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Genetics of barley tiller and leaf development[FA]

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Invited Expert Review

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Abstract In cereals, tillering and leaf development are key factors in the concept of crop ideotype, introduced in the 1960s to enhance crop yield, via manipulation of plant architecture. In the present review, we discuss advances in genetic analysis of barley shoot architecture, focusing on tillering, leaf size and angle. We also discuss novel phenotyping techniques, such as 2D and 3D imaging, that have been introduced in the era of phenomics, facilitating reliable trait measurement. We discuss the identification of genes and pathways that are involved in barley tillering and leaf development, highlighting key hormones involved in the control of plant architecture in barley and rice. Knowledge on genetic control of traits related to plant architecture provides useful resources for designing ideotypes for enhanced barley yield and performance.

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INTRODUCTION

Humans have been cultivating barley (*Hordeum vulgare* ssp. *vulgare*) for at least 10,000 years, since domestication from the wild ancestor *Hordeum vulgare* ssp. *spontaneum* (Pankin and von Korff 2017). Good adaptability to different agro-climatic conditions facilitated spreading of barley cultivation to a wide range of environments worldwide (Russell et al. 2016). Today, barley is among the top four cereal crops with a global production of over 141 million tonnes, 41% of which comes from the European Union (http://faostat.fao.org). Barley is mainly used as animal feed and in malting for the brewing and distilling industries. While currently accounting for a minor proportion of barley production, use as human food is attracting increasing interest for the nutritional benefits of beta-glucans present in grains (Munoz Amatriain et al. 2014). Recently, straw – previously considered a byproduct of minimal value – is also receiving attention as a source of renewable energy, so barley may be considered as a dual-purpose crop for production of grains and lignocellulosic biomass.

As for other cereals, the Green Revolution has brought innovation in barley breeding with the introduction of semi-dwarfing genes to reduce lodging and increase partitioning of photosynthates to seeds (Dockter and Hansson 2015). The resultant varieties are considered paradigms of the ideotype concept, that is, a model crop plant rationally designed to combine morpho-physiological features predicted to improve quantity and/or quality of the end product(s) (Donald 1968). Over the past 50 years, different cereal ideotypes have been proposed, placing major emphasis on shoot architecture traits. Indeed, beside plant height, tillering, leaf size, morphology and arrangement play a fundamental role in light interception, photosynthetic efficiency, and ultimately, plant performance, biomass, and grain yield (Hussien et al. 2014; Mathan et al. 2016).

Numerous studies suggest that the optimal plant architecture would be achieved by smaller leaf angles

from the upper canopy and more horizontally oriented leaves in the lower canopy (Duncan 1971; Long et al. 2006; Ku et al. 2010; Zhu et al. 2010). This was also recently emphasized by Ort et al. (2015) in the concept of smart canopy for crop biomass and yield. The concept refers to maximizing the potential of light harvesting at the canopy level in a cooperative (rather than competitive) manner between plants. Plant phytochromes are red (R)/far-red (FR) light photoreceptors that play key roles in sensing of light conditions and consequent adjustment of plant development and growth (Li et al. 2011). This ability to perceive changes in light condition (R/FR ratio), could be utilized to develop plants with smart canopies having leaves adapted to the prevailing light conditions (Gilbert et al. 2001; Ort et al. 2015).

Clearly, knowledge of the genetic and molecular mechanisms controlling tiller and leaf development is important for designing optimal shoot features to maximize crop productivity for different/multiple end uses, and efficient genomic and phenotyping approaches are key to identifying the genes and alleles needed to achieve this goal.

For its diploid genome ($2n = 14$, 5.1 Gb) and autogamous reproduction, barley is an established model plant in genetic research (Dawson et al. 2015). Nine decades of mutagenesis programs have generated thousands of barley mutants that have been characterized at various levels (Lundqvist 2014) (for more information the reader is referred to the International Database for Barley Genes and Barley Genetic Stocks, http://89.221.255.170/bgs/index.php) and collected in repositories such as NordGen (https://www.nordgen.org/en/). For over 800 mutants, near-isogenic lines (NILs) have been generated in the background of cv. Bowman and genotyped with a genome-wide single nucleotide polymorphism (SNP) array allowing to assign the majority to unique chromosomal positions and providing a platform for phenotypic characterization and positional cloning of the corresponding genes (Druka et al. 2011). Large collections of wild accessions, landraces and cultivars offer an additional reservoir of genetic variation for genetic research and breeding (Munoz Amatriain et al. 2014; Dawson et al. 2015).

The parallel development of genomic tools has revolutionized the characterization and exploitation of genetic resources, with barley scientists pioneering mutant analysis as well as genome-wide association studies (GWAS) in plants (Waugh et al. 2009). The recently released reference genome sequence for cultivar Morex (Mascher et al. 2017), a novel 50 k SNP array (Bayer et al. 2017) and an exome capture platform (Mascher et al. 2013) are examples of the tools now available to barley geneticists and breeders. For example, exome sequencing has been used in gene identification through mapping-by-sequencing of barley mutants (Mascher et al. 2014). As genomic tools advance, the bottleneck in genetic analyses is increasingly represented by phenotyping (Araus and Kefauver 2018).

In this review, we briefly introduce barley shoot morphology and development and revisit current knowledge of the loci and genes that control tillering, leaf size and angle. We also overview state-of-the-art phenotyping approaches that promise to accelerate genetic studies and identification of shoot architecture genes with special emphasis on leaf angle.

BARLEY SHOOT MORPHOLOGY AND DEVELOPMENT

When sowing a grass seed, within a few days (4–5 d) germination occurs and the plant starts developing along the apical-basal axis. From this axis the radicle starts to grow, giving rise to the root, and later, the epicotyl begins to grow which becomes the shoot. The tips of this axis are pre-formed in the embryo and correspond to the primary meristems of the plant, that is, the shoot and root apical meristems (SAM and RAM), respectively. The epicotyl comprises the SAM and the leaf primordia enclosed by a tubular organ called the coleoptile (Briggs 1978; Rossini et al. 2014). The SAM and RAM are the ultimate determinants of the architecture of aerial and basal parts of the plant, respectively.

Stem cells responsible for meristem maintenance constitute a small area, while other cells produced from the meristem are destined to give rise to lateral organs. The position of an individual cell in the SAM is the major determinant of its fate. As in maize, the barley SAM is thought to be structured into two clonally distinct layers: the outer layer (L1) or tunica, and the inner layer or corpus (L2), although it is possible that a third layer is also present (Doring et al. 1999). In grasses, the first leaf

primordia are produced by the SAM, during embryogenesis. For example, in barley, 3–4 leaf primordia are typically present in the seed (Kirby and Appleyard 1987); these will resume growth post-embryonically to become visible as the first leaves on the main stem (Figure 1A).

In plants, shoot architecture is modular, meaning that it consists of units named phytomers. The phytomer is comprised of a stem segment called the internode, and a node with a leaf and an axillary bud (Weatherwax 1923; Bossinger et al. 1992; Forster et al. 2007) (Figure 1B, C). The SAM originates new phytomers, in succession, ultimately resulting in the final architecture of the shoot (Figure 1D). The first phytomers, in which internodes do not elongate, form the basal region of the shoot, called the crown (Figure 1D). By contrast, internode elongation occurs in phytomers formed after the transition from the vegetative to the reproductive phase.

In a fully grown barley plant, the stem, which is called the culm in grasses, consists of alternating solid nodes and hollow internodes (Figure 1B). Leaf arrangement through the shoot is termed phyllotaxis. In barley and other cereals, successive leaves are arranged on the culm, at 180° to each other, leading to a distichous pattern (Figure 1E). This same pattern is maintained also in the spike, consisting of units called spikelets attached to the rachis (i.e., the main inflorescence axis arising as an extension of the culm). In barley, two types of spike exist: in the first, the lateral spikelets in the triplets are fertile and produce grains, and the result is the six-rowed spike, in the second, the lateral spikelets fail to develop (i.e., only central spikelets develop and produce grains), and the result is the two-rowed spike (Komatsuda et al. 2007).

Leaf morphology and development

Grass leaves have a distinctive strap-like shape with veins running parallel to the central midrib. Along the proximal-distal dimension, domains with different functions can be recognized (Figure 2A–D). The distal leaf blade projects from the stem and is the main photosynthetic organ, while the basal portion, or sheath, wraps around and supports the culm. At the blade-sheath boundary, the lamina joint, with two lateral projections called auricles, acts as a hinge for the leaf blade, while the ligule, an adaxial epidermal outgrowth, stops water and pathogens from penetrating between the leaf sheath and the stem (Figure 2A).

