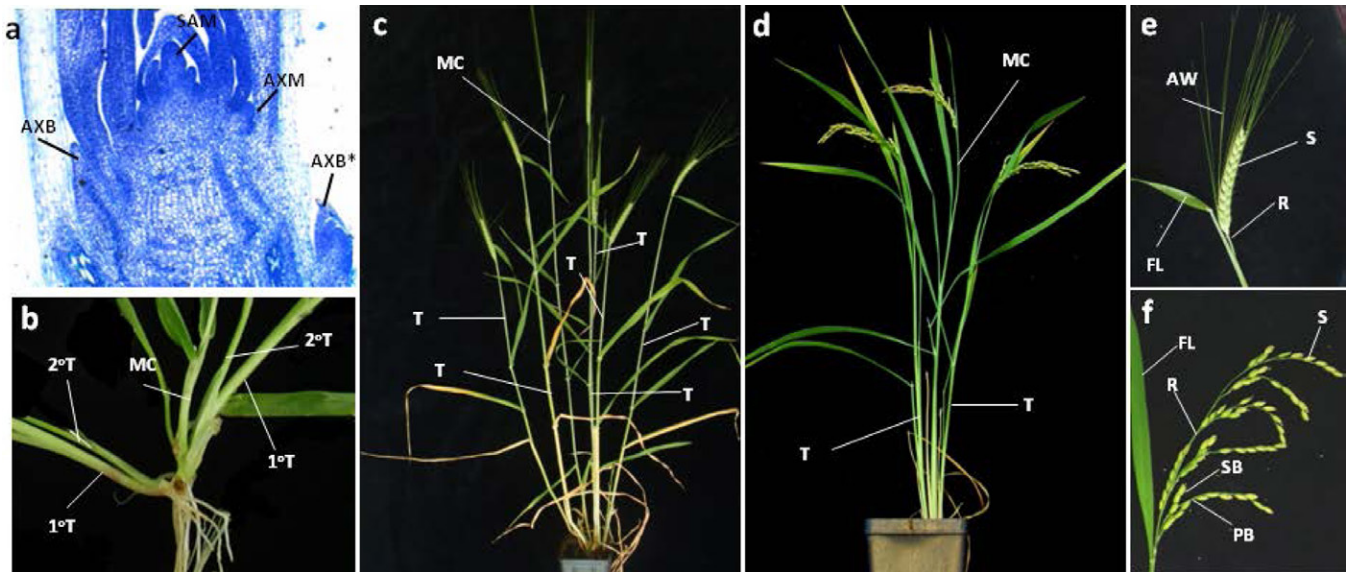


Figure 1. Tiller formation in barley and shoot architecture of barley and rice. (a) Longitudinal section of a barley shoot apex showing a shoot apical meristem (SAM), an axillary meristem (AXM, the first stage in tiller formation) and axillary buds (AXB, the second stage of tiller formation). (b) Barley plant with out growth of primary (1°T) and secondary tillers (2°T), the third stage of tiller formation. MC = main culm. (c) Barley shoot architecture showing the MC and tillers (T). (d) Rice shoot architecture showing the MC and T. (e) Barley two-rowed spike showing the flag leaf (FL), rachis (R), spikelet (S), and awn (AW). (f) Rice panicle showing the FL, R, primary branch (PB), secondary branch (SB), and S.

primordia from the AXM to form an axillary bud, and (iii) outgrowth of the axillary bud to form a tiller (Fig. 1) (Schmitz and Theres, 2005). Classically, shoot development is considered to occur in repeated units called phytomers, each consisting of an internode (stem segment), a node, a leaf, and an axillary bud (Weatherwax, 1923; Sharman, 1942). Elaborations on this basic model have been proposed for barley to account for floral organs and paired structures present at branching points (e.g., prophyll and palea) (Bossinger et al., 1992; Forster et al., 2007).

In barley and rice, the first AXMs are formed during embryogenesis. The mature barley embryo generally contains two axillary buds, one each in the axils of the coleoptile and of the first leaf primordium (Kirby and Appleyard, 1987), while the mature rice embryo generally contains one axillary bud in the axil of the coleoptile (Saha, 1957). Upon germination, both plants continue to produce more leaves and AXMs in an ordered and coordinated progression, as described in detail in rice (Itoh et al., 2005; Oikawa and Kyozuka, 2009). Leaves derive from leaf founder cells at the flanks of the SAM, which undergo a developmental transition from an indeterminate to a determinate cell fate as they are recruited into incipient leaf primordia. The time interval between the formation of two successive leaf primordia is called a plastochron, and leaf developmental stages are identified by their plastochron number (Pi), with the youngest visible leaf primordium indicated as P1, the next youngest as P2, and so on (reviewed in Itoh et al., 2005). The AXM develops in the leaf axil and stages of AXM formation are indicated with Pi of the subtending leaves. In rice, the first visible indication of AXM development is a slight protrusion on the stem surface towards the P2 leaf primordium (Oikawa and Kyozuka, 2009). Cell proliferation continues through the P3 and P4 stages when cells undergo a critical transition acquiring meristematic fate. The process is completed by the P5 stage when the new AXM has initiated its own leaf primordia originating an axillary bud (Oikawa and Kyozuka, 2009).

Depending on endogenous and environmental signals, an axillary bud may remain dormant or grow into a tiller. Each tiller is a new axis of growth, organized like the main culm in phytomer units. Each tiller harbors new axillary buds that may in turn develop new tillers in a reiterative pattern (Fig. 1b). Tillers, therefore, develop in acropetal succession with primary tillers arising from axillary buds of the main culm, secondary tillers growing out of leaf axils of primary tillers, and so on (Kirby and Appleyard, 1987). After the transition of the main culm SAM from a vegetative to a reproductive state, young tillers undergo senescence, possibly because nutrients are routed away from developing tillers to the elongating internodes (Mohapatra et al., 2011). The early developing primary tillers benefit from higher sink/source ratio, sink capacity, leaf area, spikelet number, and filled grain percentage (Choi and Kwon, 1985).

Axillary meristem establishment and formation of the axillary bud are mostly under genetic control, while bud outgrowth is regulated by a complex network of genetic, hormonal, and environmental factors (Kebrom et al., 2013), making it highly responsive to environmental conditions, such as shading and nutrient availability (Agusti and Greb, 2013). Being sessile, plant fitness in varied environmental conditions depends on their

ability to translate external signals into developmental responses. Several distinct signals are involved in the regulation of shoot branching, with key roles played by auxin, cytokinins (CK), and SL (Kebrom et al., 2013).

Upon transition to the reproductive phase, the SAM of each tiller is transformed into an inflorescence meristem and differentiates into an inflorescence, called a panicle in rice and spike in barley, organized around a main axis called a rachis (Fig. 1). In rice, each inflorescence meristem produces several AXMs that develop into rachis branches, and the AXMs generated subsequently may develop into the next order of rachis branches or lateral spikelets, resulting in a branched structure (Fig. 1) (Itoh et al., 2005; Oikawa and Kyozuka, 2009). In barley, AXMs arising from the rachis differentiate into spikelet triplet meristems, that in turn will develop into three spikelet meristems (Bossinger et al., 1992), one central and two lateral. In wild barley and two-rowed cultivars, only the central spikelet is fertile, while the lateral spikelets are sterile and remain underdeveloped. In six-rowed barley cultivars and mutants, all three spikelets mature to produce grains (Kirby and Appleyard, 1987; Komatsuda et al., 2007).

## Genetic and Hormonal Control of Tillering in Rice

Thanks to its importance as a crop and also as a model system for other cereals, the genetic basis of shoot branching in rice has received growing attention, and over the last decade, a number of genes involved in tiller development have been identified (Table 1, Fig. 2). Some of these genes specifically affect tiller development, while others affect other agronomically important traits such as inflorescence (panicle) architecture and plant height. Here we review the isolated and characterized genes involved in rice tillering and related hormonal pathways including auxin, CK, gibberellins (GA), and SL.

**Table 1. List of genes and mutants involved in rice tillering with their phenotypes, homologs, molecular function, and pathway.†**

| Gene or mutant name, protein or gene family | Phenotype | Homologs | Molecular function or pathway | References |
|---|---|---|---|---|
| AXM establishment and maintenance | | | | |
| *MOC1*—GRAS family | reduced tillers‡<br>increased tillers and reduced plant height§ | tomato *Lateral suppressor* (*Ls*)<br>*LAS* | TF up-regulates *OsTB1* and *OSH1*, works with LAX1 and LAX2 in AXM establishment; degraded by TAD1 | Li et al., 2003; Xu et al., 2012; Lin et al., 2012 |
| *TAD1* and TE, Cdh1-type coactivators | increased tillers and reduced plant height‡ | *CCS52A* | APC/C, a multisubunit E3 ligase; forms a complex with OsAPC10; activates APC/C to target MOC1 for degradation by the ubiquitin-26S proteasome pathway | Xu et al., 2012; Lin et al., 2012 |
| *MIP1*, Brefeldin A-sensitivity protein 1 (*OsBre1A* and *OsBre1B*) | increased tillers and reduced plant height§ | *Arabidopsis At_HUB1*, Maize *Zm_Bre1* | Bre1 protein family is E3 ubiquitin-protein ligase; *At_HUB1* involved in chromatin modification and gene regulation; interacts with MOC1 | Sun et al., 2010 |
| *LAX1*, containing basic helix-loop-helix domain | reduced tillers and panicle branches§ | *Arabidopsis AtBA1/LAX1* Maize *BA1* | TF; interacts with MOC1 and LAX2 in AXM establishment; maintenance | Komatsu et al., 2003; Oikawa and Kyozuka, 2009 |
| *LAX2*, Novel plant nuclear protein | reduced tillers and panicle branches§ | *Arabidopsis DRIP1* and *DRIP2* (although lack the amino acid stretches) | potentially works as coactivator of LAX1; interacts with MOC1 and LAX1 in AXM establishment; maintenance | Tabuchi et al., 2011 |
| Auxin | | | | |
| *OsPIN1*-PIN1 family | increased tillers¶ | *Arabidopsis AtPIN1* | auxin efflux carrier/Transports Auxin | Xu et al., 2005 |
| *OsPIN2*-PIN2 family | increased tillers and tiller angle, reduced plant height§ | *Arabidopsis AtPIN2* | auxin efflux carrier; transports auxin, down-regulates *OsLazy1* (negative regulator of polar auxin transport) | Chen et al., 2012 |
| *Increased number of Tillers/ Enlarged Leaf angles/Dwarfism TLD1/Gretchen Hagen3 OsGH3.13-GH3* | increased tillers, leaf angle and drought tolerance, reduced panicle length, plant height and spikelets no# | *Arabidopsis WES1/GH3.5* | multifunctional acetyl-amino synthetase; Conjugates IAA to amino acids; regulates negatively free IAA; *Arabidopsis* homologs respond to ABA and salicylic acid pathways | Zhang et al., 2009 |
| *ASP1/Ramosa1 Enhancer Locus2*-Transcriptional corepressor | increased primary tillers and reduced secondary tillers/ disrupted phyllotaxy of tillers arrangement‡ | *TPL*, *REL2* | transcriptional corepressor; derepression of axillary bud growth; involved in auxin signaling | Kwon et al., 2012; Yoshida et al., 2012 |
| *OsmiR393*, MIR393 noncoding miRNA | increased tillers, early flowering, salt and drought susceptibility§ | *Arabidopsis miR393* | represses *OsTIR1* and *OsAFB2*, that further represses *OsAUX1*, auxin transport to axillary buds and down-regulates *OsTB1* | Xia et al., 2012 |

*(cont'd)*

**Table 1. Continued.**

| Gene or mutant name, protein or gene family | Phenotype | Homologs | Molecular function or pathway | References |
|---|---|---|---|---|
| Cytokinins (CK) | | | | |
| *OsIPT1,2,3,4,7*, Adenosine 5′ phosphate isopentenyl transferase | overproliferation of axillary shoots§ | *Arabidopsis Isopentenyl Transferase* genes | catalyses prenylation of adenosine 5′ phosphates at the N6-terminus with dimethylallyldiphosphate (involved in CK biosynthesis | Sakamoto et al., 2006 |
| Gibberellin (GA) | | | | |
| *OsGA2ox5/6* oxidases | increased tillers and adventitious root growth, semidwarfing§ | *AtGA2oxs*, *ZmGA2oxs* | catalyse 2-β-hydroxylation reaction/inactivate bioactive GA | Lo et al., 2008 |
| Strigolactones (SL) | | | | |
| *D1/D17/HTD1*, CCD7 | increased tillers‡ | *MAX3* | cleaves β-carotene into 13-apo-β-carotenone/ involves in SL biosynthesis/up-regulated by auxin | Ishikawa et al., 2005, Kebrom et al., 2013, Zou et al., 2006 |
| *D10/CCD8b*, CCD8 family | increased tillers‡ | *MAX4* | cleaves β-carotene into 13-apo-β-carotenone/ involves in SL biosynthesis/Up-regulates by auxin | Ishikawa et al., 2005, Kebrom et al., 2013, Arite et al., 2007 |
| *D27*, Iron-containing protein with isomerase activity | increased tillers‡ | *AtD27* | produces 9-cis-β-carotine from all-trans-β-carotine in SL biosynthesis pathway/ involved in SL biosynthesis | Ishikawa et al., 2005, Lin et al., 2009; Kebrom et al., 2013 |
| *D14*, hydrolase/esterase | increased tillers‡ | *AtD14* | involved in SL signaling, likely as SL receptor and SL catabolic enzyme/interacts with GA signaling repressor SLR1/regulated by OsMADS57 | Ishikawa et al., 2005; Guo et al., 2013; Nakamura et al. 2013 |
| *D3*, F-box leucin-rich repeat protein | increased tillers‡ | *Arabidopsis MAX2* | mediates signaling of SL and karrikins; involved in SL biosynthesis | Ishikawa et al., 2005; Kebrom et al., 2013 |
| SL pathway regulation and integration of different signals | | | | |
| *OsTEF1*, Elf1 superfamily | reduced tillers, seminal roots growth and salt tolerance‡ | *Arabidopsis Transcription elongation factor-like 1* | involved in transcription elongation by RNA polymerase II; Induces cytochrome P450, potentially a member of SL pathway in *Arabidopsis* | Paul et al., 2012 |
| *OsTB1/FC1*, class II proteins of TCP family | excessive tillers and thin culm‡ | TB, *BRC1/TBL1* | TF; regulates SL signal transduction by interaction with OsMADS57 and reduces its inhibition for *D14*; target for repression by CK and GA; up-regulated by auxin | Minakuchi et al., 2010; Guo et al., 2013; Takeda et al., 2003 |
| *OsMADS57*, MADS-box domain protein | increased tillers,§ reduced tillers¶ | | involved in SL signaling by inhibiting D14; inhibits directly D14 and its inhibition activity reduced by interaction with OsTB1 | Guo et al., 2013 |
| *OsMIR444a*, *MIR444* noncoding miRNA | reduced tillers§ | | enhances the SL biosynthesis by repressing *OsMADS57* | Guo et al., 2013 |
| *THIS*, Class III lipase family | increased tillers, shorter plants, and less seed set‡ | *Arabidopsis PRLIP8* | may be involved in auxin and SL signaling | Liu et al., 2013 |
| NSP1 and NSP2 | reduced tillers‡ | Legume NSP1 and NSP2 | TFs; down-regulates *D27* | Liu et al., 2011 |
| *OsSPL14/Os IPA11*/WFP QTL–SPL family | reduced tillering, increased lodging resistance, and higher yield†† | *AtSPLs* and maize *ZmSPLs* | TF, regulates OsTB1 | Miura et al., 2010; Chen et al., 2010; Lu et al., 2013 |
| Brassinosteroid (BR) | | | | |
| *DLT/OsGRAS32*, GRAS | reduced tillers and plant height‡ | *Arabidopsis AtGRAS8* | TF, involved in inhibition of BR biosynthesis through interaction with OsBZR1 that perceives BR signal by OsBRI1 | Tong et al., 2009, 2012 |
| *GSK2*, GSK family | reduced tillers, dark green and dwarf plants§ | *Arabidopsis GSK3/ SHAGGY-like kinase Brassinosteroid-Insensitive2* | Regulates *DLT* gene by phosphorylation | Tong et al., 2012 |