In grasses, each leaf originates as a ring of founder cells, which are recruited on the SAM flank, and grows from this disc of insertion surrounding the meristem. While the term phyllochron defines the time interval between emergence of two successive leaves (e.g., referring to appearance of the ligule), the time interval separating the initiation of two consecutive leaf primordia is called the plastochron (P: revisited in Wilhelm and McMaster 1995) and P number is conventionally used to designate the developmental

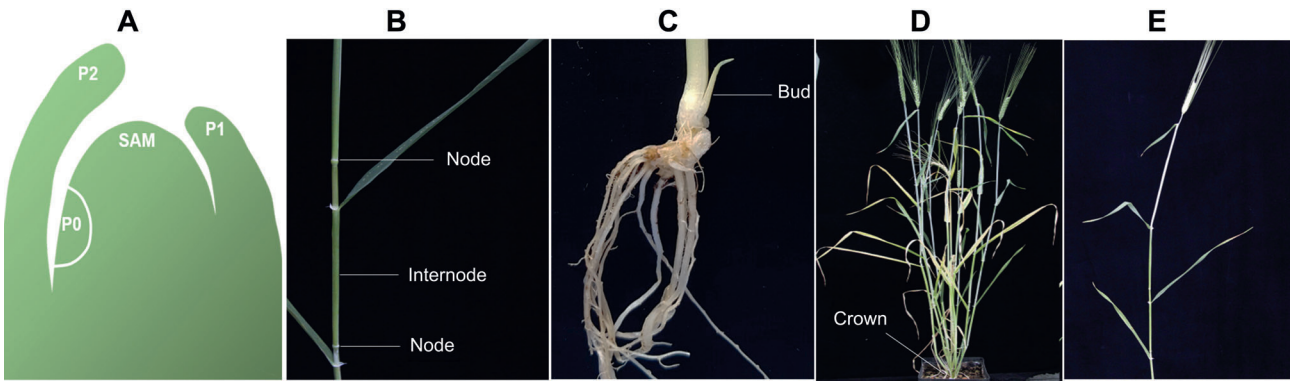

Figure 1. Illustration of barley shoot characteristics
(A) Schematic structure of the shoot apical meristem (SAM); P0, P1, and P2 are leaf primordia. **(B)** Barley nodes and internodes on a fully developed culm. **(C)** An axillary bud at the crown region (the ensheathing leaf was removed). **(D)** Barley whole-plant architecture, with the tillers producing fertile spikes. **(E)** An example illustrating leaf arrangement on the culm, with leaves positioned at 180° to each other, leading to a distichous pattern.

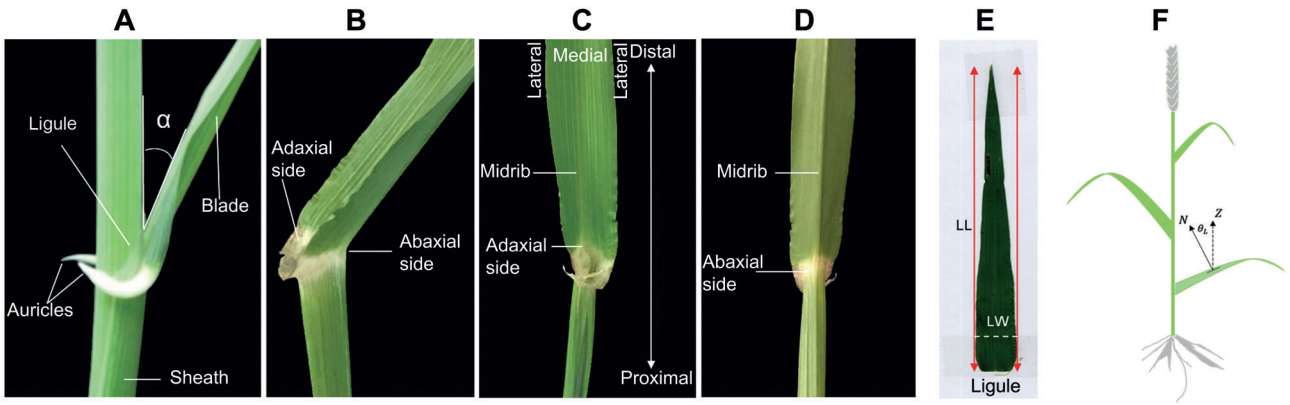

Figure 2. Illustration of barley leaf characteristics

(A) Structure of a barley leaf, comprised of the sheath and blade, the ligule and auricles; the insertion angle at the lamina joint is shown (α). **(B)** Lamina joint connecting the leaf blade to the leaf sheath. **(C)** Leaf adaxial side: proximal-distal and medial-lateral axes are indicated, along with the midrib (mid vein). **(D)** Leaf abaxial side. **(E)** Measurement of leaf blade length (LL) is taken from the ligule to the tip (red arrows), leaf blade width (LW) is taken at the widest point (dashed line). **(F)** Definition of the leaf inclination angle (LIA, θ_L), the leaf surface normal (N) is the vector perpendicular to leaf blade and the zenith (Z) is the vertical vector.

age of a leaf primordium on the shoot apex (Itoh et al. 2005) (Figure 1A). Here, P0 corresponds to the incipient leaf primordium, when founder cells – although not morphologically distinguishable from the SAM – acquire a distinct fate from meristematic cells through down-regulation of meristematic class I *KNOTTED1-like homeobox* (*KNOX*) genes (Sluis and Hake 2015). The youngest visible leaf primordium protruding from the meristem is called P1; P2 is the leaf primordium that developed immediately prior to P1, and so on.

During leaf development, polarity is established along the proximal-distal, medio-lateral and abaxial-adaxial axes (Figures 2B–D) so that growth and differentiation proceed in a coordinated fashion to attain the final structure and size of the mature leaf. At the initiation stage, founder cells are progressively recruited from the central part of the incipient primordium, proceeding laterally in both directions, organizing the medio-lateral axis, easily recognized for the bilateral symmetry around the midrib, which is formed as early as P1 in maize (Scanlon et al. 1996; Lewis and Hake 2016). Initially, the leaf primordium grows mainly along the proximal-distal axis and, at P2, it is shaped as a hood surrounding the meristem and younger leaf primordia (Itoh et al. 2005). A recent study in maize suggests that, at this stage, the developing leaf consists entirely of blade tissue (Johnston et al. 2015), placing between P3 and P4 the first emergence of the sheath from the disc of insertion. However, the exact timing of differentiation of the domains along the proximal-distal axis, may differ between species: for example, the preligular band (i.e., the group of cells that will give rise to the ligule) forms before P6 in maize (Lewis and Hake 2016), but this step occurs at P3 in rice (Itoh et al. 2005).

Leaves continue to grow from meristematic zones located at the bases of leaf blade and sheath (Briggs 1978; Itoh et al. 2005; Jöst et al. 2016). Starting from the distal end of the leaf, cells expand and mature while they stop proliferating in a basipetal progression, so that when cells at leaf tip are fully differentiated, cells at the base are still dividing (reviewed in Nelissen et al. 2016). Accordingly, the growing leaf is thought to be organized in the distal maturation, central expansion and proximal division zones (Fournier et al. 2005). In the division zone, cells undergo both longitudinal and transverse divisions to support growth in leaf width and length, respectively (Sylvester and Smith 2009) (Figure 2E). Final leaf size and shape result from spatial and temporal coordination of these processes. For example, leaf length depends on leaf elongation duration (LED) and leaf elongation rate (LER), which is closely connected to the size of the division zone (reviewed in Nelissen et al. 2016). Interestingly, studies in maize and barley suggest that LER and LED are under (at least partially) distinct control mechanisms (Baute et al. 2016; Digel et al. 2016).

Beside blade size, an important factor for photosynthetic efficiency is leaf orientation and angle, as determined at the lamina joint connecting the blade to the sheath (Figure 2A, B). During the development of the lamina joint and when the leaf blade and sheath have completed their elongation, the blade bends away from the vertical leaf sheath (culm) to form the leaf angle (Figure 2A, F) (Hoshikawa 1989). The lamina joint inclination resembles the phenomenon of epinasty caused by ethylene (Takeno et al. 1982).

During the period when expansion of cells on the adaxial side (upper leaf surface at the lamina joint region; Figure 2C) exceeds that of cells on the abaxial side (lower leaf surface at the lamina joint; Figure 2D), the leaf tends to bend outward from its vertically oriented position. This requires cell wall loosening for cell expansion on the adaxial side of the leaf (López-Bucio et al. 2002; Eklöf and Brumer 2010). This increased tendency of leaf bending with ageing is also well-known and has been observed and discussed in other species (Duan et al. 2016; Confalonieri et al. 2017).

Studies in rice have shown that leaf erectness is linked to several morphological and developmental features, such as loss of lamina joint structure, including ligule and auricles (Lee et al. 2007), prevention of elongation of parenchyma cells located on the adaxial side, and excess sclerenchyma cell division on the abaxial side of the lamina joint (Zhang et al. 2009; Sun et al. 2015). In contrast, excess in proliferation of parenchyma cells on the adaxial side results in enhanced leaf inclination (Zhao et al. 2010, 2013; Zhang et al. 2015). Abnormal mechanical tissues, such as vascular bundle formation and cell wall composition in the lamina joint also play a crucial role in modification of leaf angle (Ning et al. 2011), indicating a dynamic cytology of the lamina joint where multiple factors are involved in regulating its structure (Zhou et al. 2017).