*(cont'd)*

**Table 1. Continued.**

| Gene or mutant name, protein or gene family | Phenotype | Homologs | Molecular function or pathway | References |
|---|---|---|---|---|
| Other factors | | | | |
| *OsMIR156*, noncoding miRNA | increased tillers, reduced spikelets and grains no.§ | *Arabidopsis MIR156* | microRNA cleavage of *OsSPL14* mRNA | Luo et al., 2012 |
| ABCG/WBC | reduced tillers, reduced panicle branches‡ | *Arabidopsis Terminal Flower 1* (*TFL1*) | half-transporter, *Arabidopsis TFL1* potentially involved in transportation of lipid | Yasuno et al., 2009 |
| *FZP*, ERF TFs | reduced tillers and plant height, increased rachis-branches‡ | maize *Branched Silkless1 BD1* gene | Involved in transition from axillary meristem identity to spikelet meristem | Xing and Zhang,2010; Kato and Horibata, 2012 |
| *APO2/OsRFL* | increased tillers and leaf number, reduced panicle branching‡ | *LFY* gene | TF, interacts with APO1 | Ikeda-Kawakatsu et al., 2012 |
| *APO1*-F-box protein | increased tillers and leaf number, reduced panicle branches‡ | *UFO* | Interacts with APO2, represses class-C genes | Ikeda et al., 2007; Ikeda et al., 2005 |
| *GLDH*, Mitochondrial enzyme with FAD domain | reduced tillers and plant height, premature senescence¶ | *Arabidopsis GLDH* | Catalyzes the last step of ASA biosynthesis by converting l-GalL into ASA, potentially involved in ABA and JA pathway | Liu et al., 2013 |
| *OsEATB/AP2/ERF* gene-AP2/ERF | increased tillers and panicle branches, reduced plant height§ | *Arabidopsis AtERFs* | TF; involved in the cross talk between ethylene and GA; down-regulates ethylene-induced enhancement of GA synthase | Qi et al., 2011 |

†ABA, abscisic acid; ABCG, *OsABCG5/rcn1*-ATP-Binding Cassette subfamily G5; *AP2, APETALA2* transcription factor; APC/C, coactivator of anaphase-promoting complex and/or cyclosome; APO1, *Aberrant Panicle Organization 1; APO2, Aberrant Panicle Organization 2; ASP1, Aberrant Spikelet and Panicle1; AtD14, 17, Arabidopsis Dwarf14, 27; AtGA2oxs, Arabidopsis gibberellin 2-oxidases*; ASA, ascorbic acid; *AtSPLs, Arabidopsis SQUAMOSA Promoter Binding Protein-Like; BA1*, Maize *Barren Stalk1; BD1, Branched Silkless1* gene; *BRC1/TBL1, Arabidopsis BRANCHED 1/TB1-LIKE 1*; CCD7, CCD8, Carotenoid Cleavage Dioxygenase; *CCS52A, Arabidopsis Cell Cycle Switch52A; D1/D17, Dwarf1/17; D10, Dwarf10; DLT, DWARF AND LOW-TILLERING* mutant allele; ERF, ethylene-responsive element-binding factor; *FC1, Fine culm1; FZP*, frizzy panicle; *GLDH, l-Galactono-1,4-Lactone dehydrogenase; GSK2, Glycogen synthase kinase2; HTD1, High Tillering Dwarf1; LAS, Arabidopsis Lateral Suppressor; LAX1, 2, Lax Panicle1, 2; LFY, Arabidopsis LEAFY* gene; *MIP1, MOC1 Interacting Protein; MOC1, Monoculm1; OsEATB, ERF protein associated with tillering and panicle branching; OsIPT1,2,3,4,7, Isopentenyl Transferase;* MAX3, MAX4, Arabidopsis More Axillary Growth3, 4; *NSP1, Nodulation Signaling Pathway1; rcn1, reduced culm number1; OsBre1A, Brefeldin A-sensitivity protein1; Os IPA11, rice Ideal Plant Architecture1; OsGA2ox5/6, Gibberellin 2-Oxidases5/6;* OsPIN1, OsPIN2, PIN-FORMED protein; *OsSPL14, REL2, OsTB1, Teosinte Branched1; OsTEF1, Transcription Elongation Factor-like 1;* Maize *Ramosa Enhancer Locus2; SQUAMOSA Promoter Binding Protein-Like 14; TAD1, Tillering and Dwarf 1; TB*, maize *Teosinte Branched; TBL1, Teosinte Branched 1-Like 1; TE, Tiller Enhancer*; TF, transcription factor; *THIS, Increased Tillering, Reduced Height, and Infertile Spikelets; TLD1, Increased number of Tillers/ Enlarged Leaf angles/Dwarfism; TPL, Arabidopsis TOPLESS; UFO, Arabidopsis Unusual Floral Organs*; WBC, white–brown complex; WFP, WEALTHY FARMER'S PANICLE; *ZmGA2oxs*, Maize *Gibberellin 2-Oxidases*. AtBA1/LAX1 comes as *Arabidopsis* ortholog to maize BARREN STALK1 (BA1) and rice LAX PANICLE1 (LAX1). APC/C is a complex formed of 15-17 subunit, and called Anaphase-Promoting Complex (APC), also known as the Cyclosome (C).

‡Loss of function mutation.

§Overexpression.

¶Down-regulation.

#Gain-of-function.

††QTL, quantitative trait locus.

## Genes Involved in AXM Formation

*MOC1* was the first tillering gene to be identified in rice (Li et al., 2003). Plants carrying loss-of-function mutations in *MOC1* have only one main culm as a result of failure to establish AXMs, affecting both tiller and panicle branches (Li et al., 2003). *MOC1* encodes a GRAS (named after the first three members: GIBBERELLIC-ACID INSENSITIVE, REPRESSOR of GAI and SCARECROW) transcription factor homologous to tomato Lateral suppressor (Ls) (Schumacher et al., 1999), and *Arabidopsis* LATERAL SUPPRESSOR (LAS) (Greb et al., 2003). However, in *ls* and *las* mutants, AXM defects are mainly observed in the vegetative phase, while *moc1* shows suppression of all types of AXM, indicating that AXM control mechanisms differ at least in part between monocots and eudicots. *MOC1* expression marks the initiation of the AXM and is maintained in the developing bud, consistent with a role in axillary bud initiation and outgrowth (Li et al., 2003). Recently, a protein mediating the degradation of MOC1 protein was identified from analysis of the allelic mutants *tillering and dwarf1* (*tad1*; Xu et al., 2012) and *tillering enhancer* (*te*; Lin et al., 2012). These mutants are characterized by high tillering and reduced plant height, similar to plants overexpressing *MOC1* (Li et al., 2003). The *TAD1/TE* gene encodes a Cdh1-type coactivator orthologous to the dicot CCS52A (Vinardell et al., 2003), which interacts with the anaphase-promoting complex (APC/C), a multisubunit E3 ligase. TAD1/TE forms a complex with APC/C-OsAPC10, targeting MOC1 for degradation via the ubiquitin-26S proteasome pathway, thus repressing AXM initiation (Xu et al., 2012; Fig. 2). *MOC1* Interacting Protein 1 (*MIP1*) may be another player in this circuit (Sun et al., 2010). When overexpressed, the *MIP1* gene causes enhanced tillering and semidwarf stature similar to *MOC1* overexpression (Li et al., 2003). *MIP1* is a member of the *Brefeldin A-sensitivity protein 1* family, that includes *At_HUB1*, which encodes an E3 ligase involved in H2B (Histone 2B;

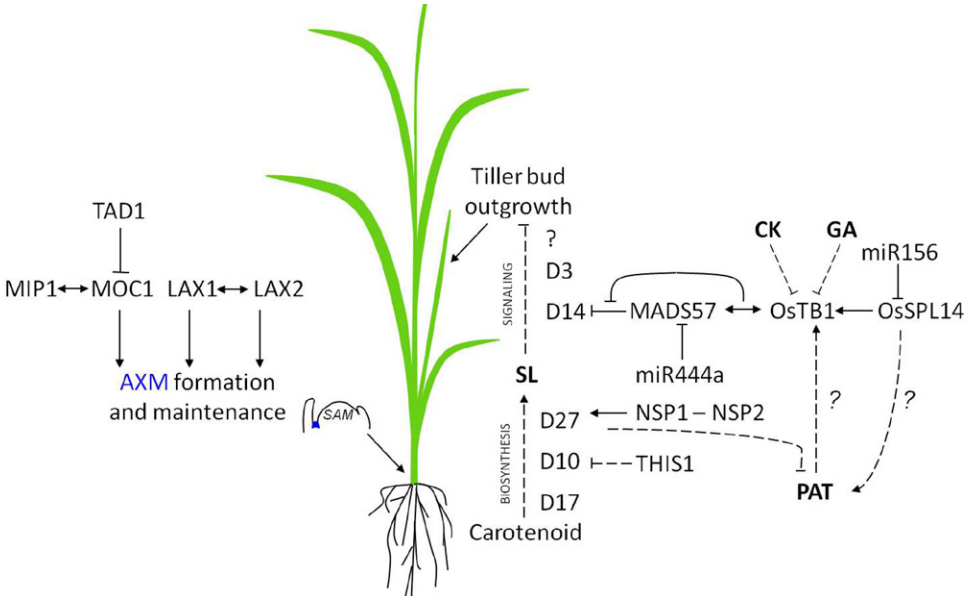


Figure 2. Key interactions among genes controlling rice tiller number. Left: genes involved in axillary meristem (AXM) initiation and establishment. Right: genes involved in axillary bud outgrowth through the strigolactone (SL) pathway (Wang and Li, 2011) and its interactions with auxin (Aux), gibberellic acid (GA), and cytokinin (CK). Arrows indicate positive regulation, blunt-ended lines indicate negative regulation, dashed lines indicate multiple steps or indirect effects, and double-headed arrows represent protein–protein interactions. See text for details.

a subunit of the nucleosome) monoubiquitination in *Arabidopsis* (Fleury et al., 2007; Liu et al., 2007).

Soon after the first visible appearance of AXM formation, the *LAX PANICLE1* (*LAX1*) gene plays a role in maintenance of AXM development. Plants carrying loss-of-function mutations in *LAX1* are characterized by reduced numbers of rachis branches and spikelets on the panicle, and reduced number of tillers (Komatsu et al., 2001; Oikawa and Kyozuka, 2009). *LAX1* encodes a putative basic-helix-loop-helix transcription factor required for formation of AXMs in both vegetative and reproductive phases (Komatsu et al., 2001; Oikawa and Kyozuka, 2009). *LAX1* acts in a noncell autonomous manner to maintain cell proliferation during AXM formation. Oikawa and Kyozuka (2009) proposed a two-step regulation of spatial and temporal *LAX1* expression and activity. Spatially, *LAX1* mRNA is specifically expressed in the boundary region at the adaxial side of the developing AXM, and later, LAX1 protein is trafficked toward the AXM. Temporally, *LAX1* mRNA is expressed in leaf axils from P4 to later stages, while LAX1 protein movement is restricted to the P4 stage, accompanying the acquisition of meristematic fate. Plants carrying mutations in the *LAX2* gene show similar phenotypes to *lax1* mutants, with reduced branching in the vegetative and reproductive phases. *LAX2* encodes a novel nuclear protein with a plant-specific conserved domain and was shown to physically interact with LAX1 (Tabuchi et al., 2011). Double mutant analyses suggest that *MOC1*, *LAX1*, and *LAX2* function in partially independent but overlapping pathways to regulate AXM establishment and maintenance (Tabuchi et al., 2011) (Fig. 2).

## Auxin

The main shoot apex suppresses the outgrowth of axillary buds via auxin that is produced in young expanding leaves and actively transported basipetally through the shoot, acting indirectly on axillary buds (Agusti and Greb, 2013). The movement of auxin from developing leaves to stem (auxin sink) is termed polar auxin transport (PAT) and depends on auxin efflux carriers of the adenosine triphosphate (ATP)-binding cassette B and the PIN-FORMED (PIN) protein families (Zazímalová et al., 2010). The PINs are integral membrane proteins with a topology similar to transporter proteins (Zazímalová et al., 2010). Auxin is transported to the organ initiation sites through the outermost epidermal layer of the shoot apex and is directed via the developing primordia into the basipetal stream of the main shoot. PIN1 proteins are localized in xylem parenchyma cells and maintain the auxin supplement to the basipetal stream of the main shoot, playing a role in PAT (Petrásek and Friml, 2009). In agreement with the role of PAT in inhibition of bud outgrowth, rice plants underexpressing *OsPIN1b* (previously known as *REH1*) showed increased number of tillers (Xu et al., 2005; Chen et al., 2012). Conversely, increased tillering and reduced stature were caused by overexpression of *OsPIN2*, suggesting that *OsPIN1b* and *OsPIN2* play distinct roles in the control of shoot architecture (Chen et al., 2012).

Additional insight into the role of auxin comes from analysis of the *ABERRANT SPIKELET AND PANICLE1* (*ASP1*; or rice *RAMOSA1 ENHANCER LOCUS2*) gene that encodes a transcriptional corepressor proposed to act in auxin signaling (Yoshida et al., 2012). A variety of developmental alterations were described for *asp1*

mutant plants, including derepression of axillary bud outgrowth and disturbed phyllotaxy in the vegetative phase, disorganized panicle branching and spikelet morphology, indicating a general role for *ASP1* in controlling meristem fate (Yoshida et al., 2012).

A member of the MIR393 miRNA family known to regulate expression of auxin receptors also affects tillering ability in rice. Plants overexpressing *OsmiR393* showed reduced expression of the auxin receptors *OsTIR1* and *OsAFB2*, which sequentially repress the auxin transporter *OsAUX1* (Xia et al., 2012). This ultimately down-regulates *OsTB1*, a tillering repressor (see below), explaining the increased outgrowth of tillers in *OsmiR393* overexpressing plants.

Another auxin-dependent pathway regulating rice tillering involves *TLD1* (increased number of Tillers/enlarged Leaf angles/Dwarfism), an indole-3-acetic acid (IAA)-amido synthetase that converts active auxin (IAA) to its inactive form via conjugation with amino acids (Zhang et al., 2009). The associated reduction of IAA concentration affects developmental traits and also influences plant resistance to biotic and abiotic stress via the abscisic acid, and salicylic acid pathways. Gain-of-function *tld1-D* mutants show pleiotropic phenotypes including increased number of tillers, reduced plant height, shorter panicle, and reduced number of spikelets (Zhang et al., 2009).

## Cytokinins

Cytokinins are key regulators of many plant developmental processes, including cell division, activation of axillary buds, inhibition of root growth, and delay of senescence (Mok, 1994). Cytokinins are mainly synthesized in the root and transported upward along the xylem (Wang and Li, 2006). Cytokinin biosynthesis and signaling are affected by nutrient availability and environmental stresses, such as drought and high salinity (Krouk et al., 2011; Ha et al., 2012). The *supershoot* (*sps*) mutants in *Arabidopsis* show massive shoot overproliferation and three- to ninefold increase in levels of Z-type CKs that indicates a role of SPS in suppression of AXM initiation and growth through the localized attenuation of CK levels at sites of bud initiation (Tantikanjana et al., 2001).

The fundamentals of CK biosynthesis were originally studied in *Arabidopsis* (Sakakibara, 2004) where the central rate-limiting step is prenylation of adenosine 5′ phosphates at the $N^6$–terminus with dimethylallyldiphosphate, catalysed by adenosine phosphate ISOPENTENYL TRANSFERASE (IPT). Auxin can down-regulate CK levels by inhibiting the expression of *IPT* genes (Ferguson and Beveridge, 2009). Other studies showed that the *Arabidopsis* KNOTTED-like homeobox (KNOX) protein SHOOTMERISTEMLESS (STM) induces expression of *AtIPT7* (Jasinski et al., 2005; Yanai et al., 2005) and down-regulates GA biosynthesis genes, creating low-GA and high-CK status in the meristem, which may be essential for the maintenance of meristematic activity (Jasinski et al., 2005). Eight *OsIPT* genes have been identified and studied in the rice genome (Sakamoto et al., 2006). Transgenic rice plants overexpressing *OsIPTs* have increased axillary bud activity and reduced root formation, which are typical of CK overexpression. Also, *OsIPT3* and *OsIPT2* transformants showed elevated content in 12 different CK species, highlighting the overall stimulation of de novo CK biosynthesis (Sakamoto et al., 2006).

## Gibberellins

Gibberellins interact with auxin in the regulation of stem elongation, with apically derived auxin regulating GA synthesis (O'Neill and Ross, 2002). In rice, GAs participate in controlling many plant developmental processes, positively regulating germination, stem and root elongation, and flower development, while negatively regulating *OSH1* (a rice *KNOX* gene) and *OsTB1* (see below) (Lo et al., 2008). The main catabolic pathway for GAs is the 2-β-hydroxylation reaction catalysed by C19- and C20-GA 2-oxidases (GA2oxs), which inactivate endogenous bioactive GAs, affecting GA-dependent developmental processes (Sakamoto et al., 2004). In total, 10 putative *GA2ox* genes were identified in the rice genome and rice lines overexpressing some C20-GA2oxs exhibit semidwarfing, early and increased tillering, and adventitious root growth (Lo et al., 2008).

The *ERF protein associated with tillering and panicle branching* (*OsEATB*) gene belongs to the APETALA2/ethylene-responsive element binding factor (ERF) family of transcription factors. Transformed plants overexpressing *OsEATB* showed enhanced tillering, reduced height, enhanced panicle branching, and overall higher grain yield (Qi et al., 2011). These phenotypes were accompanied by decreased levels of different GAs, confirming the negative correlation between GA and tillering.

## Strigolactones

Strigolactones have been recently identified as phytohormones which inhibit side branching in plants (Gomez-Roldan et al., 2008; Umehara et al., 2008). Strigolactones are synthesized in roots and move acropetally (Wang and Li, 2006). They interact with auxins in a dual-loop pathway to control axillary bud outgrowth, but the nature of this regulatory loop is unclear (Kebrom et al., 2013). Two hypotheses have emerged, mostly from studies in dicots: (i) SL act downstream of auxin (Foo et al., 2005; Bainbridge et al., 2005; Brewer et al., 2009; Hayward et al., 2009); (ii) SL negatively regulate auxin transport in the main stem, and inhibit the establishment of axillary bud PAT into the stem (Bennett et al., 2006; Crawford et al., 2010; Domagalska and Leyser, 2011). In rice, mutations in SL biosynthesis gene *DWARF27* (*D27*) result in increased PAT (Lin et al., 2009), and exogenous auxin application can up-regulate expression of *D10* and *D17*, two other genes involved in SL biosynthesis (Arite et al., 2007; Zou et al., 2006), indicating a complex interplay between auxin and SL. A scheme linking the SL pathway, shoot branching, and the rice genes characterized to date is presented in Fig. 2. More details regarding the SL pathway can be found

in some excellent reviews (Beveridge and Kyozuka, 2010; Domagalska and Leyser, 2011; Brewer et al., 2013).

## Brassinosteroids

Along with GAs, brassinosteroids (BRs) are viewed as major players in the control of plant height. Brassinosteroids are phytohormones with a structure similar to animal steroid hormones, and mutants defective in BR biosynthesis and signaling generally exhibit a dwarf phenotype and other abnormalities in leaves and branches (Clouse and Sasse, 1998; Bishop and Koncz, 2002; Gendron et al., 2012). In contrast to the general negative correlation between plant height and tiller number (Hong et al., 2003; Booker et al., 2004), rice mutants impaired in the BR pathway, such as *DWARF AND LOW-TILLERING* (*DLT*), show reductions in both tillering and stature. The *DLT* (or *OsGRAS32*) gene encodes a GRAS transcription factor involved in feedback inhibition of BR biosynthesis (Tong et al., 2009, 2012). Brassinosteroids can down-regulate the expression of *DLT* via the OsBRI1 receptor-like protein, which regulates both *DLT* and OsBZR1, a transcription factor that, in turn, regulates BR-responsive genes (Tong et al., 2009, 2012). OsBZR1 is also controlled by *GSK3/SHAGGY-like kinase* (*GSK2*), which is the ortholog of *Arabidopsis GSK2 BRASSINOSTEROID-INSENSITIVE2*. Rice *GSK2* overexpression results in dwarf plants with dark green leaves, compact structure, and fewer tillers (Tong et al., 2012).

## Strigolactone Pathway Regulation and Integration of Different Signals

Recent studies are providing insight into the regulation of the SL pathway and its cross-talk with other hormonal pathways (Fig. 2). NODULATION SIGNALING PATHWAY1 and NODULATION SIGNALING PATHWAY2 are indispensable for SL biosynthesis through positive regulation of *D27* (Liu et al., 2011; Ishikawa et al., 2005; Kebrom et al., 2013). Expression of *D10*, another SL biosynthesis gene, is increased in the rice *this1* mutant (Liu et al., 2013). The *this1* mutant is characterized by reduced height, infertile spikelets, and high tillering, due to the release of tiller bud outgrowth at the elongation stage (Arite et al., 2007; Ishikawa et al., 2005; Kebrom et al., 2013). The rice mutant *fine culm1* (*fc1*) exhibits thin culm and excessive tillering due to a loss-of-function mutation of the *OsTB1* gene, which encodes a *TB1*/CYCLOIDEA/PCF (TCP) transcription factor homologous to *TB1* in maize, and *Arabidopsis BRANCHED 1/TB1-LIKE 1* (Takeda et al., 2003; Choi et al., 2012). Thus, *FC1*/*OsTB1* functions as a negative regulator of lateral branching in rice, similar to maize *TB1* (Minakuchi et al., 2010). Based on insensitivity of the *fc1* mutant to exogenous application of SL and epistatic interaction with *d17*, Minakuchi et al. (2010) proposed that *FC1*/*OsTB1* acts downstream of SL. Negative regulation of *FC1*/*OsTB1* expression by CK and GA (Lo et al., 2008) further led to the hypothesis that *FC1*/*OsTB1* may act as an integrator of multiple pathways controlling tillering (Minakuchi et al., 2010). More details about the interplay between *OsTB1* and SL have recently emerged. OsMADS57, a MADS-box domain protein was shown to interact with OsTB1 and repress *D14*, a gene involved in SL signaling and possibly encoding a SL receptor (Guo et al., 2013). *OsmiR444a*, a member of the MIR444 miRNA family, posttranscriptionally regulates *OsMADS57* transcript accumulation (Guo et al., 2013). In contrast to the function of *FC1*/*OsTB1*, genetic and molecular analyses of *OsMADS57* indicate that it functions as a repressor of SL signaling and a positive regulator of tillering. Thus, interaction between the two transcription factors may act to fine-tune *D14* expression and consequently tiller outgrowth (Guo et al., 2013). Recently, *OsTB1* was shown to be directly regulated by *OsSPL14*, a member of the *SQUAMOSA Promoter Binding Protein* gene family (Lu et al., 2013) previously associated with the semidominant *WEALTHY FARMERS PANICLE/IDEAL PLANT ARCHITECTURE1* quantitative trait locus (QTL) (Jiao et al., 2010; Miura et al., 2010). Increased *OsSPL14* expression results in reduced tillering, prolonged plastochron duration, sturdier stems, increased number of primary branches in the panicle and, ultimately, higher grain yield, corresponding to the ideotype for rice breeding (Jiao et al., 2010; Miura et al., 2010). In the vegetative phase, *OsSPL14* is specifically expressed in leaf primordia, indicating that *OsSPL14* may affect tillering through regulation of plastochron duration, an activity shared with the highly related *Arabidopsis* genes *SPL9* and *SPL15* (Luo et al., 2012). A genome-wide screen for OsSPL14 binding sites recovered various developmental genes including *OsPIN1b*, suggesting that OsSPL14 may also be involved in regulation of PAT (Lu et al., 2013). Negative control of *OsSPL14* expression involves cleavage by *OsmiR156*, whose overexpression transformants show increased number of tillers, and reduced number of spikelets and grains per panicle (Luo et al., 2012). *ABERRANT PANICLE ORGANIZATION1* (*APO1*) and *APO2* also act upstream of *OsSPL14* (Luo et al., 2012). *APO1* encodes the ortholog of an *Arabidopsis* F-box protein UNUSUAL FLORAL ORGANS, while *APO2* is homologous to the *Arabidopsis LEAFY* gene, and the two proteins were shown to interact in vitro (Ikeda et al., 2007; Ikeda-Kawakatsu et al., 2012). Rice *apo2* mutants have shorter plastochron duration, increased number of tillers, and small panicles with reduced number of primary branches (Ikeda-Kawakatsu et al., 2012). Together, analyses of these genes indicate that regulation of plastochron duration also affects the number of tillers formed by a plant as a result of the number of leaves and axils formed on the shoot (Wang and Li, 2011).

## Other Genes

Other genes in the control of tillering have been recently characterized (Table 1). Future work will help to better understand if and how they interact with the aforementioned pathways. Among them, *FRIZZY PANICLE* (*FZP*) was initially identified as a repressor of AXM formation in the panicle, necessary to establish floral meristem

**Table 2. List of barley tillering mutants. For each mutant, the chromosomal position and relevant references are indicated, along with the corresponding (candidate) gene and rice ortholog when known.**

| Barley mutant | Map position | Mutant phenotype | Gene (rice ortholog) | References |
|---|---|---|---|---|
| *uniculm2* (*cul2*) | 6HL | no tiller, irregular INF† | ND‡ | Babb and Muehlbauer, 2003; Okagaki et al., 2013 |
| *low number of tillers1* (*lnt1*) | 3HL | few tillers, irregular INF | *JuBel2* (*qSH1*) | Dabbert et al., 2010 |
| *absent lower laterals1* (*als1*) | 3HL | few tillers, irregular INF | ND | Dabbert et al., 2009 |
| *uniculme4* (*cul4*) | 3HL | few tillers | ND | Babb and Muehlbauer, 2003; Rossini et al., 2006 |
| *intermedium spike-b* (*int-b*) | 5HL | reduced tillering, irregular INF | ND | Babb and Muehlbauer, 2003; Okagaki and Muehlbauer, unpublished data, 2013 |
| *semibrachytic* (*uzu*) | 3HL | reduced tillering and plant height, shorten spike | *HvBRI1* (*OsBRI1*) | Babb and Muehlbauer, 2003; Chono et al., 2003; Nakamura et al., 2006 |
| *granum-a* (*gra-a*) | 3HL | high tillering, dwarf, shorten spike | ND | Babb and Muehlbauer, 2003 |
| *intermedium-c* (*int-c*) | 4HS | high tillering, Reduced lateral spikelet development | *HvTB1* (*OsTB1*) | Ramsay et al., 2011 |
| *many noded dwarf1.a* (*mnd1.a*) | 7HL | high tillering, dwarf, irregular INF | ND | Babb and Muehlbauer, 2003; Nice and Muehlbauer, unpublished data, 2013 |
| *many noded dwarf6* (*mnd6*)/ *densinodosum6* (*den6*) | 5HL | high tillering, short spike | ND | Babb and Muehlbauer, 2003; Druka et al., 2011; Nice and Muehlbauer, unpublished data, 2013 |
| *semidwarf1* (*sdw1*)/*denso* | 3H | high tillering, reduced plant height | SD1 | Jia et al., 2011 |
| *intermedium spike-m* (*int-m*) | ND | high tillering, irregular INF | ND | Babb and Muehlbauer, 2003 |

†INF, inflorescence.
‡ND, not determined.

identity in rice spikelets (Komatsu et al., 2003). The *FZP* gene encodes an ethylene-responsive ERF transcription factor highly related to *Branched Silkless1* that was shown to play a similar role in maize inflorescence development (Chuck et al., 2002). Noteworthy is a loss-of-function allele of *FZP* that shows defects in tillering, suggesting that *FZP* plays additional roles in controlling vegetative AXM development (Kato and Horibata, 2011).

In summary, since the first gene involved in tillering in rice was identified 10 yr ago (Li et al., 2003), many genes involved in tillering have been rapidly identified in this species, revealing a complex genetic and hormonal network regulating tiller development. The growing number of genes associated with the regulation of tillering in rice provides a molecular framework for this process, while opening new questions about the interplay of the different factors involved.

## Genetic Control of Tillering in Barley

Several barley mutants exhibiting tillering abnormalities have been identified and characterized providing some initial insight into the genetic and hormonal regulation of tillering in the Triticeae (Dabbert et al., 2010) (Table 2 and Fig. 3). These can be classified into four classes, according to their AXM activity. The first class includes mutants that fail to develop axillary buds, and consequently, develop no tillers. The mutant *uniculm2* (*cul2*) is the best characterized example of this class with a phenotype similar to that of *moc1* mutant in rice (Babb and Muehlbauer, 2003). The second class of mutants exhibit lower number of tillers due to compromised axillary bud outgrowth, including *low number of tillers1* (*lnt1*; Dabbert et al., 2010), *absent lower laterals1* (*als1*; Dabbert et al., 2009) and *uniculme4* (*cul4*) (Babb and Muehlbauer, 2003). The third group comprises mutants with modestly reduced tillering, such as the *intermedium-b* (*int-b*) and *semibrachytic* (*uzu*) mutants (Babb and Muehlbauer, 2003). The fourth class of mutants exhibits enhanced tillering, suggesting a defect in controlling tiller bud outgrowth. The mutants *granum-a* (*gra-a*), *grassy tillers* (*grassy*), *intermedium-c* (*int-c*), *many noded dwarf1* (*mnd1*), and *many noded dwarf6* (*mnd6*) represent the high tillering class (Babb and Muehlbauer, 2003; Druka et al., 2011). Additional loci altering inflorescence architecture may also affect tillering, although such defects have not been explored in detail in barley. One example is the barley *INT-C* gene, the ortholog of maize and rice *TB1* genes, which acts in controlling spike row-type and also has an effect on seedling tiller number (Ramsay et al., 2011).

*Uniculm2* (*cul2*) mutants possess one main culm without any tiller outgrowth (Babb and Muehlbauer, 2003). The *cul2* mutation appears to be epistatic to low tillering mutations (*lnt1*, *als1*, *cul4*, *int-b*, and *uzu*) and high tillering mutations (*mnd1*, *mnd6*, and *gra*). Barley *cul2* mutants also show disorganization in the distal end of the developing inflorescence, and deviation from wild-type timing of reproductive developmental steps (Babb and Muehlbauer, 2003). Overall similarities between *cul2* and the rice *moc1* mutant include failure to develop axillary buds, reduced plant height, reduced inflorescence branching, and the epistatic effects to mutations in other loci. However, in contrast to *moc1* where AXMs are not initiated, AXMs are present in *cul2* leaf axils but do not progress to axillary