Tiller development

In addition to the SAM, shoot architecture is further determined by activities of lateral meristems, called axillary meristems (AXMs). An AXM develops in the axil between the stem and developing leaf/coleoptile. Once established, the AXM initiates its own leaf primordia, becoming an axillary bud that may remain dormant or grow out to produce a lateral shoot or tiller, similar in structure to the main culm (Hussien et al. 2014). In contrast to lateral branches in dicots, tillers are produced from the axillary buds in the axil of the leaves from basal phytomers of the stem, corresponding to the crown region where internodes do not elongate (Figure 1D). Tillers produced from the main stem are called primary tillers and those produced from the primary tillers are called secondary tillers, and so on (Hussien et al. 2014). The final number of tillers determines the entire architecture of the mature barley plant, and depends on the number of AXMs, the axillary buds, their outgrowth and subsequent plant dynamics. Tiller outgrowth is especially plastic, being strongly dependent on environmental factors that may promote, or repress lateral shoot development through a complex network of hormonal and regulatory signals (Kebrom et al. 2012). Variation of these parameters leads to high morphological diversity in different genotypes and even within the same genotype.

GENETICS OF BARLEY SHOOT ARCHITECTURE

The following sections provide a review of the genes involved in barley tillering, leaf size and angle, as well as novel phenotyping approaches that may be used in conjunction with cutting-edge genomic tools to characterize mutant and germplasm collections, toward identification of new genes and pathways involved in barley shoot architecture.

Genetic control of leaf size in barley

A recent review (Nelissen et al. 2016) summarizes conserved genetic and molecular mechanisms subtending leaf growth in dicots and monocots, drawing especially on research in *Arabidopsis*, maize and rice. By contrast, only a few genes involved in leaf-size control were identified in barley. This section assesses current knowledge of the genetic determinants of barley leaf dimensions. Studies on mutants and germplasm collections have focused especially on length and width of the lamina for its importance in photosynthesis. Effect on leaf features of major genes for spike morphology and phenology is also discussed.

Barley leaf size mutants

Compared to the wide variety of leaf mutants described in maize (Neuffer et al. 1997), barley leaf mutants are

not so well characterized. A number have been assigned chromosomal positions (Druka et al. 2011) as a starting point for identification of the underlying genes. Information for some of these loci is presented (Table 1; Figure 3). In terms of leaf size, barley mutants have been categorized as having narrow (e.g., *angustifolium*, *fol*), wide (e.g., *broad leaf1*, *blf1*), long (e.g., *curly3*, *cur3*) or short leaves (e.g., *curly dwarf1*, *cud1*), although classification is complicated by pleiotropic phenotypes in leaf and shoot architecture traits that often characterize individual mutants. The following paragraphs focus on two mutants whose causative genes have been functionally characterized, offering insights into the molecular regulation of leaf size.

Recessive *narrow leafed dwarf1* (*nld1*) mutants are characterized by reduced plant height and leaf blade width, but similar blade length compared to wild type (Yoshikawa et al. 2016). The narrow leaf phenotype is caused by a reduction in the number of cells across the lamina, and consistent phenotypic effects in all leaves indicate that normal *Nld1* function is required to promote medial-lateral, but not proximal-distal, lamina growth throughout plant development. In agreement with this interpretation, reduced width is evident already in developing leaf primordia. Histological and morphological analyses demonstrated that *nld1* leaves lack lateral domains, as reflected by the absence of auricles and sawtooth trichomes typically present on wild-type leaf margins. Further analyses demonstrated pleiotropic effects of *nld1* in leaflike organs of the inflorescence. Each barley spikelet comprises two bracts, called palea and lemma, enclosing the stamens, pistil and a pair of lodicules (organs that play a role in flower opening and anther extrusion). The lemma and its distal extension, called an awn, were shown to be homologous to the leaf sheath and blade, respectively (Pozzi et al. 2000). Based on width reduction of the palea and lemma in the *nld1* mutants, wild-type *Nld1* also regulates lateral development of foliar organs during the reproductive phase, although other reproductive organs are not affected (Yoshikawa et al. 2016). Positional cloning demonstrated that the *Nld1* gene encodes a WUSCHEL-RELATED HOMEOBOX (WOX) transcription factor, related to redundant maize factors NARROW SHEATH1 (NS1) and NS2 (Yoshikawa et al. 2016). Several similarities support conserved functions between *Nld1* and its maize homologs (Nardmann et al. 2004). For example, like *NS1/2*, *Nld1* is expressed in lateral domains of leaf primordia to promote margin development; expression is also evident in the marginal edges of palea and lemma, supporting shared functions in margin development of different foliar organs (Nardmann et al. 2004; Yoshikawa et al. 2016). In maize *ns1 ns2* double mutants, leaf founder cells of the marginal leaf domains are not recruited into the leaf primordium because of a failure to downregulate *KNOTTED1* gene expression (Scanlon et al. 1996; Nardmann et al. 2004). It would be interesting to test whether *Nld1* also acts through repression of class I *KNOX* genes such as *Bkn3*, the barley ortholog of maize *KNOTTED1* (Müller et al. 1995). However, the role of *Bkn3* in barley leaf development is not known and speculation about the possible interaction between *Nld1* and *Bnk3* in development of other organs is difficult. A gain-of-function mutation causing ectopic expression of *Bkn3* in the developing lemma was shown to have profound effects on morphogenesis of this organ, including formation of wing-like marginal outgrowths (Müller et al. 1995; Richardson et al. 2016). These findings indicate that control of *Bkn3* expression is needed for correct patterning of the lemma margins, but contrasts with the phenotype of *nld1* lemmas.

Contrary to *nld1*, *broad leaf1* (*blf1*) mutants are characterized by wider leaf blades, as a result of increased numbers of cells along the medial-lateral axis (Jöst et al. 2016). Interestingly, no significant effect was detected on the leaf sheath, whereas the palea and lemma also showed increased width, further supporting the existence of shared genetic mechanisms for control of medial-lateral growth between these organs and leaves. The effect on blade width appears from P6 onward, indicating that *Blf1* functions to limit cell proliferation in the medial-lateral axis, during blade outgrowth, but does not affect recruitment of leaf founder cells as *NS1/2* do (Jöst et al. 2016). The *Blf1* locus encodes an INDETERMINATE-domain (IDD) protein expressed in nuclei of SAM cells, epidermal and subepidermal cells at the base of P2 and P3 leaf primordia and later throughout the epidermis (P5/P6), especially in correspondence with presumptive veins (Jöst et al. 2016). Based on the role of related *Arabidopsis* IDD proteins and expression in presumptive veins, BLF1 was speculated to affect auxin transport (Jöst et al. 2016). Studies on narrow leaf mutants in rice and maize also

Table 1. Barley shoot architecture mutants: description of barley mutants and their relevant genes involved in leaf size/shape, angle, and tillering along with their chromosomal position and phenotype(s)

Gene name	Trait	Gene abbreviation	Chromosome	Gene product annotation	Phenotypes	References
Angustifolium-a	Leaf size	*fol-a*	2HL	No candidate gene	Semi-dwarf, narrow and dark green leaves, other organs reduced in size	Druka et al. (2011)
Broad leaf 2	Leaf size	*blf2*	5HL	No candidate gene	Narrow leaf blades	Druka et al. (2011)
Narrow leafed dwarf 1	Leaf size	*nld1*	5HL	WUSCHEL-RELATED HOMEOBOX 3 (HvWOX3)	Narrow and dark green leaves, degenerated auricles, altered marginal development of lateral organs	Druka et al. (2011); Yoshikawa et al. (2016)
Scirpoides leaf-b	Leaf size	*scl-b*	6HS or 3HL	No candidate gene	Narrow and folded inward leaf blades	Druka et al. (2011)
Scirpoides-a	Leaf size	*sci-a*	5H	No candidate gene	Narrow and folded inward leaf blades, short spikes	Druka et al. (2011)
Scirpoides-b	Leaf size	*sci-b*	1H or 6H	No candidate gene	Narrow leaves, lower leaf blades folded inward	Druka et al. (2011)
Angustifolium-b	Leaf size	*Fol-b*	1HS	No candidate gene	Homozygotes: short thread-like leaves, often die at the 3 to 4 leaf stage; heterozygotes: narrow leaves, small spikes and kernels	Druka et al. (2011)
Broad leaf 1	Leaf size	*blf1*	5HL	INDETERMINATE DOMAIN (IDD) protein	Broad and crinkled leaf blades, wide lemmas, paleas and kernels, light green plant	Jöst et al. (2016)
Eligulum-a	Leaf size	*eli-a*	2HS	RNaseH-like domain containing protein	Semi-dwarf, weak culms, broad leaf blades, liguleless, altered auricles, short peduncle, compact spikes	Druka et al. (2011); Okagaki et al. (2018)
Curly 1/2	Leaf shape	*cur1/2*	3HL	No candidate gene	Curved or wavy tillers, curved or twisted leaves, bent rachis, curly lemmas and awns, curly roots	Druka et al. (2011)
Curly 3	Leaf size	*cur3*	6HL	No candidate gene	Curved stem internodes, long leaves, slightly coiled awns	Druka et al. (2011)
Curly 4	Leaf shape	*cur4*	2HL	No candidate gene	Slightly bent culms at the nodes, coiled or bent leaf blades with wrinkles at the margins, spiral or kinky peduncles, slightly coiled awns, curved roots	Druka et al. (2011)