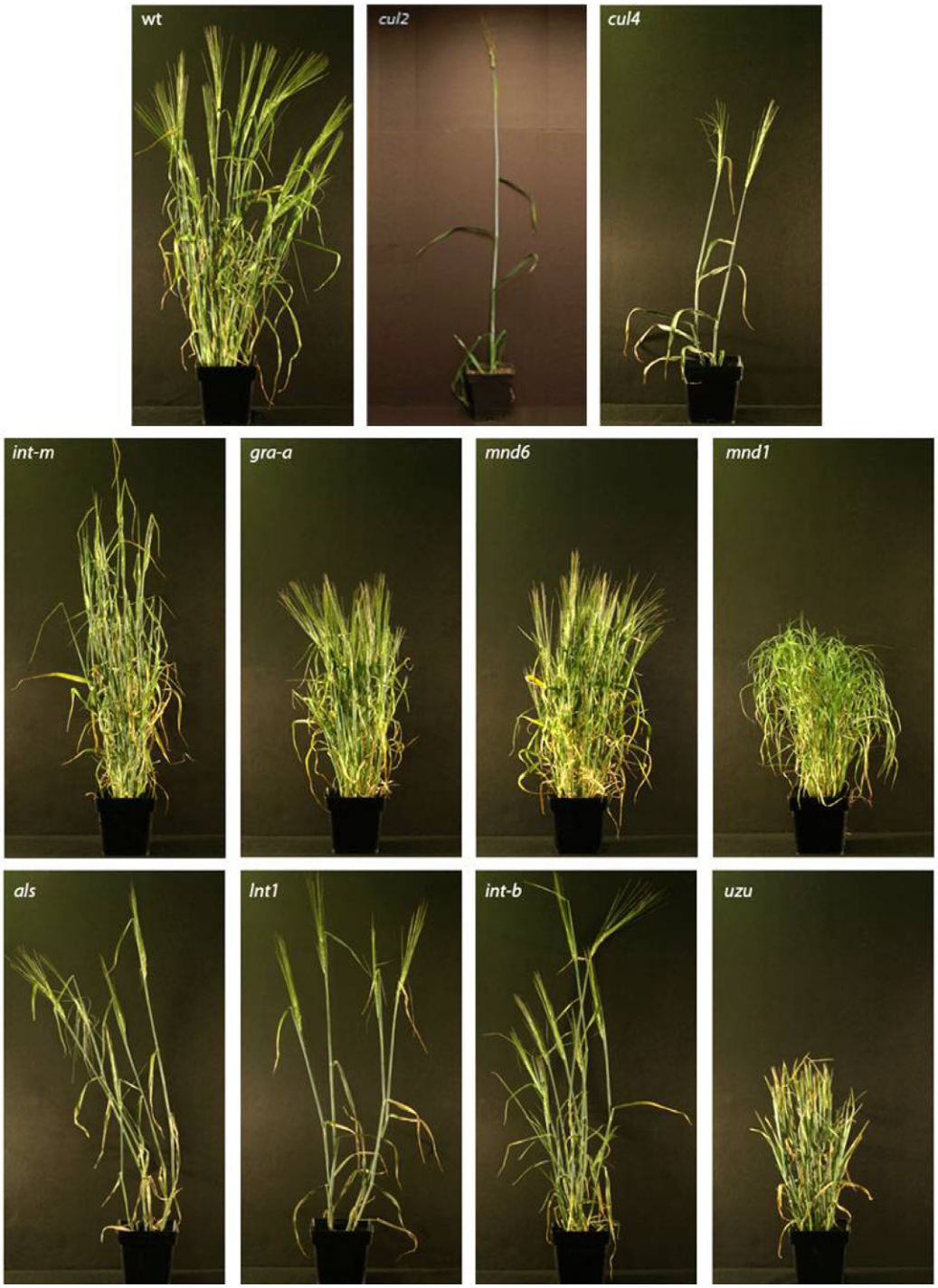


Figure 3. Phenotypes of barley tillering mutants. The first row contains the wild-type 'Bowman' (wt), and the low-tillering mutants *uniculm2* (*cul2*) and *uniculme4* (*cul4*). The second row represents the high-tillering mutants *intermedium spike-m* (*int-m*), *granum-a* (*gra-a*), *many noded dwarf6* (*mnd6*), and *many noded dwarf1* (*mnd1*). The last row contains the low-tillering mutants *absent lower laterals* (*als*), *low number of tillers1* (*lnt1*), *intermedium spike-b* (*int-b*), and *semi rachitic* (*uzu*).

buds, indicating that *Cul2* acts at the stage of bud development. The *cul2* locus was positioned on chromosome 6H near the centromeric region, but no candidate genes have been identified (Okagaki et al., 2013). Transcriptome analysis of *cul2* mutants and corresponding wild-type plants using the Affymetrix Barley1 GeneChip (Close et al., 2004) indicated that *CUL2* is necessary for coordinating signaling pathways and stress response and integrating them into AXM development (Okagaki et al., 2013).

The *als1*, *lnt1*, and *cul4* mutants typically develop only 1 to 3 tillers compared with their wild-type background (Dabbert et al., 2009, 2010; Babb and Muehlbauer, 2003). These loci, mapped at different positions on chromosome 3H, are epistatic to the high tillering mutants, based on the low tillering phenotype of the

double mutants (Dabbert et al., 2009, 2010; Muehlbauer, unpublished results, 2013). Transcriptomics studies showed that stress-related genes are up-regulated in the *als1*, but not in the *lnt1* mutant. Gene expression, mapping, and sequence analyses supported the *JuBel2* gene as a candidate for the *Lnt1* locus (Dabbert et al., 2010). The JuBEL2 protein is a member of BELL-family of homeodomain transcription factors (Müller et al., 2001), sharing high similarity with qSH1, a rice QTL for seed shattering on chromosome 1 (Konishi et al., 2006) and the transcription factor *Arabidopsis BELLRINGER* (*BLR*, wild-type) in *Arabidopsis* (Smith and Hake, 2003; Byrne, 2003; Roeder et al., 2003). The mutant *qSH1* allele in cultivated rice is a regulatory mutation that prevents *qSH1* expression in the pedicel at the base of the rice seed, resulting in resistance to shattering (Konishi et al., 2006). No effect of this mutation was detected on expression of *qSH1* in other tissues and no phenotypic effect on tillering was reported. However, a *qSH1* loss-of-function allele has not been isolated in rice, and the *qSH1* locus may control other traits in addition to shattering (Konishi et al., 2006). In *Arabidopsis*, *blr* mutants show reduced plant height, additional axillary branches and leaves, and disrupted phyllotaxy in vegetative and inflorescence units (Smith and Hake, 2003; Byrne, 2003; Roeder et al., 2003). A two-hybrid protein–protein interaction experiment showed that barley JuBEL2 can bind to class I KNOX proteins including *Hooded/BKN3*, which is a barley homolog of *Arabidopsis STM* (Müller et al., 2001). Similar results were obtained in *Arabidopsis*, where BLR protein interacts with the STM protein, assisting in its transportation to the nucleus (Cole et al., 2006; Rutjens et al., 2009). *STM* is required to maintain the meristematic identity of cells in both the SAM and AXM (Long and Barton, 2000). Plants mutated in *BLR* and two other related *BELL-like* genes, *POUND-FOOLISH* and *ARABIDOPSIS THALIANA HOMEOBOX GENE 1*, lack a SAM, indicating that BELL-like proteins are essential for normal *STM* function (Rutjens et al., 2009). Together, these results suggest that interactions between *JuBel2* and class I *KNOX* genes may promote AXM development and tiller development in barley.

Recessive mutations in the *Int-b* (located on chromosome 5H) and *Uzu* (wild-type, located on chromosome 3H) genes also reduce tiller number, but to a lesser extent compared with the mutants of the previous class (Babb and Muehlbauer, 2003). The *Uzu* gene encodes a putative BR receptor HvBRI1 (Chono et al., 2003) and its use as a dwarfing gene has become widespread in Asian breeding programs (Hoskins and Poehlman, 1971; Tsuchiya, 1976; Zhang, 1994, 2000; Saisho et al., 2004). A similar correlation between tiller number and plant height has been associated with altered BR responses in rice *DLT* mutants (Tong et al., 2009, 2012), indicating BR plays a role in tillering and plant height in both barley and rice. Rice *d61* is a mutant of the *BRASSINOSTERD-INSENSITIVE1* (*OsBRI1*) gene, the ortholog of barley *HvBRI1*. Reduced plant height in *uzu* and *d61* mutants indicates that these BR-receptor genes play similar roles in regulation of stem elongation in barley and rice (Chono et al., 2003). However, no effect on tillering was reported for *OsBRI1*-defective mutants and severe alleles cause complete loss of fertility and malformed dark green leaves (Nakamura et al., 2006), pointing to diverse developmental roles of *BRI* genes in the two species.

In barley, a different link between hormones, plant stature, and tillering is supported by *semidwarf1* (*sdw1*)/*denso* (mapped on chromosome 3H), an agronomically important dwarfing gene with pleiotropic effects on tillering (Jia et al., 2011). Although *sdw1* and *denso* are known to be allelic, the two alleles exhibit different phenotypic effects. A barley GA 20-oxidase gene (*Hv20ox2*) has been proposed as a candidate for *sdw1*/*denso* (Jia et al., 2009). Compared with wild-type, *Hv20ox2* expression is reduced four- and 60-fold in the *denso* and *sdw1* mutants, respectively. These data indicate that low expression decreased plant height while increasing tillering (Jia et al., 2011) and are consistent with a negative correlation between GA and tillering observed in rice (see above). The rice genomic region collinear to the *denso*/*sdw1* locus hosts the rice *sd1*/*Os20ox2* gene, the likely ortholog of *Hv20ox2* (Jia et al., 2009). While *denso*/*sdw1* and *sd1* have similar phenotypic effects on plant height (Sasaki et al., 2002; Spielmeyer et al., 2002), we could not find information about the involvement of the rice gene in tillering.

Semidwarf phenotypes and excessive development of tillers also characterize plants carrying recessive mutations in the *Gra-a* (3H), *Mnd1* (7HL), and *Mnd6* (5HL) genes (Druka et al., 2011). In histological studies, *gra-a* mutants exhibit increased numbers of AXMs and axillary buds, with an occasional appearance of two shoot apical meristems (Babb and Muehlbauer, 2003), while the *mnd6* mutant is characterized by the development of side branches from aerial nodes (Babb and Muehlbauer, 2003). Although the genes that correspond to *gra-a* and *mnd* mutations have not been identified, their phenotypes resemble those of rice mutants defective in SL biosynthesis and signal transduction pathways (Ishikawa et al., 2005; Zou et al., 2006; Arite et al., 2007). Characterization of these mutants may thus offer a foundation for the study of the SL pathway in barley.

Abnormal formation of lateral shoots from aerial nodes was also observed on virus-induced gene silencing of the *P23k* gene, involved in synthesis of (1,3;1,4)-β-D-glucan (Oikawa et al., 2009), suggesting a link between cell wall polysaccharide synthesis and branch development.

Beside these classical mutants, screening of novel mutagenized populations (see below) may uncover new loci and alleles conditioning tiller development. Screening of TILLMore—A population obtained from sodium azide mutagenesis of the reference genotype Morex (IBSC, 2012; Talamè et al., 2008; http://www.dista.unibo.it/TILLMore/, verified 21 Jan. 2014)—Identified a set of lines exhibiting decreased tillering that our group is currently characterizing.

In addition to mutants, QTLs involved in barley tillering have also been identified. Three QTLs for tiller number were mapped on chromosomes 1H bin 6-8, 2H bin 3, and 6H bin 10-11, each explaining 10.3 to 15.7% of the phenotypic variation in a cross between cultivated and wild barley (Gyenis et al., 2007), and also four QTLs for tiller number were detected on 1H, 2H, 3H, and 4H in a cross of a Syrian barley line, Arta, with a wild barley (*H. vulgare* ssp. *spontaneum*) (Baum et al., 2003).

In the following section we discuss how the development of new genomics tools and approaches, coupled with the synteny between the rice and barley genomes, can accelerate the isolation of barley genes underlying tillering phenotypes.

## Resources and Perspectives for Further Dissection of Tillering in Rice and Barley

Monocots include three subfamilies of the grasses (Poaceae): the Panicoideae (e.g., *Sorghum bicolor*, *Zea mays*), Ehrhartoideae (e.g., *Oryza sativa*) and Pooideae (including *Brachypodium distachyon* and species of the tribe Triticeae such as barley and wheat) (Abrouk et al., 2010). They diverged from a common ancestor, with five proto-chromosomes around 60 to 75 million years ago (MYA), while rice and barley diverged 46 MYA, and wheat and barley diverged only 12 MYA (Petsko, 2002; Gaut, 2002; Bolot et al., 2009; Salse et al., 2009; Murat et al., 2010). Rice (*O. sativa* ssp. *japonica* 'Nipponbare') was the first cereal genome to be sequenced (International Rice Genome Sequencing Project, 2005). A recent release of the Os-Nipponbare-Reference-IRGSP-1.0 assembly (IRGSP-1.0; http://rapdb.dna.affrc.go.jp/ and http://rice.plantbiology.msu.edu/, verified 21 Jan. 2014) provides a valuable resource for cereal geneticists, and genomic platforms for functional analysis of rice genes were developed including high-quality genomic, physical, and transcriptome resources and integrated bioinformatics databases (reviewed by Yang et al., 2013). Additionally, various mutant libraries from T-DNA insertion, Ds/dSpm tagging, Tos17 tagging, and chemical or irradiation mutagenesis (reviewed by Jiang and Ramachandran, 2010; Yang et al., 2013; Wang et al., 2013) were developed to support both forward and reverse genetics approaches. In total, 37,869 loci were annotated in rice by mapping transcript and protein sequences including 1626 loci, currently incorporating literature-based annotation data (Sakai et al., 2013). Among these loci, the rice genes related to tillering described above (Table 1) were isolated using these resources and represent a set of candidates for barley loci that still await molecular characterization.

Comparative genomics has become a fundamental approach for the identification of candidate genes, often in conjunction with map-based cloning (Goff et al., 2002; Droc et al., 2006; Zhang et al., 2006; Zou et al., 2006; Quraishi et al., 2009; Jaiswal, 2011; Matsumoto et al., 2011; Dibari et al., 2012; Sakai et al., 2013). Syntenic analysis among rice, wheat, Brachypodium, sorghum, and maize based on short conserved sequence regions indicated that wheat orthologs can be identified for 73% of rice genes, and on average, around 90% of cereal genomes can be considered part of macrosyntenic blocks (Abrouk et al., 2010). Several studies have focused on the high conservation of genomic arrangement in grasses to extract the maximum information from conserved syntenic associations. Numerous tools have been developed to compare plant genomes and tentatively identify orthologs (Salse et al., 2009). Such approaches were applied to identify candidate genes for a number of barley morphological mutants (Rossini et al., 2006; Druka et al., 2011; Ramsay et al., 2011). Because of the fact that many more genes controlling tillering have been identified in rice than barley, we were interested in determining the utility of rice–barley synteny to identify candidates for barley genes controlling tillering. We placed the known barley tillering mutants on the rice genome in relationship to the location of the rice genes that control tillering, and found that the majority of the known barley genes are not located in syntenic regions of the rice genome where genes controlling tillering are located (Fig. 4). Considering also the different phenotypes associated to the rice homologues of known barley tillering genes (e.g., *qSH1*, *OsBRI1*), these results suggest that there may be differences in the genetic control between rice and barley, and that identifying additional barley tillering mutants will be necessary to obtain a better understanding of the commonalities and differences between the two species.

Recent progress in developing genomics tools is augmenting the power of comparative approaches between barley, rice, and other cereal genomes. For example, combining chromosome sorting, next-generation sequencing, array hybridization, and systematic exploitation of conserved synteny with model grasses including rice, the virtual chromosomal order of 21,766 barley genes (out of the estimated 32,000) was reconstructed and represented in tables known as "genome zippers" (Mayer et al., 2011). A deep whole-genome shotgun assembly and deep RNA sequence data supporting 26,159 "high-confidence" genes have become available (IBSC, 2012). Moreover, 22,651 representative full-length cDNA (???) sequences, including 17,773 novel barley full-length cDNAs, 1699 of which are barley-specific, are now available from 12 libraries from various organs or under different conditions (Matsumoto et al., 2011). Recently, these resources have been integrated with a new approach based on high through-put sequencing of reference mapping populations (Mascher et al., 2013), providing a much improved reference sequence resource for gene discovery and comparative genomics.

The implementation of efficient systems for high-throughput transformation has proved elusive for most cereals apart from rice, although some new methods have been proposed for activation tagging and insertional mutagenesis in barley (Ayliffe and Pryor, 2010). The development of barley genomics resources (see above) and the availability of new genomic technologies have accelerated the establishment of platforms

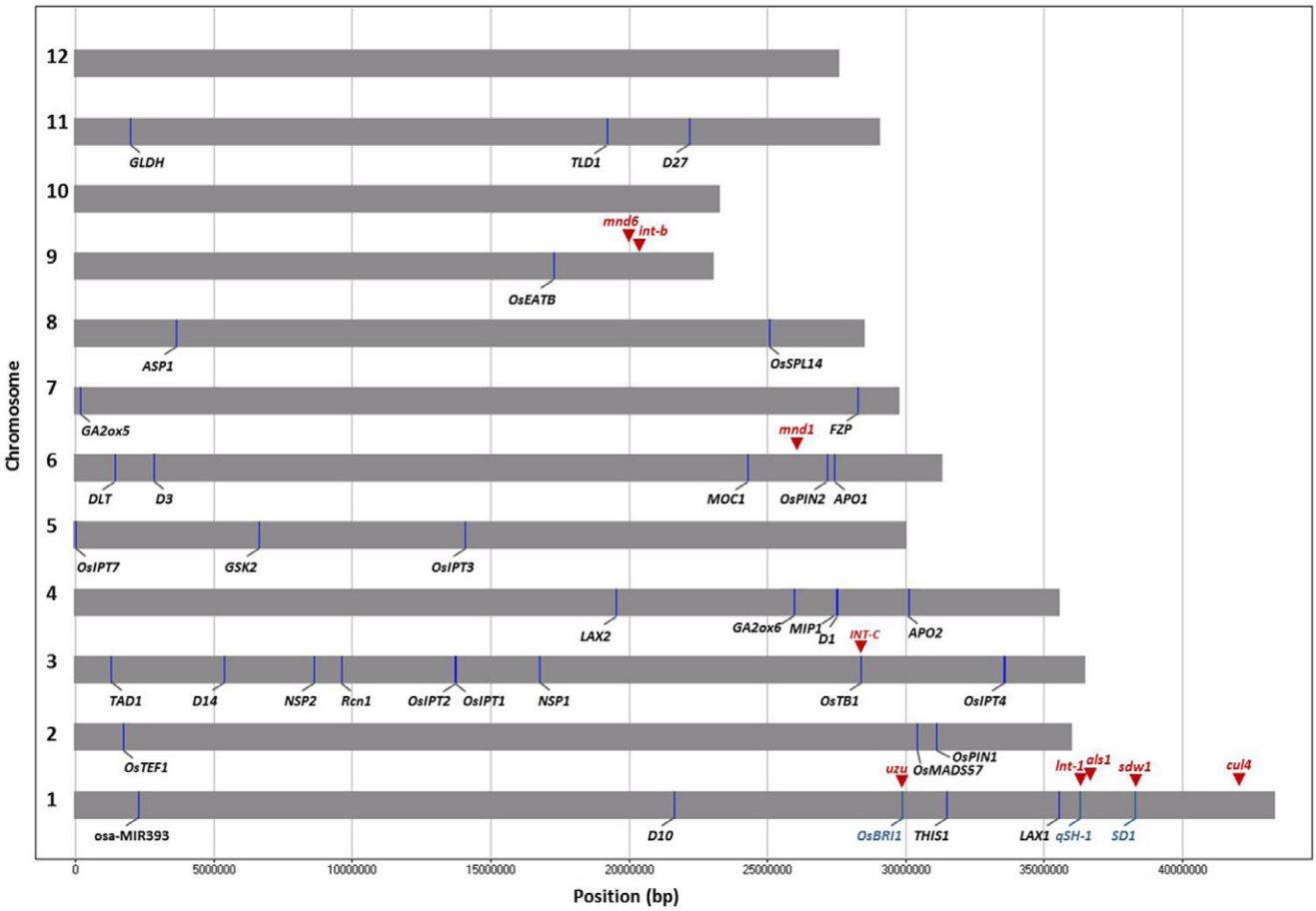


Figure 4. Chromosomal location of the rice and barley genes controlling tillering in the rice genome. All rice genes from Table 1 with known locations are represented in blue, and the barley genes with known chromosomal location and exhibiting genomic synteny to rice are indicated in red. Rice genes homologous to barley tillering genes are also added to the figure and are represented in light blue. The chromosomal position of the rice genes was assigned by blasting their nucleotide sequence against the genes in MSU Rice Genome Annotation Project Release 7 or by searching the rice locus identifier in the same database (http://rice.plantbiology.msu.edu/, verified 17 Jan. 2014). The barley genes were placed on their syntenic rice positions when possible, based on the nucleotide sequence of either the barley gene (when available) or the genetic markers identifying the gene mutation. The figure was plotted using Spotfire DecisionSite software (Tibco Software Inc., Palo Alto, CA).

for barley functional genomics. The recently developed barley hybridization-based exome capture tool (Mascher et al., 2013) provides a valuable instrument for the study of gene structure and variation in barley, while RNaseq technologies are offering new insight into transcriptome dynamics. Finally, bioinformatics tools to establish associations between genes, loci, and traits of interest from available barley transcriptome data have been developed (GeneNetwork, http://www.genenetwork.org, verified 21 Jan. 2014; Druka et al., 2008). These genomics tools can be applied to the systematic investigation of gene-trait relationships using classical mutant resources generated by physical and chemical mutagenesis and barley TILLING populations (Talamè et al., 2008; Gottwald et al., 2009; Druka et al., 2011).

The availability of complete or nearly complete genome sequences for many model organisms, in conjunction with the use of ultra-high-throughput sequencing technologies, has recently prompted the development of new forward genetic mapping approaches, based on the existing principle of Bulked Segregant Analysis (BSA) for the identification of recessive monogenic traits (Schneeberger and Weigel, 2011). In classical BSA, a cross or backcross between a mutant and wild-type plant is generated, and the phenotyped mutant and wild-type offspring are separately pooled and subjected to genotyping analysis (Michelmore et al., 1991). Only markers closely linked to a causal locus are expected to segregate consistently in mutant pools. Ultra-high throughput sequencing allows the combination of marker discovery and genetic mapping into a single step, potentially affording particularly high mapping resolution if bulk sizes, sequencing depth, and variability between individuals is high (Schneeberger and Weigel, 2011). Indeed, the basic principle has been applied in several species, both animal and plant, using statistical inference methods of varying degrees of sophistication (e.g., Blumenstiel et al., 2009; Schneeberger et al., 2009; Uchida et al., 2011; Austin et al., 2011; del Viso et al., 2012; Abe et al., 2012; Fekih et al., 2013; Krothapalli et al., 2013). In plants, different types

of segregating populations have been used. Some studies were based on populations derived from crossing the mutant to a distinct genetic background, which segregate for a number of polymorphisms, as well as the causal mutation (Schneeberger et al., 2009; Galvão et al., 2012). A different approach was proposed for mutants derived from chemically mutagenized populations where the mutant is crossed to its own background, using only the mutagen-induced changes as segregating markers (Abe et al., 2012; Zhu et al., 2012; Hartwig et al., 2012; Fekih et al., 2013).

While the aforementioned approach is most reliable when a complete genome sequence is available, it can be adapted to incorporate information from synteny (Galvão et al., 2012), potentially allowing its use in organisms such as barley, taking advantage of the high resolution draft of the barley genome and its extensive EST and cDNA resources. Mutants isolated from chemically mutagenized populations are expected to be particularly amenable to mapping by this approach, as point mutations underlying developmental phenotypes are likely to be predominantly located in, or close to coding regions—the great majority of which have been sequenced in barley and are represented in an available exome capture array (Mascher et al., 2013). These considerations also negate the need for whole genome resequencing and would substantially reduce experimental costs.

An exciting variation on this theme has been employed in several systems with less well-characterized genomes. As a proxy for exome enrichment, deep sequencing of the transcriptome can be used to identify genes with an allele frequency close to one in mutant bulks (Trick et al., 2012; Liu et al., 2012; Hill et al., 2013). A possible limitation of this strategy is the difficulty in obtaining suitable sequencing coverage, particularly for genes expressed at low levels (Schneeberger and Weigel, 2011). On the other hand, some functional inferences regarding downstream effects of mutations under study might be obtained from identification of genes differentially expressed between mutant and wild-type bulks.

These new high-throughput approaches are expected to radically accelerate the identification of genes and causal mutations underlying tillering and other traits, particularly in grasses where extensive synteny exists. Beyond barley, other species, even those with large and complex genomes might be studied in this manner.

## Concluding Remarks

In this review we have attempted to provide an overview of the known similarities and possible differences in the molecular and hormonal regulation of shoot branching, or tillering, in barley and rice. We have also dwelt on the ongoing development of genomic, comparative genomic, and postgenomic resources in these two species, with the intention of underlining how high-throughput approaches might complement classical genetic methodologies in coming years. Beside the feasibility of transferring knowledge between experimental systems, analysis of additional species beyond rice is expected to provide a more comprehensive understanding of the genetic basis and molecular evolution of tillering in cereals. A number of questions remain open. For example, how many genes are involved in controlling tillering in different grasses? How many of them are playing similar roles across species? In-depth comparisons based on phylogeny and functional characterization of genes identified from different species are needed to evaluate this. Even assuming overall conservation of regulation of tillering in grasses, recent gene duplications in various species are likely to lead to distinct degrees of functional redundancy in different points of tillering pathways—implying that different genes are likely to be identified from spontaneous or induced mutants in distinct systems. In this context, despite its relatively large and complex genome, barley represents an experimental system of great value, both intrinsically, and as a model for other Triticeae genomes. The availability of extensive genetic resources, ever-improving genomic and comparative genomic data, as well as novel and affordable high-throughput genotyping and sequencing platforms suggest that barley will continue to be a key system for the study of tillering and other developmental processes in grasses.


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### Note Added in Proof

After acceptance of the manuscript, two groups reported the identification of *Dwarf53* (*D53*) as a new gene in the SL signalling pathway [Jiang, L., X. Liu, G. Xiong, H. Liu, F. Chen, L. Wang, X. Meng, G. Liu , H. Yu, Y. Yuan, W. Yi, L. Zhao, H. Ma, Y. He, Z. Wu, K. Melcher, Q. Qian, H.E. Xu, Y. Wang, and J. Li. 2013. DWARF 53 acts as a repressor of strigolactone signalling in rice. Nature 2013 Dec 19, 504(7480):401–405, doi:10.1038/nature12870; and Zhou, F., Q. Lin, L. Zhu, Y. Ren, K. Zhou, N. Shabek, F. Wu, H. Mao, W. Dong, L. Gan, W. Ma, H. Gao, J. Chen, C. Yang, D. Wang, J. Tan, X. Zhang, X. Guo, J. Wang, L. Jiang, X. Liu, W. Chen, J. Chu, C. Yan, K. Ueno, S. Ito, T. Asami, Z. Cheng, J. Wang, C. Lei, H. Zhai, C. Wu, H. Wang, N. Zheng, and J. Wan. 2013. D14-SCF D3-dependent degradation of D53 regulates strigolactone signaling. Nature 2013 Dec 19, 504(7480):406–410, doi:10.1038/nature12878].

### References


Abe, A., S. Kosugi, K. Yoshida, S. Natsume, H. Takagi, H. Kanzaki, H. Matsumura, K. Yoshida, C. Mitsuoka, M. Tamiru, H. Innan, L. Cano, S. Kamoun, and R. Terauchi. 2012. Genome sequencing reveals agronomically important loci in rice using MutMap. Nat. Biotechnol. 30(2):174–178. doi:10.1038/nbt.2095

Abrouk, M., F. Murat, C. Pont, J. Messing, S. Jackson, T. Faraut, E. Tannier, C. Plomion, R. Cooke, C. Feuillet, and J. Salse. 2010. Palaeogenomics of plants: Synteny-based modelling of extinct ancestors. Trends Plant Sci. 15(9):479–487. doi:10.1016/j.tplants.2010.06.001.

Aguilar-Martínez, J.A., C. Poza-Carrión, and P. Cubas. 2007. *Arabidopsis* BRANCHED1 Acts as an Integrator of Branching Signals within Axillary Buds. Plant Cell Online 19(2):458–472. doi:10.1105/tpc.106.048934

Agusti, J., and T. Greb. 2013. Going with the wind-adaptive dynamics of plant secondary meristems. Mech. Dev. 130(1):34–44. doi:10.1016/j.mod.2012.05.011

Arite, T., H. Iwata, K. Ohshima, M. Maekawa, M. Nakajima, M. Kojima, H. Sakakibara, and J. Kyozuka. 2007. DWARF10, an RMS1/MAX4/DAD1 ortholog, controls lateral bud outgrowth in rice. Plant J. 51(6):1019–1029. doi:10.1111/j.1365-313X.2007.03210.x

Atsmon, D., and E. Jacobs. 1977. A newly bred 'Gigas' form of bread wheat (*Triticum aestivum*: Morphological features and thermo-photoperiodic responses. Crop Sci. 17(1):31–35. doi:10.2135/cropsci1977.0011183X001700010010x

Austin, R.S., D. Vidaurre, G. Stamatiou, R. Breit, N.J. Provart, D. Bonetta, J. Zhang, P. Fung, Y. Gong, P.W. Wang, P. McCourt, and D.S. Guttman. 2011. Next-generation mapping of *Arabidopsis* genes. Plant J. 67(4):715–725. doi:10.1111/j.1365-313X.2011.04619.x

Ayliffe, M.A., and A.J. Pryor. 2010. Activation tagging and insertional mutagenesis in barley. In: A. Pereira, editor, Plant reverse genetics. Humana Press, New York. p. 107–128.

Babb, S., and G.J. Muehlbauer. 2003. Genetic and morphological characterization of the barley *uniculm2* (*cul2*) mutant. Theor. Appl. Genet. 106(5):846–857. doi:10.1007/s00122-002-1104-0.

Bainbridge, K., K. Sorefan, S. Ward, and O. Leyser. 2005. Hormonally controlled expression of the *Arabidopsis* MAX4 shoot branching regulatory gene. Plant J. 44(4):569–580. doi:10.1111/j.1365-313X.2005.02548.x

Baum, M., S. Grando, G. Backes, A. Jahoor, A. Sabbagh, and S. Ceccarelli. 2003. QTLs for agronomic traits in the Mediterranean environment identified in recombinant inbred lines of the cross 'Arta' × *H. spontaneum* 41-1. Theor. Appl. Genet. 107(7):1215–1225. doi:10.1007/s00122-003-1357-2

Bennett, T., T. Sieberer, B. Willett, J. Booker, C. Luschnig, and O. Leyser. 2006. The *Arabidopsis* MAX pathway controls shoot branching by regulating auxin transport. Curr. Biol. 16(6):553–563. doi:10.1016/j.cub.2006.01.058

Bennetzen, J.L., and M. Freeling. 1997. The unified grass genome: Synergy in synteny. Genome Res. 7(4):301–306. doi:10.1101/gr.7.4.301.

Beveridge, C.A., and J. Kyozuka. 2010. New genes in the strigolactone-related shoot branching pathway. Curr. Opin. Plant Biol. 13(1):34–39. doi:10.1016/j.pbi.2009.10.003

Bishop, G.J., and C. Koncz. 2002. Brassinosteroids and plant steroid hormone signaling. Plant Cell S97-S110(Supplement 2002):97–110. doi:10.1105/tpc.001461.

Blumenstiel, J.P., A.C. Noll, J.A. Griffiths, A.G. Perera, K.N. Walton, W.D. Gilliland, R.S. Hawley, and K. Staehling-Hampton. 2009. Identification of EMS-induced mutations in Drosophila melanogaster by whole-genome sequencing. Genetics 182(1):25–32. doi:10.1534/genetics.109.101998

Bolot, S., M. Abrouk, U. Masood-Quraishi, N. Stein, J. Messing, C. Feuillet, and J. Salse. 2009. The "inner circle" of the cereal genomes. Curr. Opin. Plant Biol. 12(2):119–125. doi:10.1016/j.pbi.2008.10.011

Booker, J., M. Auldridge, S. Wills, D. Mccarty, H. Klee, and O. Leyser. 2004. MAX3/CCD7 is a carotenoid cleavage dioxygenase required for the synthesis of a novel plant signaling molecule. Curr. Biol. 14:1232–1238. doi:10.1016/j.cub.2004.06.061

Bossinger, G., W. Rohde, U. Lundqvist, and F. Salamini. 1992. Genetics of barley development: Mutant phenotypes and molecular aspects. *In* P.R. Shewry, editor, Barley: Genetics, biochemistry, molecular biology and biotechnology. CAB International, Wallingford, UK. p. 231–263.

Brewer, P.B., E. Dun, B.J. Ferguson, C. Rameau, and C. Beveridge. 2009. Strigolactone acts downstream of auxin to regulate bud outgrowth in pea and *Arabidopsis*. Plant Physiol. 150(1):482–493. doi:10.1104/pp.108.134783

Brewer, P.B., H. Koltai, and C.A. Beveridge. 2013. Diverse roles of strigolactones in plant development. Mol. Plant 6(1):18–28. doi:10.1093/mp/sss130

Byrne, M.E. 2003. Phyllotactic pattern and stem cell fate are determined by the *Arabidopsis* homeobox gene BELLRINGER. Development 130(17):3941–3950. doi:10.1242/dev.00620

Chen, Y., X. Fan, W. Song, Y. Zhang, and G. Xu. 2012. Over-expression of OsPIN2 leads to increased tiller numbers, angle and shorter plant height through suppression of OsLAZY1. Plant Biotechnol. J. 10(2):139–149. doi:10.1111/j.1467-7652.2011.00637.x

Chen, X., Z. Zhang, D. Liu, K. Zhang, A. Li, and L. Mao. 2010. SQUAMOSA promoter-binding protein-like transcription factors: Star players for plant growth and development. J. Integr. Plant Biol. 52(11):946–951. doi:10.1111/j.1744-7909.2010.00987.x

Choi, H.C., and Y.W. Kwon. 1985. Evaluation of varietal difference and environmental variation for some characters related to source and sink in the rice plants. Korean J. Crop Sci. 30(4):460–470.