(Continued)

Table 1. Continued

Gene name	Trait	Gene abbreviation	Chromosome	Gene product annotation	Phenotypes	References
Curly 5	Leaf size	*cur5*	2HS	No candidate gene	Semi-dwarf, short, narrow and partially coiled leaves, short spikes, slightly coiled awns, narrow kernels	Druka et al. (2011)
Curly dwarf 1	Leaf size	*cud1*	5HL	No candidate gene	Short culms, short and twisted leaves, compact spike, short awns, small and round kernels	Druka et al. (2011)
Curly dwarf 2	Leaf size	*cud2*	1HL	No candidate gene	Short culms, curved stem internodes, short and slightly twisted leaves	Druka et al. (2011)
Revoluted leaf 1	Leaf shape	*rvl1*	1HL	No candidate gene	Tips of young leaf blades rolled into a tube through a counter-clockwise spiral	Druka et al. (2011)
Breviaristatum-e	Leaf angle	*ari-e*	5HL	Heterotrimeric G protein AGG3-type γ subunit (HvDep1)	Semi-dwarf, erect leaves, short and erect awns, small kernels	Druka et al. (2011); Liu et al. (2015); Wendt et al. (2016)
Liguleless 1	Leaf angle	*lig1*	2HL	Putative SBP-domain Transcription Factor (HvLG1)	Erect leaf blades, liguleless, auricleless	Rossini et al. (2006); Druka et al. (2011)
Breviaristatum-245	Leaf angle	*ari-u.245*	2HS	Cytochrome P450 CYP85A (HvBRD)	Short culm, shorter rachis internode length, short awns, and acute leaf angles	Kucera et al. (1975); Druka et al. (2011); Dockter et al. (2014)
Brachytic 13	Leaf angle	*brh13.p*	5HS	C-23α-hydroxylase cytochrome P450 (HvCPD)	Reduced culm length due to short upper internodes, irregular rachis internode length, short awns, and acute leaf angles	Franckowiak (1995); Druka et al. (2011); Dockter et al. (2014)
Breviaristatum-o	Leaf angle	*ari-o, brh.a, brh14.q, brh16.v, ert-u, ert-zd*	7HL	Δ5-sterol-Δ24-reductase (HvDIM)	Short culms, shorter rachis internodes, short awns, acute leaf angles, slightly undulating basal leaf blade margins, and a slightly elongated basal rachis internode	Kucera et al. (1975); Druka et al. (2011); Dockter et al. (2014)

(Continued)

Table 1. Continued

Gene name	Trait	Gene abbreviation	Chromosome	Gene product annotation	Phenotypes	References
Semi-brachytic	Leaf angle	*uzu1.a*	3HL	Brassinosteroid receptor (HvBRI1)	Acute leaf angle, short awn, compact spike with dense basal spikelets, irregular elongation of rachis internodes. Slightly udulating leaf blade margins and auricles	Chono et al. (2003); Druka et al. (2011); Dockter et al. (2014)
brassinosteroid deficient1	Leaf angle	*brd1*	2HS	BR-6-oxidase (HvDWARF)	Reduced plant height, shorter awn, and mild dense spike compared to the parent variety Delisa	Gruszka et al. (2011); Gruszka et al. (2016)
Brachytic 1	Leaf angle	*brh1.a, ari-i*	7HS	Heterotrimeric G protein AGG3-type α subunit (HvD1)	Short leaves, culms, spikes, awns, and kernels	Druka et al. (2011); Braumann et al. (2017); Ito et al. (2017)
Brachytic 2	Leaf angle	*brh2, ari-l*	4HL	U-box E3 ubiquitin ligase (HvTUD1)	Reduced plant height and vigor, shorter leaf and kernel, semi compact spikes	Druka et al. (2011); Braumann et al. (2018)
Uniculm 2	Leaf size and tillering	*cul2*	6HL	No candidate gene	No tillers, thick culm, wide leaves	Babb and Muehlbauer (2003); Druka et al. (2011); Okagaki et al. (2013)
Absent lower laterals 1	Leaf size and tillering	*als1*	3HL	No candidate gene	Low tillering, thick culms, wide leaves, altered lateral spikelets development	Babb and Muehlbauer (2003); Dabbert et al. (2009); Druka et al. (2011)
Low number of tillers 1	Leaf size and tillering	*lnt1*	3HL	JuBel2 Homeodomain Transcription Factor	Low tillering, thick culms, wide and dark green leaves	Babb and Muehlbauer (2003); Dabbert et al. (2010); Druka et al. (2011)
Granum-a	Leaf size and tillering	*gra-a*	7H	No candidate gene	Numerous and thin tillers with short internodes, narrow leaves, short spikes, thin and small seeds	Babb and Muehlbauer (2003); Druka et al. (2011); Okagaki et al. (2013)

(Continued)

Table 1. Continued

Gene name	Trait	Gene abbreviation	Chromosome	Gene product annotation	Phenotypes	References
Many noded dwarf 1/5	Leaf size and tillering	*mnd1/5*	2H/7HL	No candidate gene	Dwarf, high tillering, narrow leaves, small spikes	Babb and Muehlbauer (2003); Druka et al. (2011); Franckowiak and Lundqvist (2013)
Many noded dwarf 3	Leaf size and tillering	*mnd3*	4HS	No candidate gene	Dwarf, high tillering, narrow leaves	Franckowiak and Lundqvist (2002); Druka et al. (2011)
Many noded dwarf 6	Leaf size and tillering	*mnd6*	5HL	CYP78A subfamily of cytochrome P450 enzymes (HvMND)	Semi-dwarf, decreased culm internode length, high tillering, erect and narrow leaves, short plastochron, short spikes	Franckowiak and Lundqvist (2002); Druka et al. (2011); Mascher et al. (2014)
Grassy tillers	Leaf size and tillering	*grassy*	unknown	No candidate gene	High tillering, narrow leaves	Druka et al. (2011); Hussien et al. (2014)
Corn stalk 1	Tillering	*cst1*	5HL	No candidate gene	Semi-dwarf, single thick culm (in six-rowed barley)	Druka et al. (2011)
Single internode dwarf 1	Tillering	*sid1*	4HL	No candidate gene	Culms with single elongated internode, lax spikes, weak and partially sterile plant	Druka et al. (2011)
Intermedium spike-b	Tillering	*int-b*	5HL	No candidate gene	Low tillering, altered spikelets architecture	Babb and Muehlbauer (2003); Druka et al. (2011)
Opposite spikelets 1	Tillering	*ops1*	7HS	AT-hook Transcriptional Regulator (HvBaf1)	Low tillering, altered spikelets architecture	Druka et al. (2011); Franckowiak and Lundqvist (2013)

(Continued)

Table 1. Continued

Gene name	Trait	Gene abbreviation	Chromosome	Gene product annotation	Phenotypes	References
Uniculme 4	Tillering	*cul4*	3HL	BOP-like BTB-ankyrin protein	Low tillering, alterations in leaf proximal-distal patterning; liguleless	Babb and Muehlbauer (2003); Druka et al. (2011); Tavakol et al. (2015)
Uzu 1 (semi-brachytic)	Tillering	*uzu1.a*	3HL	BR receptor (HvBRI1)	Semi-dwarf, low tillering, reduced organ length	Chono et al. (2003); Druka et al. (2011); Dockter et al. (2014)
Hordeum vulgare D14	Tillering	*HvD14*	4H	SL receptor α/β hydrolase	Dwarf, high tillering	Marzec et al. (2016)
Intermedium spike-c	Tillering	*int-c*	4HS	TCP Transcription Factor (HvTB1)	High tillering in seedlings, altered spike architecture	Druka et al. (2011); Ramsay et al. (2011)
Intermedium spike-m	Tillering	*int-m*	5HL	No candidate gene	Semi-dwarf, high tillering, altered spike architecture	Babb and Muehlbauer (2003); Druka et al. (2011)
Semidwarf 1	Tillering	*sdw1*	3HL	GA biosynthesis (HvGA20ox2)	Semi-dwarf, high tillering	Druka et al. (2011); Jia et al. (2011); Xu et al. (2017)

Gene nomenclature is based on the NordGen database (https://www.nordgen.org/bgs/).