Choi, M.-S., M.-O. Woo, E.-B. Koh, J. Lee, T.-H. Ham, H.S. Seo, and H.-J. Koh. 2012. Teosinte Branched 1 modulates tillering in rice plants. Plant Cell Rep. 31(1):57–65. doi:10.1007/s00299-011-1139-2

Chono, M., I. Honda, H. Zeniya, K. Yoneyama, D. Saisho, K. Takeda, S. Takatsuto, T. Hoshino, and Y. Watanabe. 2003. A Semidwarf phenotype of barley *uzu* results from a nucleotide substitution in the gene encoding a putative brassinosteroid receptor. Plant Physiol. 133(3):1209–1219. doi:10.1104/pp.103.026195

Chuck, G., M. Muszynski, E. Kellogg, S. Hake, and R.J. Schmidt. 2002. The control of spikelet meristem identity by the branched silkless1 gene in maize. Science 298(5596):1238–1241. doi:10.1126/science.1076920.

Close, T.J., S.I. Wanamaker, R.A. Caldo, S.M. Turner, D.A. Ashlock, J.A. Dickerson, R.A. Wing, G.J. Muehlbauer, A. Kleinhofs, and R.P. Wise. 2004. A new resource for cereal genomics: 22K Barley GeneChip comes of age. Plant Physiol. 134:960–968. doi:10.1104/pp.103.034462

Clouse, S.D., and J.M. Sasse. 1998. BRASSINOSTEROIDS: Essential regulators of plant growth and development. Annu. Rev. Plant Physiol. Plant Mol. Biol. 49:427–451. doi:10.1146/annurev.arplant.49.1.427

Cole, M., C. Nolte, and W. Werr. 2006. Nuclear import of the transcription factor SHOOT MERISTEMLESS depends on heterodimerization with BLH proteins expressed in discrete sub-domains of the shoot apical meristem of *Arabidopsis thaliana*. Nucleic Acids Res. 34(4):1281–1292. doi:10.1093/nar/gkl016

Crawford, S., N. Shinohara, T. Sieberer, L. Williamson, G. George, J. Hepworth, D. Müller, M. Domagalska, and O. Leyser. 2010. Strigolactones enhance competition between shoot branches by dampening auxin transport. Development 137(17):2905–2913. doi:10.1242/dev.051987

Dabbert, T., R.J. Okagaki, S. Cho, J. Boddu, and G.J. Muehlbauer. 2009. The genetics of barley low-tillering mutants: Absent lower laterals (als). Theor. Appl. Genet. 118(7):1351–1360. doi:10.1007/s00122-009-0985-6

Dabbert, T., R.J. Okagaki, S. Cho, S. Heinen, J. Boddu, and G.J. Muehlbauer. 2010. The genetics of barley low-tillering mutants: Low number of tillers-1 (lnt1). Theor. Appl. Genet. 121(4):705–715. doi:10.1007/s00122-010-1342-5

del Viso, F., D. Bhattacharya, Y. Kong, M. Gilchrist, and M. Khokha. 2012. Exon capture and bulk segregant analysis: Rapid discovery of causative mutations using high-throughput sequencing. BMC Genomics 13(1):649. doi:10.1186/1471-2164-13-649

Dibari, B., F. Murat, A. Chosson, V. Gautier, C. Poncet, P. Lecomte, I. Mercier, H. Bergès, C. Pont, A. Blanco, and J. Salse. 2012. Deciphering the genomic structure, function and evolution of carotenogenesis related phytoene synthases in grasses. BMC Genomics 13(1):221. doi:10.1186/1471-2164-13-221

Doebley, J.F., B.S. Gaut, and B.D. Smith. 2006. The Molecular genetics of crop domestication. Cell 127:1309–1321. doi:10.1016/j.cell.2006.12.006

Domagalska, M.A., and O. Leyser. 2011. Signal integration in the control of shoot branching. Nat. Rev. Mol. Cell Biol. 12(4):211–221. doi:10.1038/nrm3088

Donald, C.M. 1968. The breeding of crop ideotypes. Euphytica 17(3):385–403. doi:10.1007/BF00056241

Droc, G., M. Ruiz, P. Larmande, A. Pereira, P. Piffanelli, J.B. Morel, A. Dievart, B. Courtois, E. Guiderdoni, and C. Périn. 2006. OryGenesDB: A database for rice reverse genetics. Nucleic Acids Res. 34(suppl 1):D736–D740. doi:10.1093/nar/gkj012

Druka, A., I. Druka, A. Centeno, H. Li, Z. Sun, W. Thomas, N. Bonar, B. Steffenson, S. Ullrich, A. Kleinhofs, R. Wise, T. Close, E. Potokina, Z. Luo, C. Wagner, G. Schweizer, D. Marshall, M. Kearsey, R. Williams, and R. Waugh. 2008. Towards systems genetic analyses in barley: Integration of phenotypic, expression and genotype data into GeneNetwork. BMC Genet. 9(1):73. doi:10.1186/1471-2156-9-73

Druka, A., J. Franckowiak, U. Lundqvist, N. Bonar, J. Alexander, K. Houston, S. Radovic, F. Shahinnia, V. Vendramin, M. Morgante, N.

Stein, and R. Waugh. 2011. Genetic dissection of barley morphology and development. Plant Physiol. 155(2):617–627. doi:10.1104/pp.110.166249

FAOSTAT. 2012. Food and Agriculture Organization of the United Nations. http://faostat.fao.org/ (verified 27 Jan. 2014).

Fekih, R., H. Takagi, M. Tamiru, A. Abe, S. Natsume, H. Yaegashi, S. Sharma, S. Sharma, H. Kanzaki, H. Matsumura, H. Saitoh, C. Mitsuoka, H. Utsushi, A. Uemura, E. Kanzaki, S. Kosugi, K. Yoshida, L. Cano, S. Kamoun, and R. Terauchi. 2013. MutMap+: Genetic mapping and mutant identification without crossing in rice. PLoS ONE 8(7):E68529. doi:10.1371/journal.pone.0068529

Ferguson, B.J., and C.A. Beveridge. 2009. Roles for auxin, cytokinin, and strigolactone in regulating shoot branching. Plant Physiol. 149(4):1929–1944. doi:10.1104/pp.109.135475

Fleury, D., K. Himanen, G. Cnops, H. Nelissen, T.M. Boccardi, S. Maere, G.T.S. Beemster, P. Neyt, S. Anami, P. Robles, J.L. Micol, D. Inzé, and M. Van Lijsebettens. 2007. The *Arabidopsis thaliana* homolog of yeast BRE1 has a function in cell cycle regulation during early leaf and root growth. Plant Cell 19(2):417–432. doi:10.1105/tpc.106.041319

Foo, E., E. Bullier, M. Goussot, F. Foucher, C. Rameau, and C.A. Beveridge. 2005. The branching gene RAMOSUS1 mediates interactions among two novel signals and auxin in pea. Plant Cell 17(2):464–474. doi:10.1105/tpc.104.026716

Forster, B.P., J.D. Franckowiak, U. Lundqvist, J. Lyon, I. Pitkethly, and W.T.B. Thomas. 2007. The barley phytomer. Ann. Bot. 100(4):725–733. doi:10.1093/aob/mcm183

Galvão, V.C., K.J.V. Nordström, C. Lanz, P. Sulz, J. Mathieu, D. Posé, M. Schmid, D. Weigel, and K. Schneeberger. 2012. Synteny-based mapping-by-sequencing enabled by targeted enrichment. Plant J. 71(3):517–526. doi:10.1111/j.1365-313x.2012.04993.x.

Gaut, B.S. 2002. Evolutionary dynamics of grass genomes. New Phytol. 154(1):15–28. doi:10.1046/j.1469-8137.2002.00352.x

Gendron, J.M., J. Liu, M. Fan, M. Bai, S. Wenkel, and P.S. Springer. 2012. Brassinosteroids regulate organ boundary formation in the shoot apical meristem of *Arabidopsis*. Proc. Natl. Acad. Sci. USA 109(51):21,152–21,157. doi:10.1073/pnas.1210799110

Goff, S.A., D. Ricke, T.-H. Lan, G. Presting, R. Wang, et al. 2002. A draft sequence of the rice genome (*Oryza sativa* L. ssp. *japonica*). Science 296(5565):92–100. doi:10.1126/science.1068275

Gomez-Roldan, V., S. Fermas, P.B. Brewer, V. Puech-Pagès, E. a Dun, J.-P. Pillot, F. Letisse, R. Matusova, S. Danoun, J.-C. Portais, H. Bouwmeester, G. Bécard, C. a Beveridge, C. Rameau, and S.F. Rochange. 2008. Strigolactone inhibition of shoot branching. Nature 455(7210):189–194. doi:10.1038/nature07271

Gottwald, S., P. Bauer, T. Komatsuda, U. Lundqvist, and N. Stein. 2009. TILLING in the two-rowed barley cultivar "Barke" reveals preferred sites of functional diversity in the gene *HvHox1*. BMC Res. Notes 2:258. doi:10.1186/1756-0500-2-258

Greb, T., O. Clarenz, E. Scha, and G. Schmitz. 2003. Molecular analysis of the LATERAL SUPPRESSOR gene in *Arabidopsis* reveals a conserved control mechanism for axillary meristem formation. Genes Dev. 17:1175–1187. doi:10.1101/gad.260703

Guo, S., Y. Xu, H. Liu, Z. Mao, C. Zhang, Y. Ma, Q. Zhang, Z. Meng, and K. Chong. 2013. The interaction between OsMADS57 and OsTB1 modulates rice tillering via DWARF14. Nat. Commun. 4:1566. doi:10.1038/ncomms2542

Gyenis, L., S.J. Yun, K.P. Smith, B.J. Steffenson, E. Bossolini, M.C. Sanguineti, and G.J. Muehlbauer. 2007. Genetic architecture of quantitative trait loci associated with morphological and agronomic trait differences in a wild by cultivated barley cross. Genome 50(8):714–723. doi:10.1139/G07-054

Ha, S., R. Vankova, K. Yamaguchi-Shinozaki, K. Shinozaki, and L.-S.P. Tran. 2012. Cytokinins: Metabolism and function in plant adaptation to environmental stresses. Trends Plant Sci. 17(3):172–179. doi:http://dx.doi.org/10.1016/j.tplants.2011.12.005.

Hartwig, B., G.V. James, K. Konrad, K. Schneeberger, and F. Turck. 2012. Fast ssogenic mapping-by-sequencing of ethyl methanesulfonate-induced mutant bulks. Plant Physiol. 160(2):591–600. doi:10.1104/pp.112.200311

Hayes, P.M., A. Castro, L. Marquez-Cedillo, A. Corey, C. Henson, B.L. Jones, J. Kling, D. Mather, I. Matus, C. Rossi, and K. Sato. 2003. Genetic diversity for quantitatively inherited agronomic and malting quality traits. In: R. von Bothmer et al., editors, Developments in plant genetics and breeding. Elsevier, Atlanta, GA. p. 201–226.

Hayward, A., P. Stirnberg, C. Beveridge, and O. Leyser. 2009. Interactions between auxin and strigolactone in shoot branching control. Plant Physiol. 151(1):400–412. doi:10.1104/pp.109.137646

Hill, J.T., B.L. Demarest, B.W. Bisgrove, B. Gorsi, Y.-C. Su, and H.J. Yost. 2013. MMAPPR: Mutation mapping analysis pipeline for pooled RNA-seq. Genome Res. 23(4):687–697. doi:10.1101/gr.146936.112

Hong, Z., M. Ueguchi-Tanaka, K. Umemura, S. Uozu, S. Fujioka, S. Takatsuto, S. Yoshida, M. Ashikari, H. Kitano, and M. Matsuoka. 2003. A rice brassinosteroid-deficient mutant, *ebisu dwarf* (*d2*), is caused by a loss of function of a new member of cytochrome P450. Plant Cell 15:2900–2910. doi:10.1105/tpc.014712

Hoskins, P.H., and J.M. Poehlman. 1971. Pleiotropic effects of *Uzu* and spike-density genes in a barley cross. J. Hered. 62(3):153–156. doi:10.1093/jhered/62.3.153

IBSC. 2012. A physical, genetic and functional sequence assembly of the barley genome. Nature 491(7426):711–716. doi:10.1038/nature11543.

Ikeda, K., M. Ito, N. Nagasawa, J. Kyozuka, and Y. Nagato. 2007. Rice ABERRANT PANICLE ORGANIZATION 1, encoding an F-box protein, regulates meristem fate. Plant J. 51(6):1030–1040. doi:10.1111/j.1365-313X.2007.03200.x

Ikeda, K., N. Nagasawa, and Y. Nagato. 2005. ABERRANT PANICLE ORGANIZATION 1 temporally regulates meristem identity in rice. Dev. Biol. 282(2):349–360. doi:10.1016/j.ydbio.2005.03.016

Ikeda-Kawakatsu, K., M. Maekawa, T. Izawa, J.-I. Itoh, and Y. Nagato. 2012. ABERRANT PANICLE ORGANIZATION 2/RFL, the rice ortholog of *Arabidopsis* LEAFY, suppresses the transition from inflorescence meristem to floral meristem through interaction with APO1. Plant J. 69(1):168–180. doi:10.1111/j.1365-313X.2011.04781.x

International Rice Genome Sequencing Project. 2005. The map-based sequence of the rice genome. Nature 436:793–800. doi:10.1038/nature03895

Ishikawa, S., M. Maekawa, T. Arite, K. Onishi, I. Takamure, and J. Kyozuka. 2005. Suppression of tiller bud activity in tillering dwarf mutants of rice. Plant Cell Physiol. 46(1):79–86. doi:10.1093/pcp/pci022

Itoh, J.-I., K.-I. Nonomura, K. Ikeda, S. Yamaki, Y. Inukai, H. Yamagishi, H. Kitano, and Y. Nagato. 2005. Rice plant development: From zygote to spikelet. Plant Cell Physiol. 46(1):23–47. doi:10.1093/pcp/pci501

Izawa, T., and K. Shimamoto. 1996. Becoming a model plant: The importance of rice to plant science. Trends Plant Sci. 1(3):95–99. doi:10.1016/S1360-1385(96)80041-0

Jaiswal, P. 2011. Gramene Database: A hub for comparative plant genomics. In: A. Pereira, editor, Methods in molecular biology—Plant reverse genetics. Humana Press, New York. p. 247–275.

Jasinski, S., P. Piazza, J. Craft, A. Hay, L. Woolley, I. Rieu, A. Phillips, P. Hedden, and M. Tsiantis. 2005. KNOX action in *Arabidopsis* is mediated by coordinate regulation of cytokinin and gibberellin activities. Curr. Biol. 15(17):1560–1565. doi:10.1016/j.cub.2005.07.023

Jia, Q., X.-Q. Zhang, S. Westcott, S. Broughton, M. Cakir, J. Yang, R. Lance, and C. Li. 2011. Expression level of a gibberellin 20-oxidase gene is associated with multiple agronomic and quality traits in barley. Theor. Appl. Genet. 122(8):1451–1460. doi:10.1007/s00122-011-1544-5

Jia, Q., J. Zhang, S. Westcott, X.-Q. Zhang, M. Bellgard, R. Lance, and C. Li. 2009. GA-20 oxidase as a candidate for the semidwarf gene sdw1/denso in barley. Funct. Integr. Genomics 9(2):255–262. doi:10.1007/s10142-009-0120-4

Jiang, S.-Y., and S. Ramachandran. 2010. Natural and artificial mutants as valuable resources for functional genomics and molecular breeding. Int. J. Biol. Sci. 6(3):228–251. doi:10.7150/ijbs.6.228

Jiao, Y., Y. Wang, D. Xue, J. Wang, M. Yan, G. Liu, G. Dong, D. Zeng, Z. Lu, X. Zhu, Q. Qian, and J. Li. 2010. Regulation of OsSPL14 by OsmiR156 defines ideal plant architecture in rice. Nat. Genet. 42(6):541–544. doi:10.1038/ng.591

Kato, T., and A. Horibata. 2011. A novel frameshift mutant allele, fzp-10, affecting the panicle architecture of rice. Euphytica 184(1):65–72. doi:10.1007/s10681-011-0547-2

Kato, T., and A. Horibata. 2012. A novel frameshift mutant allele, *fzp-10*, affecting the panicle architecture of rice. Euphytica 184(1):65–72. doi:10.1007/s10681-011-0547-2

Kebrom, T.H., and R.A. Richards. 2013. Physiological perspectives of reduced tillering and stunting in the *tiller inhibition* (*tin*) mutant of wheat. Funct. Plant Biol. 40(10):977. doi:10.1071/FP13034

Kebrom, T.H., W. Spielmeyer, and E.J. Finnegan. 2013. Grasses provide new insights into regulation of shoot branching. Trends Plant Sci. 18(1):41–48. doi:10.1016/j.tplants.2012.07.001

Keller, T., J. Abbott, T. Moritz, and P. Doerner. 2006. *Arabidopsis REGULATOR OF AXILLARY MERISTEMS1* controls a leaf axil stem cell niche and modulates vegetative development. Plant Cell 18(3):598–611. doi:10.1105/tpc.105.038588

Khush, G. 2001. Green revolution: The way forward. Nat. Rev. Genet. 2(10):815–822 10.1038/35093585. doi:10.1038/35093585

Khush, G. 2003. Productivity improvements in rice. Nutr. Rev. 61(6):114–116. doi:10.1301/nr.2003.jun.S114-S116

Kirby, E., and M. Appleyard. 1987. Cereal development guide. 2nd ed. Arable Unit, Stoneleigh, Warwickshire.

Komatsu, M., M. Maekawa, K. Shimamoto, and J. Kyozuka. 2001. The LAX1 and FRIZZY PANICLE 2 genes determine the inflorescence architecture of rice by controlling rachis-branch and spikelet development. Dev. Biol. 231(2):364–373. doi:10.1006/dbio.2000.9988

Komatsu, K., M. Maekawa, S. Ujiie, Y. Satake, I. Furutani, H. Okamoto, K. Shimamoto, and J. Kyozuka. 2003. LAX and SPA: Major regulators of shoot branching in rice. Proc. Natl. Acad. Sci. USA 100(20):11,765–11,770. doi:10.1073/pnas.1932414100

Komatsuda, T., M. Pourkheirandish, C. He, P. Azhaguvel, H. Kanamori, D. Perovic, N. Stein, A. Graner, T. Wicker, A. Tagiri, U. Lundqvist, T. Fujimura, M. Matsuoka, T. Matsumoto, and M. Yano. 2007. Six-rowed barley originated from a mutation in a homeodomain-leucine zipper I-class homeobox gene. Proc. Natl. Acad. Sci. USA 104(4):1424–1429. doi:10.1073/pnas.0608580104

Konishi, S., T. Izawa, S.Y. Lin, K. Ebana, Y. Fukuta, T. Sasaki, and M. Yano. 2006. An SNP caused loss of seed shattering during rice domestication. Science 312(5778):1392–1396. doi:10.1126/science.1126410.

Krothapalli, K., E.M. Buescher, X. Li, E. Brown, C. Chapple, B.P. Dilkes, and M.R. Tuinstra. 2013. Forward genetics by genome sequencing reveals that rapid cyanide release deters insect herbivory of Sorghum bicolor. Genetics 195(2):309–318. doi:10.1534/genetics.113.149567

Krouk, G., S. Ruffel, R.A. Gutiérrez, A. Gojon, N.M. Crawford, G.M. Coruzzi, and B. Lacombe. 2011. A framework integrating plant growth with hormones and nutrients. Trends Plant Sci. 16(4):178–182. doi:10.1016/j.tplants.2011.02.004

Kumlehn, J., and G. Hensel. 2009. Genetic transformation technology in the Triticeae. Breed. Sci. 59(5):553–560. doi:10.1270/jsbbs.59.553

Kwon, Y., S. Yu, J. Park, Y. Li, J. Han, H. Alavilli, J. Cho, T. Kim, J. Jeon, and B. Lee 2012. *OsREL2*, a rice TOPLESS homolog functions in axillary meristem development in rice inflorescence. Plant Biotech Rep. 6(3):213–224. doi:10.1007/s11816-011-0214-z

Li, X.Y., Q. Qian, Z.M. Fu, Y.H. Wang, G.S. Xiong, D.L. Zeng, X.Q. Wang, X.F. Liu, S. Teng, F. Hiroshi, M. Yuan, D. Luo, B. Han, and J.Y. Li. 2003. Control of tillering in rice. Nature 422(6932):618–621. doi:10.1038/nature01518

Lin, Q., D. Wang, H. Dong, S. Gu, Z. Cheng, J. Gong, R. Qin, L. Jiang, G. Li, J.L. Wang, F. Wu, X. Guo, X. Zhang, C. Lei, H. Wang, and J. Wan. 2012. Rice APC/C(TE) controls tillering by mediating the degradation of MONOCULM 1. Nat. Commun. 3:752. doi:10.1038/ncomms1716

Lin, H., R. Wang, Q. Qian, M. Yan, X. Meng, Z. Fu, C. Yan, B. Jiang, Z. Su, J. Li, and Y. Wang. 2009. DWARF27, an iron-containing protein required for the biosynthesis of strigolactones, regulates rice tiller bud outgrowth. Plant Cell 21(5):1512–1525. doi:10.1105/tpc.109.065987

Liu, W., W. Kohlen, A. Lillo, R. Op den Camp, S. Ivanov, M. Hartog, E. Limpens, M. Jamil, C. Smaczniak, K. Kaufmann, W.C. Yang, G.J. Hooiveld, T. Charnikhova, H.J. Bouwmeester, T. Bisseling, and R. Geurts. 2011. Strigolactone biosynthesis in *Medicago truncatula* and rice requires the symbiotic GRAS-type transcription factors $NSP_1$ and $NSP_2$. Plant Cell 23(10):3853–3865. doi:10.1105/tpc.111.089771

Liu, Y., M. Koornneef, and W.J.J. Soppe. 2007. The absence of histone H2B monoubiquitination in the *Arabidopsis hub1* (*rdo4*) mutant reveals a role for chromatin remodeling in seed dormancy. Plant Cell 19(2):433–444. doi:10.1105/tpc.106.049221

Liu, S., C.-T. Yeh, H.M. Tang, D. Nettleton, and P.S. Schnable. 2012. Gene mapping via bulked segregant RNA-Seq (BSR-Seq). PLoS ONE 7(5):E36406. doi:10.1371/journal.pone.0036406

Liu, W., D. Zhang, M. Tang, D. Li, Y. Zhu, L. Zhu, and C. Chen. 2013. THIS1 is a putative lipase that regulates tillering, plant height, and spikelet fertility in rice. J. Exp. Bot. 64(14):4389–4402. doi:10.1093/jxb/ert256

Lo, S.-F., S.-Y. Yang, K.-T. Chen, Y.-I. Hsing, J.A.D. Zeevaart, L.-J. Chen, and S.-M. Yu. 2008. A novel class of gibberellin 2-oxidases control semidwarfism, tillering, and root development in rice. Plant Cell 20(10):2603–2618. doi:10.1105/tpc.108.060913

Long, J., and M.K. Barton. 2000. Initiation of axillary and floral meristems in *Arabidopsis*. Dev. Biol. 218(2):341–353. doi:10.1006/dbio.1999.9572.

Lu, Z., H. Yu, G. Xiong, J. Wang, Y. Jiao, G. Liu, Y. Meng, X. Hu, Q. Qian, X. Fu, Y. Wang, and J. Li. 2013. Genome-wide binding analysis of the transcription activator IDEAL PLANT ARCHITECTURE1 reveals a complex network regulating rice plant architecture. Plant Cell 25(10):3743–3759. doi:10.1105/tpc.113.113639

Luo, L., W. Li, K. Miura, M. Ashikari, and J. Kyozuka. 2012. Control of tiller growth of rice by OsSPL14 and strigolactones, which work in two independent pathways. Plant Cell Physiol. 53(10):1793–1801. doi:10.1093/pcp/pcs122

Mäkelä, P., and S. Muurinen. 2011. Uniculm and conventional tillering barley accessions under northern growing conditions. J. Agric. Sci. 150(03):335–344. doi:10.1017/S002185961100058X

Mascher, M., G.J. Muehlbauer, D.S. Rokhsar, J. Chapman, J. Schmutz, K. Barry, M. Muñoz-Amatriaín, T.J. Close, R.P. Wise, A.H. Schulman, A. Himmelbach, K.F.X. Mayer, U. Scholz, J. a Poland, N. Stein, and R. Waugh. 2013. Anchoring and ordering NGS contig assemblies by population sequencing (POPSEQ). Plant J. 76(4):718–727. doi:10.1111/tpj.12319.

Matsumoto, T., T. Tanaka, H. Sakai, N. Amano, H. Kanamori, K. Kurita, A. Kikuta, K. Kamiya, M. Yamamoto, H. Ikawa, N. Fujii, K. Hori, T. Itoh, and K. Sato. 2011. Comprehensive sequence analysis of 24,783 barley full-length cDNAs derived from 12 clone libraries. Plant Physiol. 156(1):20–28. doi:10.1104/pp.110.171579

Mayer, K.F.X., M. Martis, P.E. Hedley, H. Simková, H. Liu, J.A. Morris, B. Steuernagel, S. Taudien, S. Roessner, H. Gundlach, M. Kubaláková, P. Suchánková, F. Murat, M. Felder, T. Nussbaumer, A. Graner, J. Salse, T. Endo, H. Sakai, T. Tanaka, T. Itoh, K. Sato, M. Platzer, T. Matsumoto, U. Scholz, J. Dolezel, R. Waugh, and N. Stein. 2011. Unlocking the barley genome by chromosomal and comparative genomics. Plant Cell 23(4):1249–1263. doi:10.1105/tpc.110.082537

Michelmore, R.W., I. Paran, and R.V. Kesseli. 1991. Identification of markers linked to disease-resistance genes by bulked segregant analysis: A rapid method to detect markers in specific genomic regions by using segregating populations. Proc. Natl. Acad. Sci. USA 88(21):9828–9832. doi:10.1073/pnas.88.21.9828

Minakuchi, K., H. Kameoka, N. Yasuno, M. Umehara, L. Luo, K. Kobayashi, A. Hanada, K. Ueno, T. Asami, S. Yamaguchi, and J. Kyozuka. 2010. FINE CULM1 (FC1) works downstream of strigolactones to inhibit the outgrowth of axillary buds in rice. Plant Cell Physiol. 51(7):1127–1135. doi:10.1093/pcp/pcq083

Mitchell, J.H., G.J. Rebetzke, S.C. Chapman, and S. Fukai. 2013. Evaluation of reduced-tillering (*tin*) wheat lines in managed, terminal water deficit environments. J. Exp. Bot. 64(11):3439–3451. doi:10.1093/jxb/ert181

Miura, K., M. Ikeda, A. Matsubara, X.-J. Song, M. Ito, K. Asano, M. Matsuoka, H. Kitano, and M. Ashikari. 2010. OsSPL14 promotes panicle branching and higher grain productivity in rice. Nat. Genet. 42(6):545–549. doi:10.1038/ng.592

Mohapatra, P.K., B.B. Panda, and E. Kariali. 2011. Plasticity of tiller dynamics in wild rice *Oryza rufipogon* Griff.: A strategy for resilience in suboptimal environments. Int. J. Agron. 2011:543237. doi:10.1155/2011/543237