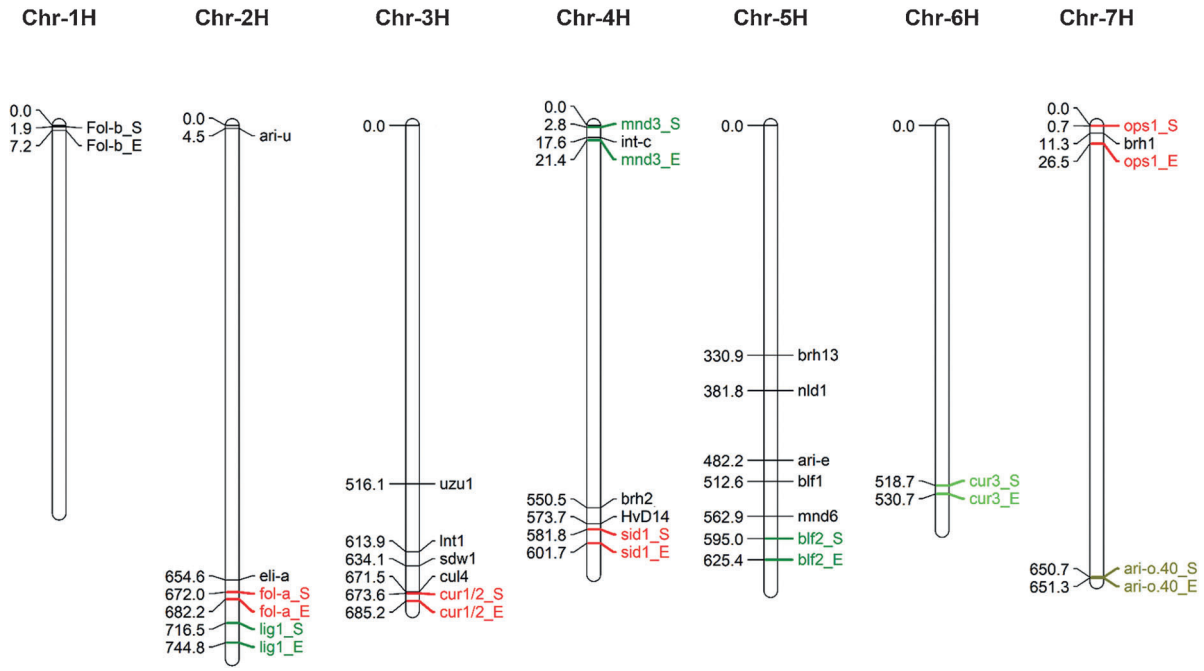

Figure 3. Physical map of barley genes controlling leaf morphology and tiller number
This map illustrates the physical position (Mb) of barley genes controlling leaf angle, leaf size, and tiller number. Only genes with unique positions are shown. Positions of genes in black color were obtained either using BLAST searches against the barley genome available in the IPK database (http://webblast.ipk-gatersleben.de/barley_ibsc/) (Mascher et al. 2017), or the James Hutton Institute database (https://ics.hutton.ac.uk/morexGenes/). Other genes highlighted in red or green color were mapped based on markers developed by Druka et al. (2011) and available in the Nordgen database (https://www.nordgen.org/bgs/). Only genes with an inter-marker distance of 30 Mb or less are represented. The suffix "_S" or "_E" denotes the "start" and the "end" of the area that contains the gene.

show the importance of auxin-related genes in control of leaf width (reviewed in Yoshikawa and Taketa 2017).

Ongoing and future work on additional leaf mutants (e.g., Table 1) will be important to improve our understanding of the genes and genetic interactions that regulate leaf size in barley and their effects on other traits.

GWAS analysis for leaf size in barley

Recent association mapping studies have provided a different perspective, by analyzing natural genetic variation for leaf size, linking it to other morphological and life history traits.

Two major growth habits are known in barley: in winter types, flowering is promoted by an extended period at low temperatures (vernalization), whereas spring barleys do not respond to vernalization. In addition, winter barley flowering is generally stimulated by long days (LDs; Turner et al. 2005). This response to photoperiod (accelerated flowering under LDs) is under the control of the *PHOTOPERIOD-H1* (*Ppd-H1*) gene, encoding a PSEUDO-RESPONSE-REGULATOR (PRR) protein (Turner et al. 2005): the wild-type *Ppd-H1* allele is widespread in winter barley, whereas a natural recessive mutation (*ppd-H1*) reduces photoperiod sensitivity and has been selected in some spring barleys to delay flowering in areas with extended growing seasons (Turner et al. 2005; von Korff et al. 2006; Jones et al. 2008; von Korff et al. 2010; Wang et al. 2010).

Variability for leaf blade width and length, as well as flowering date, was explored by GWAS in a collection of European winter cultivars (Digel et al. 2016): integrating data collected from field-grown plants in two different locations provided robust evidence for the association between all three traits and the *Ppd-H1* locus, whereby the recessive late flowering allele correlated with larger blade width and length. The direct effect of *Ppd-H1* on leaf blade size was confirmed by photoperiod-dependent increases in width and length in *ppd-H1*

spring barley cultivars compared to the respective introgression lines (ILs) carrying the *Ppd-H1* allele (Digel et al. 2016). Although LER was similar in *Ppd-H1* and *ppd-H1* genotypes, longer leaf blades in the spring barley lines were shown to derive from increased phyllochron, extended LED, and increased number of cells along the proximal-distal axis. Under LDs, *ppd-H1* lines produced more leaves compared to *Ppd-H1* ILs, showing that *Ppd-H1* affects multiple aspects of canopy development (Digel et al. 2016). Consistent results on association between *Ppd-H1* and leaf blade area were obtained under LD greenhouse conditions in a spring barley association panel, where additional quantitative trait loci (QTLs) were identified and associated to potential candidate genes (Alqudah et al. 2018). QTLs for flag leaf length were also identified in chromosomes 1H, 3H, and 4H from a recent analysis of a doubled-haploid population (Vafadar Shamasbi et al. 2017).

In addition to growth habit and photoperiod response, spike row-type is another major trait partitioning barley varieties. Two-row cultivars and wild barley accessions carry the wild-type allele of the major row-type gene *VRS1*, while recessive mutants were selected by ancient farmers giving rise to modern six-row cultivars (Komatsuda et al. 2007). A recent study on a worldwide collection of spring barley accessions showed that the *VRS1* gene impacts leaf size, at different developmental stages, with six-row barleys having increased leaf area (LA) compared to two-row (Thirulogachandar et al. 2017). Detailed analyses on *vrs1* mutants and their wild-type backgrounds showed that *VRS1* affects leaf width from as early as the P1 primordium stage, possibly by controlling cell proliferation (Thirulogachandar et al. 2017). Interestingly, QTL analysis in a double haploid progeny detected a major QTL for flag leaf area, width and length in correspondence with the *VRS1* locus (Liu et al. 2015). As row-type genes are also known to affect tillering (Liller et al. 2015), understanding the pleiotropic effects of these genes on tiller number and leaf size is a prerequisite to optimize source-sink relationships and improve yield.

In summary, studies of natural genetic variation are providing essential information on the genetic links between leaf size and other agronomically relevant traits, and lay the foundations for rational development of new crop ideotypes.

Genetic control of leaf angle in barley

Studies in rice have demonstrated that most of the genes associated with lamina joint bending and leaf angle are involved in signalling, or biosynthesis of phytohormones, including brassinosteroids (BRs), gibberellins (GAs), and auxin (IAA) (reviewed by Luo et al. 2016). Among these phytohormones, BRs have the major role in regulating leaf angle (Sakamoto et al. 2006; Hartwig et al. 2011). BRs are endogenous plant hormones which have similar structures to animal steroid hormones and were first characterized by Mitchell et al. (1970).

Many physiological and developmental processes and traits are controlled by BRs, such as cell expansion, stomata development, vascular differentiation, reproductive development, photomorphogenesis, plant height, grain size, and stress responses (Clouse and Sasse 1998; Bishop and Koncz 2002; Fukuda 2004; Yang et al. 2011). In fact, both GAs and BRs are major determinants of plant height or dwarfism with pleiotropic effects on other traits (Mandava 1988; Clouse and Sasse 1998; Taiz and Zeiger 2002; Fujioka and Yokota 2003); however, BR-related genes have a more distinctive effect on leaf angle (Fujioka et al. 1998; Hong et al. 2003). BRs regulate leaf angle, at the lamina joint, by promotion of cell proliferation on the adaxial side and suppression of cell division on the abaxial side (Sun et al. 2015): increased BR content or enhanced BR signaling are associated with lamina joint inclination, or enlarged leaf angle, whereas BR-deficient mutants display erect leaves.

Numerous BR-related genes in rice have been well studied and cloned, and most control leaf angle, including key genes that are involved in BR signalling (*D1*, *BRI1*, *BAK1*, *BZR1*, *DLT*, *GSK2*, *TUD1*, *ILI1*, *IBH1*, *LIC1*, *BU1*, *LC2*, and *OsGSR1*) (Yamamuro et al. 2000; Nakamura et al. 2006; Wang et al. 2006; Bai et al. 2007; Li et al. 2009; Tong et al. 2009, 2012; Wang et al. 2009; Zhang et al. 2009; Zhao et al. 2010; Zhang et al. 2012; Hu et al. 2013) and BR biosynthesis (*BRD1*, *BRD2*, *D2*, *D4*, *OsDWARF*, and *OsDWARF4*) (Hong et al. 2002, 2003, 2005; Tanabe et al. 2005; Sakamoto et al. 2006).

Among barley BR-related mutants, *uzu* was the first to be cloned and shown to correspond to the ortholog of *Arabidopsis* and rice *BRASSINOSTEROID-INSENSITIVE1* (*BRI1*) encoding a BR receptor (Li and Chory 1997; Chono et al. 2003). Barley cultivars carrying the *uzu1.a* allele are widely cultivated in East Asia, mainly due to their short

and sturdy culm that provides lodging resistance, and tolerance to dense planting.

By screening 160 near-isogenic lines (NILs) belonging to the *brachytic (brh)*, *erectoides (ert)* and *breviaristatum (ari)* classes, Dockter et al. (2014) were able to select 16 short-culm mutants fulfilling the BR phenotype criteria, that is, reduced seedling leaf length, reduced number of seminal roots (*brh* group), increased size of the outer metaxylem vessels in seminal roots, lower density of lateral roots, and insensitivity to lamina inclination by exogenous brassinolide in seedlings (*ert* group). By comparing genomic introgressions of different mutant NILs to the Bowman background, different mutants were suggested to be alleles of three BR biosynthetic genes, *BRASSINOSTEROID-6-OXIDASE* (*Ari* or *Brh*/*HvBRD*), *CONSTITUTIVE PHOTOMORPHOGENIC DWARF* (*Brh*/*HvCPD*), and *DIMINUTO* (*Ari*/*HvDIM*), or of the BR receptor gene *Uzu*/*HvBRI1* (Dockter et al. 2014).

Interestingly, *HvDIM* was also associated with biomass-related traits by using a high-throughput phenotyping approach in a diverse collection of two-rowed barleys under both controlled and field conditions (Neumann et al. 2017). Seven major biomass QTLs were identified explaining 55% of the genetic variance at the seedling stage, and 43% at the booting stage. The most important locus for biomass co-located with *HvDIM* independent from phenology: this locus explained approximately 20% of the genetic variance and was shown to act at different growth stages. These results indicate that *HvDIM*, or genes responsible for BR pathway or signalling, could be major targets for the modification of such characters including leaf angle.

In rice, mutation of the *OsDWARF* gene causes reduced plant height due to defective BR synthesis, as well as erect leaves and defects in skotomorhogenesis (dark-adapted morphogenesis) (Hong et al. 2002). Similar to rice, the barley HvDWARF protein is expected to be a BR-6-oxidase, participating in the last step of BR biosynthesis. Two semi-dwarf (BR-deficient) mutants, 522DK and 527DK, from barley variety "Delisa", were identified by exogenous BR assay using a lamina inclination test. Resequencing of the mutant lines identified missense substitutions in different fragments of the *HvDWARF* coding sequence potentially affecting the conserved fragment of the protein (Gruszka et al. 2011). These authors also detected a significant reduction in the transcription level of barley *HvBAK1* in the *HvDWARF* mutant 527DK. *HvBAK1* is highly similar to rice and *Arabidopsis BAK1* genes encoding a component of the BR signalling (Gruszka et al. 2011). The expression of *OsBAK1* was shown to be associated with changes in plant height, leaf erectness, grain morphological features, and resistance to disease (Li et al. 2009). The function of the gene is highly conserved between rice and *Arabidopsis*, but further studies are required in order to know if the function is also conserved in barley.

Rice has two partially redundant C-22 hydroxylases encoding genes called CYP90B2/ DWARF4 and CYP724B1/D11, that catalyse C-22 hydroxylation in a rate-limiting step of BR biosynthesis (Sakamoto et al. 2006). These two genes have distinctive effects on shoot architecture, with DWARF4 playing a predominant role in control of leaf angle as supported by phenotypic effects seen in the knockout mutant: this causes erect leaves, a mild semi-dwarf stature and enhances crop yield, under dense planting, even without increased fertilizers, suggesting allelic variation in this gene may have agronomic value (Sakamoto et al. 2006). Unlike *OsDWARF4*, mutation at the rice gene *D2* causes severe dwarfism. This gene encodes a cytochrome P450 enzyme (CYP90D) involved in the late BR biosynthesis (Hong et al. 2003).

Currently the functions of the barley orthologs of *HvDWARF4* and *HvCYP90D* are unknown as mutants have yet to be identified (Dockter et al. 2014). Future work on their functional characterization may be possible through targeted mutagenesis, for example by genome editing.

The barley *ari.e-GP* semi-dwarf locus was widely used in breeding because of desirable effects, including early flowering, salt tolerance, sturdy culms, and shorter awns. This locus was recently shown to correspond to the barley ortholog of the rice *Dense and erect panicle1* (*Ari-e*/*HvDEP1*) gene encoding a γ subunit of heterotrimeric G proteins: phenotypic characterization showed pleiotropic effects on plant architecture similar to those known in rice (Wendt et al. 2016). Heterotrimeric G proteins consist of three α, β and γ subunits, with the latter (also called AGG3 type) being present only in plants. Their impact on the aboveground plant architecture including plant height, branching, and seed size were studied in model plants (Wendt et al. 2016). Unlike rice, the barley genome contains only one gene encoding an AGG3-type γ-subunit protein and the effect of *HvDEP1* on barley yield is environmentally dependent

(Wendt et al. 2016). Temperature-conditional effects were also described for the *uzu1.a* allele, with larger leaf angle at higher temperatures, but less sensitive mutants such as *ert-ii.79* or *uzu1.256* have been also identified (Dockter et al. 2014). The role of heterotrimeric G proteins appears to be important in leaf angle and plant architecture, as was supported by further studies.

Recently, Ito et al. (2017) explored the barley *Brh1* locus and identified some mutants resembling the rice dwarf mutant, *daikoku* (*dwarf1*; *d1*) (Akemin 1925; Kadam 1937). The *daikoku* mutant has a mutation in the heterotrimeric G protein α subunit (Gα) (Ashikari et al. 1999, Fujisawa et al. 1999). Genetic studies have located *Brh1* on chromosome 7H (Li et al. 2002; Dahleen et al. 2005; Druka et al. 2011), and a candidate gene approach identified a gene coding the Gα in close proximity to *Brh1* (*HvD1*), indicating that the *brh1* mutant has mutations in the Gα gene, similar to rice *d1* which is involved in BR signaling.

Another *brh* mutant was also characterized by Braumann et al. (2018): studying a group of allelic *brh2* and *ari-l* mutants in the background of cv. Bowman, lines BW050 (*ari-l.3*), BW090 (*brh2.b*) were shown to respond to exogenous brassinolide in a leaf lamina-inclination assay, indicating that these genes are not in the BR signalling pathway. Based on previous mapping of the *Brh2* locus on chromosome 4H (Takahashi et al. 1971), a candidate gene was identified as the ortholog of rice *OsTUD1*. The *HvTUD1* gene encodes a protein with 92% identity to OsTUD1 which encodes a U-box E3 ubiquitin ligase (Hu et al. 2013). The *brh2* and *ari-l* mutants display BR-deficient phenotypes and responded to exogenous application of brassinolide (Dockter et al. 2014), indicating they are related to BR biosynthesis.

Novel phenotyping approaches for leaf morphological traits

Classically, measurements of leaf length and width can be taken with a ruler (Figure 2E), but these will not fully describe leaf shape, perimeter and area. Measuring leaf angle is even more complex as it requires knowledge on the 3D single leaf surface, in a complex canopy architecture, with changing leaf orientations both in space and time (Wirth et al. 2001; Müller-Linow et al. 2015). This complexity is further increased by the effect of environmental cues, such as irrigation, light condition, and temperature (Müller-Linow et al. 2015). Lack of accurate measurement is a bottleneck that will negatively affect linking phenotype to genomics data in plant genetics and breeding (Houle et al. 2010).

The most widely used measurements of leaf angle are the leaf insertion angle (LI) and leaf inclination angle (LIA) (Confalonieri et al. 2017). Other important parameters of the vegetation canopy directly related to grain yield are derived from LIA. LI is a direct measurement and is the angle between the proximal part of the leaf with respect to the stem (α, Figure 2A). This value, especially in cases of species with curved leaves, like barley, wheat, and oat, does not provide the actual distribution of photosynthetic tissues (Confalonieri et al. 2017). LIA, is defined as the angle between the zenith direction and the leaf surface normal, measured along the whole leaf length (θ_L, Figure 2F).