Mok, M. 1994. Cytokinins and plant development—An overview. In: D. Mok and M. Mok, editors, Cytokinins—Chemistry, activity, and function. CRC Press, Boca Raton, FL. p. 155–166.
Müller, D., G. Schmitz, and K. Theres. 2006. *Blind* homologous *R2R3 Myb* genes control the pattern of lateral meristem initiation in *Arabidopsis*. Plant Cell 18(3):586–597. doi:10.1105/tpc.105.038745
Müller, J., Y. Wang, R. Franzen, L. Santi, F. Salamini, and W. Rohde. 2001. *In vitro* interactions between barley TALE homeodomain proteins suggest a role for protein–protein associations in the regulation of *Knox* gene function. Plant J. 27(1):13–23. doi:10.1046/j.1365-313x.2001.01064.x
Murat, F., J.-H. Xu, E. Tannier, M. Abrouk, N. Guilhot, C. Pont, J. Messing, and J. Salse. 2010. Ancestral grass karyotype reconstruction unravels new mechanisms of genome shuffling as a source of plant evolution. Genome Res. 20(11):1545–1557. doi:10.1101/gr.109744.110
Nakamura, A., S. Fujioka, H. Sunohara, N. Kamiya, Z. Hong, Y. Inukai, K. Miura, S. Takatsuto, S. Yoshida, M. Ueguchi-Tanaka, Y. Hasegawa, H. Kitano, and M. Matsuoka. 2006. The role of *OsBRI1* and its homologous genes, *OsBRL1* and *OsBRL3*, in rice. Plant Physiol. 140(2):580–590. doi:10.1104/pp.105.072330
Nakamura, H., Y.L. Xue, T. Miyakawa, F. Hou, H.M. Qin, K. Fukui, X. Shi, E. Ito, S. Ito, S.H. Park, Y. Miyauchi, A. Asano, N. Totsuka, T. Ueda, M. Tanokura, and T. Asami. 2013. Molecular mechanism of strigolactone perception by DWARF14. Nat Commun. 4:2613. doi:10.1038/ncomms3613.
O'Neill, D.P., and J.J. Ross. 2002. Auxin regulation of the gibberellin pathway in Pea. Plant Physiol. 130:1974–1982. doi:10.1104/pp.010587
Oikawa, T., and J. Kyozuka. 2009. Two-step regulation of LAX PANICLE1 protein accumulation in axillary meristem formation in rice. Plant Cell 21(4):1095–1108. doi:10.1105/tpc.108.065425
Oikawa, A., K. Nagai, K. Kato, and S. Kidou. 2009. Gene silencing of barley P23k involved in secondary wall formation causes abnormal tiller formation and intercalary elongation. Breed. Sci. 59(5):664–670. doi:10.1270/jsbbs.59.664
Okagaki, R.J., S. Cho, W.M. Kruger, W.W. Xu, S. Heinen, and G.J. Muehlbauer. 2013. The barley UNICULM2 gene resides in a centromeric region and may be associated with signaling and stress responses. Funct. Integr. Genomics 13(1):33–41. doi:10.1007/s10142-012-0299-7
Paul, P., A. Awasthi, A. Rai, S.K. Gupta, R. Prasad, T.R. Sharma, H.S. Dhaliwal. 2012. Reduced tillering in Basmati rice T-DNA insertional mutant OsTEF1 associates with differential expression of stress related genes and transcription factors. Funct. Integr. Genomics. 12(2):291–304. doi:10.1007/s10142-012-0264-5
Petrásek, J., and J. Friml. 2009. Auxin transport routes in plant development. Development 136(16):2675–2688. doi:10.1242/dev.030353
Petsko, G.A. 2002. Grain of truth. Genome Biol. 3(5):Comment1007. doi:10.1186/gb-2002-3-5-comment1007.
Qi, W., F. Sun, Q. Wang, M. Chen, Y. Huang, Y.-Q. Feng, X. Luo, and J. Yang. 2011. Rice ethylene-response AP2/ERF factor OsEATB restricts internode elongation by down-regulating a gibberellin biosynthetic gene. Plant Physiol. 157(1):216–228. doi:10.1104/pp.111.179945
Quraishi, U., M. Abrouk, S. Bolot, C. Pont, M. Throude, N. Guilhot, C. Confolent, F. Bortolini, S. Praud, A. Murigneux, G. Charmet, and J. Salse. 2009. Genomics in cereals: From genome-wide conserved orthologous set (COS) sequences to candidate genes for trait dissection. Funct. Integr. Genomics 9(4):473–484. doi:10.1007/s10142-009-0129-8
Ramsay, L., J. Comadran, A. Druka, D.F. Marshall, W.T.B. Thomas, M. Macaulay, K. MacKenzie, C. Simpson, J. Fuller, N. Bonar, P.M. Hayes, U. Lundqvist, J.D. Franckowiak, T.J. Close, G.J. Muehlbauer, and R. Waugh. 2011. INTERMEDIUM-C, a modifier of lateral spikelet fertility in barley, is an ortholog of the maize domestication gene TEOSINTE BRANCHED 1. Nat. Genet. 43(2):169–172. doi:10.1038/ng.745
Ray, D.K., N. Ramankutty, N.D. Mueller, P.C. West, and J.A. Foley. 2012. Recent patterns of crop yield growth and stagnation. Nat. Commun. 3:1293. doi:10.1038/ncomms2296
Roeder, A.H.K., C. Ferrándiz, and M.F. Yanofsky. 2003. The role of the REPLUMLESS homeodomain protein in patterning the *Arabidopsis* fruit. Curr. Biol. 13(18):1630–1635. doi:http://dx.doi.org/10.1016/j.cub.2003.08.027.
Rossini, L., A. Vecchietti, L. Nicoloso, N. Stein, S. Franzago, F. Salamini, and C. Pozzi. 2006. Candidate genes for barley mutants involved in plant architecture: An *in silico* approach. Theor. Appl. Genet. 112(6):1073–1085. doi:10.1007/s00122-006-0209-2
Rutjens, B., D. Bao, E. Van Eck-Stouten, M. Brand, S. Smeekens, and M. Proveniers. 2009. Shoot apical meristem function in *Arabidopsis* requires the combined activities of three BEL1-like homeodomain proteins. Plant J. 58(4):641–654. doi:10.1111/j.1365-313X.2009.03809.x
Saha, B. 1957. Studies on the development of the embryo of *Oryza sativa* and the homologies of its parts. Proceeding Natl. Inst. Sci. India 22(2):86–101.
Saisho, D., K. Tanno, M. Chono, I. Honda, H. Kitano, and K. Takeda. 2004. Spontaneous brassinolide-insensitive barley mutants "*uzu*" adapted to East Asia. Breed. Sci. 54(4):409–416. doi:10.1270/jsbbs.54.409
Sakai, H., S.S. Lee, T. Tanaka, H. Numa, J. Kim, Y. Kawahara, H. Wakimoto, C. Yang, M. Iwamoto, T. Abe, Y. Yamada, A. Muto, H. Inokuchi, T. Ikemura, T. Matsumoto, T. Sasaki, and T. Itoh. 2013. Rice Annotation Project Database (RAP-DB): An integrative and interactive database for rice genomics. Plant Cell Physiol. 54(2):e6. doi:10.1093/pcp/pcs183
Sakakibara, H. 2004. Cytokinin biosynthesis and metabolism. In: P. Davies, editor, Plant hormones: Biosynthesis, signal transduction, action. Springer, Dordrecht, the Netherlands. p. 95–114.
Sakamoto, T., and M. Matsuoka. 2004. Generating high-yielding varieties by genetic manipulation of plant architecture. Curr. Opin. Biotechnol. 15(2):144–147. doi:10.1016/j.copbio.2004.02.003
Sakamoto, T., K. Miura, H. Itoh, T. Tatsumi, and M. Ueguchi-Tanaka. 2004. An overview of gibberellin metabolism enzyme genes and their related mutants in rice. Plant Physiol. 134(4):1642–1653. doi:10.1104/pp.103.033696
Sakamoto, T., H. Sakakibara, M. Kojima, Y. Yamamoto, H. Nagasaki, Y. Inukai, Y. Sato, and M. Matsuoka. 2006. Ectopic expression of KNOTTED1-like homeobox protein induces expression of cytokinin biosynthesis genes in rice. Plant Physiol. 142(1):54–62. doi:10.1104/pp.106.085811
Salse, J., M. Abrouk, F. Murat, U.M. Quraishi, and C. Feuillet. 2009. Improved criteria and comparative genomics tool provide new insights into grass paleogenomics. Brief. Bioinform. doi:10.1093/bib/bbp037
Sasaki, A., M. Ashikari, M. Ueguchi-Tanaka, H. Itoh, A. Nishimura, D. Swapan, K. Ishiyama, T. Saito, M. Kobayashi, G.S. Khush, H. Kitano, and M. Matsuoka. 2002. Green revolution: A mutant gibberellin-synthesis gene in rice. Nature 416(6882):701–702. doi:10.1038/416701a
Schmitz, G., and K. Theres. 2005. Shoot and inflorescence branching. Curr. Opin. Plant Biol. 8(5):506–511. doi:10.1016/j.pbi.2005.07.010
Schmitz, G., E. Tillmann, F. Carriero, C. Fiore, F. Cellini, and K. Theres. 2002. The tomato *Blind* gene encodes a MYB transcription factor that controls the formation of lateral meristems. Proc. Natl. Acad. Sci. USA 99(2):1064–1069. doi:10.1073/pnas.022516199
Schneeberger, K., S. Ossowski, C. Lanz, T. Juul, A.H. Petersen, K.L. Nielsen, J.-E. Jorgensen, D. Weigel, and S.U. Andersen. 2009. SHOREmap: Simultaneous mapping and mutation identification by deep sequencing. Nat. Methods 6(8):550–551. doi:10.1038/nmeth0809-550
Schneeberger, K., and D. Weigel. 2011. Fast-forward genetics enabled by new sequencing technologies. Trends Plant Sci. 16(5):282–288. doi:http://dx.doi.org/10.1016/j.tplants.2011.02.006.
Schumacher, K., T. Schmitt, M. Rossberg, G. Schmitz, and K. Theres. 1999. The *Lateral suppressor* (*Ls*) gene of tomato encodes a new member of the VHIID protein family. Proc. Natl. Acad. Sci. USA 96(1):290–295. doi:10.1073/pnas.96.1.290
Seavers, G.P., and K.J. Wright. 1999. Crop canopy development and structure influence weed suppression. Weed Res. 39:319–328. doi:10.1046/j.1365-3180.1999.00148.x
Sharman, B.C. 1942. Developmental anatomy of the shoot of *Zea mays* L. Ann. Bot. 6(2):245–282.
Shiferaw, B., M. Smale, H.-J. Braun, E. Duveiller, M. Reynolds, and G. Muricho. 2013. Crops that feed the world 10. Past successes and future

challenges to the role played by wheat in global food security. Food Secur. 5(3):291–317. doi:10.1007/s12571-013-0263-y
Smith, H.M.S., and S. Hake. 2003. The interaction of two homeobox genes, BREVIPEDICELLUS and PENNYWISE, regulates internode patterning in the *Arabidopsis* inflorescence. Plant Cell 15(8):1717–1727. doi:10.1105/tpc.012856
Spielmeyer, W., M.H. Ellis, and P.M. Chandler. 2002. Semidwarf sd-1, "green revolution" rice, contains a defective gibberellin 20-oxidase gene. Proc. Natl. Acad. Sci. USA 99(13):9043–9048. doi:10.1073/pnas.132266399
Sreenivasulu, N., and T. Schnurbusch. 2012. A genetic playground for enhancing grain number in cereals. Trends Plant Sci. 17(2):91–101. doi:10.1016/j.tplants.2011.11.003
Sun, F., W. Zhang, G. Xiong, M. Yan, Q. Qian, J. Li, and Y. Wang. 2010. Identification and functional analysis of the MOC1 interacting protein 1. J. Genet. Genomics 37(1):69–77. doi:10.1016/S1673-8527(09)60026-6
Tabuchi, H., Y. Zhang, S. Hattori, M. Omae, S. Shimizu-Sato, T. Oikawa, Q. Qian, M. Nishimura, H. Kitano, H. Xie, X. Fang, H. Yoshida, J. Kyozuka, F. Chen, and Y. Sato. 2011. LAX PANICLE2 of rice encodes a novel nuclear protein and regulates the formation of axillary meristems. Plant Cell 23(9):3276–3287. doi:10.1105/tpc.111.088765
Takeda, T., Y. Suwa, M. Suzuki, H. Kitano, M. Ueguchi-Tanaka, M. Ashikari, M. Matsuoka, and C. Ueguchi. 2003. The OsTB1 gene negatively regulates lateral branching in rice. Plant J. 33(3):513–520. doi:10.1046/j.1365-313X.2003.01648.x
Talamè, V., R. Bovina, M.C. Sanguineti, R. Tuberosa, U. Lundqvist, and S. Salvi. 2008. TILLMore, a resource for the discovery of chemically induced mutants in barley. Plant Biotechnol. J. 6(5):477–485. doi:10.1111/j.1467-7652.2008.00341.x
Tantikanjana, T., J.W.H. Yong, D.S. Letham, M. Griffith, M. Hussain, K. Ljung, G. Sandberg, and V. Sundaresan. 2001. Control of axillary bud initiation and shoot architecture in *Arabidopsis* through the SUPERSHOOT gene. Genes Dev. 15(12):1577–1588. doi:10.1101/gad.887301
Tilman, D., C. Balzer, J. Hill, and B.L. Befort. 2011. Global food demand and the sustainable intensification of agriculture. Proc. Natl. Acad. Sci. USA 108:20260–20264. doi:10.1073/pnas.1116437108
Tong, H., and C. Chu. 2009. Roles of *DLT* in fine modulation on brassinosteroid response in rice. Plant Signal. Behav. 4(5):438–439. doi:10.4161/psb.4.5.8317
Tong, H., Y. Jin, W. Liu, F. Li, J. Fang, Y. Yin, Q. Qian, L. Zhu, and C. Chu. 2009. DWARF AND LOW-TILLERING, a new member of the GRAS family, plays positive roles in brassinosteroid signaling in rice. Plant J. 58(5):803–816. doi:10.1111/j.1365-313X.2009.03825.x
Tong, H., L. Liu, Y. Jin, L. Du, Y. Yin, Q. Qian, L. Zhu, and C. Chu. 2012. DWARF AND LOW-TILLERING acts as a direct downstream target of a GSK3/SHAGGY-like kinase to mediate brassinosteroid responses in rice. Plant Cell 24(6):2562–2577. doi:10.1105/tpc.112.097394
Trick, M., N. Adamski, S. Mugford, C.-C. Jiang, M. Febrer, and C. Uauy. 2012. Combining SNP discovery from next-generation sequencing data with bulked segregant analysis (BSA) to fine-map genes in polyploid wheat. BMC Plant Biol. 12(1):14. doi:10.1186/1471-2229-12-14
Tsuchiya, T. 1976. Allelism testing in barley. II. Allelic relationships of three *uzu* genes. Crop Sci. 16(4):496–499. doi:10.2135/cropsci1976.0011183X001600040013x
Uchida, N., T. Sakamoto, T. Kurata, and M. Tasaka. 2011. Identification of EMS-induced causal mutations in a non-reference *Arabidopsis thaliana* accession by whole genome sequencing. Plant Cell Physiol. 52(4):716–722. doi:10.1093/pcp/pcr029
Umehara, M., A. Hanada, S. Yoshida, K. Akiyama, T. Arite, N. Takeda-Kamiya, H. Magome, Y. Kamiya, K. Shirasu, K. Yoneyama, J. Kyozuka, and S. Yamaguchi. 2008. Inhibition of shoot branching by new terpenoid plant hormones. Nature 455(7210):195–200. doi:10.1038/nature07272
Vinardell, J.M., E. Fedorova, A. Cebolla, Z. Kevei, G. Horvath, Z. Kelemen, S. Tarayre, F. Roudier, P. Mergaert, A. Kondorosi, and E. Kondorosi. 2003. Endoreduplication mediated by the anaphase-promoting complex activator CCS52A is required for symbiotic cell differentiation in *Medicago truncatula* nodules. Plant Cell 15:2093–2105. doi:10.1105/tpc.014373
Wang, Y., and J. Li. 2006. Genes controlling plant architecture. Curr. Opin. Biotechnol. 17(2):123–129. doi:10.1016/j.copbio.2006.02.004
Wang, Y., and J. Li. 2008. Molecular basis of plant architecture. Annu. Rev. Plant Biol. 59:253–279. doi:10.1146/annurev.arplant.59.032607.092902
Wang, Y., and J. Li. 2011. Branching in rice. Curr. Opin. Plant Biol. 14(1):94–99. doi:http://dx.doi.org/10.1016/j.pbi.2010.11.002.
Wang, N., T. Long, W. Yao, L. Xiong, Q. Zhang, and C. Wu. 2013. Mutant resources for the functional analysis of the rice genome. Mol. Plant 6(3):596–604. doi:10.1093/mp/sss142
Weatherwax, P. 1923. The story of the maize plant. University of Chicago Press.
Xia, K., R. Wang, X. Ou, Z. Fang, C. Tian, J. Duan, Y. Wang, and M. Zhang. 2012. OsTIR1 and OsAFB2 downregulation via OsmiR393 overexpression leads to more tillers, early flowering and less tolerance to salt and drought in rice. PLoS ONE 7(1):E30039. doi:10.1371/journal.pone.0030039
Xing, Y., and Q. Zhang. 2010. Genetic and molecular bases of rice yield. Annu. Rev. Plant Biol. 61:421–442. doi:10.1146/annurev-arplant-042809-112209
Xu, C., Y. Wang, Y. Yu, J. Duan, Z. Liao, G. Xiong, X. Meng, G. Liu, Q. Qian, and J. Li. 2012. Degradation of MONOCULM 1 by APC/C(TAD1) regulates rice tillering. Nat. Commun. 3:750. doi:10.1038/ncomms1743
Xu, M., L. Zhu, H. Shou, and P. Wu. 2005. A PIN1 family gene, OsPIN1, involved in auxin-dependent adventitious root emergence and tillering in rice. Plant Cell Physiol. 46(10):1674–1681. doi:10.1093/pcp/pci183
Yanai, O., E. Shani, K. Dolezal, P. Tarkowski, R. Sablowski, G. Sandberg, A. Samach, and N. Ori. 2005. *Arabidopsis* KNOXI proteins activate cytokinin biosynthesis. Curr. Biol. 15(17):1566–1571. doi:10.1016/j.cub.2005.07.060
Yang, Y., Y. Li, and C. Wu. 2013. Genomic resources for functional analyses of the rice genome. Curr. Opin. Plant Biol. 16(2):157–163. doi:10.1016/j.pbi.2013.03.010.
Yasuno, N., I. Takamure, S. Kidou, Y. Tokuji, A.N. Ureshi, A. Funabiki, K. Ashikaga, U. Yamanouchi, M. Yano, and K. Kato. 2009. Rice shoot branching requires an ATP-binding cassette subfamily G protein. New Phytol. 182(1):91–101. doi:10.1111/j.1469-8137.2008.02724.
Yoshida, A., Y. Ohmori, H. Kitano, F. Taguchi-Shiobara, and H.-Y. Hirano. 2012. Aberrant spikelet and panicle1, encoding a TOPLESS-related transcriptional co-repressor, is involved in the regulation of meristem fate in rice. Plant J. 70(2):327–339. doi:10.1111/j.1365-313X.2011.04872.x
Zazímalová, E., A.S. Murphy, H. Yang, K. Hoyerová, and P. Hosek. 2010. Auxin transporters—Why so many? Cold Spring Harb. Perspect. Biol. 2(3):A001552 doi:10.1101/cshperspect.a001552.
Zhang, J. 1994. Analyses on changes in plant height of varieties and dwarf sources of barley breeding in China. Barley Sci. 4:11–13.
Zhang, J. 2000. Inheritance of agronomic traits from the Chinese barley dwarfing gene donors 'Xiaoshan Lixiahuang' and 'Cangzhou Luodamai'. Plant Breed. 119(6):523–524. doi:10.1046/j.1439-0523.2000.00543.x
Zhang, S.-W., C.-H. Li, J. Cao, Y.-C. Zhang, S.-Q. Zhang, Y.-F. Xia, D.-Y. Sun, and Y. Sun. 2009. Altered architecture and enhanced drought tolerance in rice via the down-regulation of indole-3-acetic acid by TLD1/OsGH3.13 activation. Plant Physiol. 151(4):1889–1901. doi:10.1104/pp.109.146803
Zhang, J., C. Li, C. Wu, L. Xiong, G. Chen, Q. Zhang, and S. Wang. 2006. RMD: A rice mutant database for functional analysis of the rice genome. Nucleic Acids Res. 34(suppl 1):D745–D748. doi:10.1093/nar/gkj016
Zhu, Y., H. Mang, Q. Sun, J. Qian, A. Hipps, and J. Hua. 2012. Gene discovery using mutagen-induced polymorphisms and deep sequencing: Application to plant disease resistance. Genetics 192(1):139–146. doi:10.1534/genetics.112.141986
Zou, J., S. Zhang, W. Zhang, G. Li, Z. Chen, W. Zhai, X. Zhao, X. Pan, Q. Xie, and L. Zhu. 2006. The rice HIGH-TILLERING DWARF1 encoding an ortholog of *Arabidopsis* MAX3 is required for negative regulation of the outgrowth of axillary buds. Plant J. 48(5):687–698. doi:10.1111/j.1365-313X.2006.02916.x