Assuming a uniform leaf azimuth distribution, for flat leaves without curvature, the LIA along the whole leaf is expected to be uniform and can be also representative even for unmeasured leaves. In such cases, LIA and leaf size become independent of each other and no additional measurement of leaf size (length and width) is required. However, in crops with narrow and curved leaves, like barley, the LIA will not be unique and differs along the leaf (Zou et al. 2014). In addition, the inclination angle and leaf weight along the leaf segments (larger leaf width, higher weight) are no longer independent. In such cases, and when the values are extracted from photographic images, the leaves are visually divided into small segments and both area and leaf inclination angles are recorded at each segment (Zou et al. 2014). The relative values of the leaf segment areas become the weights for calculation of the statistical characteristics of LIA.

Another approach for this situation was proposed by Confalonieri et al. (2017), where they developed a bending index (BI), which is derived from the LIA values to derive the structural characteristics of the vegetation canopy. The most commonly used characteristic of the canopy structure is the leaf angle distribution (LAD). In reality, direct LAD measurement in the field (e.g., using a clinometer) is time-demanding and tedious, as it requires field-based sampling.

Indirect measurements of LAD, for example leaf mean tilt angle (MTA), the central moment of LAD, also have been associated with large uncertainties and

require specialized equipment. Therefore, mathematical descriptions were introduced to approximate canopy LAD. In most plant canopies, the LAD function is the probability density function of θ_L, assuming that the distribution of LIA values approaches azimuthal symmetry (de Wit 1965). There are several distributions to describe the probability density function of LIA, such as Wit's six special (de Wit 1965), Beta (Goel and Strebel 1984), ellipsoidal (Campbell 1990), Verhoef's linear combination of trigonometric (Verhoef 1997), and rotated-ellipsoidal functions (Thomas and Winner 2000). Among them, the Beta distribution with two parameters has been shown to be the best for describing the probability density function of LIA (Wang et al. 2007), especially for complex canopies with various fractions of LA and leaf angles. LAD influences the leaf area index (LAI), an important index with relevance to many biological processes, such as photosynthesis, transpiration, respiration, and grain yield. Assuming the two-parameter Beta distribution, the distribution function of θ_L can be estimated as follows:

$$f(t) = \frac{1}{B(\mu,\nu)}(1-t)^{\mu-1}(t)^{\nu-1} \quad (1)$$

where, $t = 2\theta_L/\pi$. The two parameters μ and ν are calculated as

$$\mu = (1-\bar{t})\left(\frac{\sigma_0^2}{\sigma_t^2}-1\right) \quad (2)$$

$$\nu = \bar{t}\left(\frac{\sigma_0^2}{\sigma_t^2}-1\right) \quad (3)$$

where $\bar{t}$ and σ_t^2 are the mean and variance of t, respectively. σ_0^2 is the maximum variance of t calculated as $\sigma_0^2 = \bar{t}(1-\bar{t})$. $f(t)$ can be used to calculate the G-function, the most common function to describe the leaf angle effect on radiation attenuation (Ross and Nilson 1965). The other important parameter representing the degree of erectness of the leaf is Campbell's one-parameter χ of the ellipsoidal leaf angle distribution. χ is used for the calculation of extinction coefficient (K), an important variable to correctly estimate canopy LAI (see below).

Several authors defined K as the proportion of shadow area by the canopy on the horizontal surface divided by the total area of leaves, or the average projection of leaves onto a horizontal surface (Monsi and Saeki 1953; Monteith and Unsworth 1973; Campbell 1986). Assuming that the distribution of LA follows the distribution of the surface on spheres or cylinders, the K values can be approximated (Monteith and Unsworth 1975; Campbell and Thomson 1977).

LAD and LAI are closely related and are among the major determinants of canopy light absorption (Monsi and Saeki. 1953; de Wit 1965; Duncan et al. 1967; Anderson and Denmead 1969). A model to describe light interception, by the plant canopy, can be described as Beer's law:

$$S_b(LAI) = S_b(0)\exp(-K * LAI) \quad (4)$$

In this model, $S_b(0)$ denotes the photon flux density (PFD) of light penetration above the canopy on a horizontal surface, $S_b(L)$ is the flux density below LAI, K is the light extinction coefficient and depends on the species composition of the canopy (Monsi and Saeki 1953; Hikosaka and Hirose 1997). Erect canopies with predominantly vertical leaf angles have lower K values and *vice versa*.

Many studies have shown that K is among the most important traits that determine canopy photosynthesis. Assuming the same LAI, in canopies with high K values, leaves at the uppermost layer receive stronger PFD than those in canopies with low K (Hikosaka and Hirose 1997). Thus, when the LAI is low, horizontal leaves are preferred, as they would have higher light extinction, resulting in higher light capture. LAI is a critical parameter, along with the leaf angle, for manipulation of light transmission and photosynthesis (de Wit 1965).

Manual measurement of leaf angle has a major drawback because it is labour- and time-consuming or even destructive, for example manual direct measure of LAD using inclinometers in contact with the leaf surface (Campbell and Norman 1998). In addition, traditional methods (e.g., inclinometer or protractor) overestimate the angle due to the tendency of the leaves to curve, which affects the light interception in a 3D distribution of leaves in the canopy (Tadrist et al. 2013; Confalonieri et al. 2017).

Novel phenotyping methods are important in order to gain a more complete understanding of the genetic determinants of leaf architecture traits. High-throughput phenotyping is becoming the preferred approach in capturing variability and precise

phenotyping of various traits, such as stress responses, root and shoot architecture, photosynthetic capacity, and growth and developmental traits, especially in breeding programs where hundreds, or even thousands of genotypes must be evaluated under either greenhouse or field conditions (Araus and Cairns 2014). The concept of "phenomics", introduced in plant science by Finkel (2009), is an attempt to integrate different technologies (high-resolution cameras, imaging sensors, software and processing data tools, and computer and mobile devices) to facilitate and accelerate plant phenotyping. Novel approaches are largely based on image-based phenotyping techniques, which have the added benefit of allowing simultaneous extraction of data for different traits, including leaf angle and size.

2D imaging

Visible light imaging: this process, also known as color digital camera imaging, employs cost-effective digital cameras, or red-green-blue / color-infrared cameras, made up mostly from silicon sensors (charged-coupled device or complementary metal-oxide semiconductor arrays). These cameras are sensitive to light wavelength ranges visible to the human eye (400–750 nm). These sensors allow for detecting 2D images and present color information of the object with similar wavelengths to the human eye. These cameras can be used for analyzing numerous characters of complex structures, and different scales, such as leaf morphology, shoot biomass, growth dynamics, imbibition and germination rates, flowering, plant height, spike morphology, and root architecture (Li et al. 2014).

The acquired images can be processed with software that can extract several parameters, such as counting pixels to determine percent canopy cover, based on the ratio of the selected versus the total number of pixels, per image. Regarding individual leaf size traits, as an example, 2D image analysis was used for accurate measurement of detached leaf blades to characterize the *blf1* mutant in barley (Jöst et al. 2016). If the images from multiple viewing angles (left, right, and top sides) are available, then some commercial systems can be used to determine a mathematical relationship between three images to extract shoot biomass and total LA.

To derive leaf angle parameters, such as LIA, the color images can be processed, based on a spatial matrix, with values of photon fluxes in red, green, and blue wavelengths. The skeleton of images is extracted to obtain the structure of stem and leaves, and LIA are obtained by calculating branched angles of the skeleton. This type of 2D imaging technique is well suited for physiological parameters, but has some drawbacks; for example measurement of the leaves with curved features is difficult from such 2D images. Another problem is that, in field canopies, leaves usually overlap each other and, hence, it is difficult to abstract the leaves or shoots, resulting in biased measurements of biomass and LAI. Soil background also presents some challenges for image processing and its segmentation (Fiorani and Schurr 2013; Li et al. 2014; Rahaman et al. 2015).

3D imaging

To overcome biases associated with the 2D techniques, 3D-based imaging is recommended, as it can more accurately address the above-mentioned problems. These imaging techniques provide useful information on plant architecture, the fundamental target of plant breeders for high-yield breeding, biomass, and plant shape or volume. In 3D imaging, electromagnetic energy is projected onto an object and the reflected energy is recorded in the active form (Sansoni et al. 2009). There are many 3D imaging techniques which can be grouped into several categories and are interesting for measurement of leaf angle and leaf size, such as stereo imaging, time-of-flight (ToF), laser sensors, and Kinect sensors (Müller-Linow et al. 2015; Li et al. 2017).

Stereo imaging or structure-from-motion (SFM): This is an imaging technique where images are collected from two cameras that are mounted a few metres above the canopy and then 3D point clouds of plants are generated (Gibbs et al. 2017). These stereo images are further processed, using computer pipelines, for the segmentation of leaves and calculation of leaf orientation. This approach was further developed on different sugar beet varieties to quantify leaf surface properties within natural canopies, via polygon smoothing or surface model fitting (Müller-Linow et al. 2015). Based on the resulting surface meshes, LAD are calculated at the whole leaf level. This method was proven to be useful to differentiate various genotypes under different seasonal and fertilization conditions.

Laser sensors: This system is based on light detection and ranging (LiDAR), where laser beams are projected onto plants. The projected laser beams (scattered energy from the plant or the surface) can then be measured using triangulation and a dense 3D map of point clouds is constructed (Kjaer and Ottosen 2015; Li et al. 2017). This laser sensor approach can measure the distance between sensor and the object, based on the elapsed time between the emission and return of laser pulse from the sensor (the ToF method), or based on trigonometry (Omasa et al. 2007). Having this information, LiDAR can record the 3D coordinates (XYZ), 3D structure properties, and intensity information of an object. The resultant surfaces can then be constructed and multiple traits, such as LA, LAI, and LIA can be extracted. A high-resolution portable version of the LiDAR was developed for cereals, including barley, in which the barley plants were scanned in multi-view and their 3D was reconstructed (Paulus et al. 2014). These authors were able to extract multiple characters, including leaf angle and area and proposed the method for high-throughput phenotyping of different barley organs.

ToF cameras or range imaging techniques: These are distance-based systems that can measure the speed, or ToF from the camera to the plant. These cameras, similar to laser techniques, provide suitable tools for measuring biomass, plant volume, and traits that require 3D information. ToF cameras are based on active lighting and are therefore sensitive to environmental conditions, such as sunlight, humidity, precipitation, and dust. The sensor region must be shaded to reduce the impact of environmental variations (e.g., sunlight or presence of persistant dust). Therefore, cross-sensitivities must be considered when designing a specific phenotyping platform.

Cell phone-based and other techniques: This approach provides low-cost, rapid, and reliable instruments for field phenotyping. To date, few such instruments have been developed and proposed as reliable measurement tools for extracting multiple parameters on canopy structure (Escribano-Rocafort et al. 2014; Confalonieri et al. 2017). One example is PocketPlant3D, a newly developed cell phone-based phenotyping instrument that can extract both LI (the first value at the proximal parts between the stem and the leaf, Figure 2A) and LIA (Figure 2F) (Confalonieri et al. 2017). In addition, the app provides indirect measurements of several important canopy parameters, such as parameters of ellipsoidal distribution and BI. Another advantage of the app is that it is inexpensive, does not require specific skills, and data are automatically geo-referenced and stored without any further processing. The cell phone must be positioned parallel to the leaf and pointed toward the lamina joint without touching the leaf surface. The device can then be moved along the leaf while keeping it parallel to the lamina until reaching the leaf tip.

Unfortunately, the use of 3D imaging techniques is expensive and resource-demanding, and for many crops this information is still lacking (Zou et al. 2014). As an alternative, Ryu et al. (2010) introduced a photographic measurement of LADs based on a leveled digital camera, by combining red-green-blue images with an LAI-2000 plant canopy analyzer, allowing for rapid and accurate measurement of LAD. The method was extended to short canopies, such as field crops including barley and wheat and successfully shown to be applicable in such canopies (Zou et al. 2014). In this method, MTA can be estimated from light reflectance data in blue, red and near infrared wavebands (Zou et al. 2014).

Overall, innovative phenotyping methods provide powerful means to perform large-scale screens of mutagenized and germplasm collections to accelerate discovery of barley genes involved in leaf growth and angle by positional cloning and association mapping approaches.

Genetics of barley tillering

Tillering is a highly complex trait and its genetic determinants are best studied in rice, while knowledge in barley is relatively limited (Hussien et al. 2014). However, recent progress in cloning and characterization of tillering mutants is beginning to unravel the genetic regulation of tillering in barley (Table 1).

Barley tillering mutants

Barley geneticists have identified and characterized numerous mutants that show either increased or decreased tiller numbers, and many have been introgressed into the genetic background of cv. Bowman to produce NILs for accurate phenotypic comparisons (Druka et al. 2011). These mutants can be classified into four categories: (i) mutants which fail to

develop axillary buds and, consequently, develop one single culm without any tillers, for example *uniculm2* (*cul2*; Babb and Muehlbauer 2003); (ii) mutants that produce low tiller numbers due to weak axillary bud outgrowth and suppressed formation of secondary tillers, for example *low number of tillers1* (*lnt1*; Dabbert et al. 2010), *absent lower laterals1* (*als1*; Dabbert et al. 2009), and *uniculme4* (*cul4*; Tavakol et al. 2015); (iii) mutants displaying modestly reduced tillering, for example *intermedium-b* (*int-b*) and the already mentioned *semibrachytic* (*uzu*) mutant (Babb and Muehlbauer 2003); and (iv) mutants presenting high tiller numbers, including mutations at the genes *Granum-a* (*gra-a*), *Grassy tillers* (*Grassy*), *Intermedium-c* (*Int-c*), *Many noded dwarf1* (*Mnd1*), and *Many noded dwarf6* (*Mnd6*) (Babb and Muehlbauer 2003; Druka et al. 2011). However, the identification and classification of mutants for tillering is challenging due to the presence of genes that have pleiotropic effects on this trait. For example, the barley *Int-c* gene, the homolog of maize *Teosinte Branched1* (*TB1*; Studer et al. 2011), controls lateral spikelet development and also represses tillering at early stages of barley development (Ramsay et al. 2011). Morphological characterization of barley tillering mutants demonstrated their effects on multiple traits. For example, *cul2* mutants exhibit disarrangement in the distal end of the developing inflorescence and altered timing of reproductive developmental steps (Babb and Muehlbauer 2003). In rice, the *MONOCULM 1* (*MOC1*) gene which controls tiller number is also involved in inflorescence architecture (Li et al. 2003b). Both *moc1* and *cul2* mutants show some similarities in their phenotypes, such as lack of axillary bud development, reduction in plant height, decreased branching of the inflorescence, and epistatic effects to mutations in other loci. However, AXMs are not initiated in *moc1*, whereas in *cul2* AXMs are present in leaf axils but do not produce axillary buds, which indicates that *cul2* acts at the stage of bud development (Hussien et al. 2014). Presently, no candidate gene has been identified for the *cul2* mutant, but the locus was located near the centromeric region of chromosome 6H (Okagaki et al. 2013).

The *als1*, *lnt1*, and *cul4* loci, which have been mapped on chromosome 3H, develop only 1–3 tillers (Babb and Muehlbauer 2003; Druka et al. 2011). *Lnt1* was proposed to correspond to the *JuBel2* gene, encoding a homeodomain transcription factor of the Three Amino acid Loop Extension (TALE) superfamily (Müller et al. 2001; Dabbert et al. 2010). *Cul4* was shown to encode a BTB-ankyrin transcriptional co-activator related to *Arabidopsis* BLADE-ON-PETIOLE1 (BOP1) and BOP2 (Tavakol et al. 2015). Morphological analyses demonstrated that *Cul4* affects multiple aspects of tiller development, regulating the number of AXMs that form in each axil and the formation of secondary buds on primary tillers, as well as being required for proper tiller outgrowth (Tavakol et al. 2015). Consistent with these findings, the gene is expressed at the leaf axil boundary, prior to AXM formation and later more diffusely in the axillary bud (Tavakol et al. 2015). Interestingly, *cul4* mutants lack ligules and in wild-type plants the *Cul4* gene is expressed in developing ligules, suggesting a shared genetic control of tiller and ligule development (Tavakol et al. 2015). Intriguingly, another liguleless mutant, *eligulum-a* (*eli-a*), was recently identified as a suppressor of the *cul2* mutant (Okagaki et al. 2018). Plants carrying mutations in the *Eli-a* gene exhibit reduced stature and fewer tillers, as well as abnormality of the leaf blade-sheath boundary. The *Eli-a* gene encodes a protein of unknown function containing an RNaseH-like domain and is conserved in different plant species: the transcript is expressed at the preligule boundary and the developing ligule; however, in contrast to *Cul4*, it is not expressed at the AXM boundary in the leaf axil, so the role of *Eli-a* in tiller development remains unclear (Okagaki et al. 2018).

By contrast to the previously mentioned mutants, recessive mutations in genes like *Mnd1* (7HL), *Mnd6* (5HL) and *Gra-a* (3H) show excessive development of tillers and semi-dwarf phenotypes (Druka et al. 2011). In *mnd6* mutants, side branches develop from aerial nodes (Babb and Muehlbauer 2003), whereas *gra-a* mutants unveil increased numbers of AXMs and axillary buds, with an infrequent appearance of two SAMs (Babb and Muehlbauer 2003). The gene for the *mnd6* locus, named *HvMND*, encodes a member of the CYP78A subfamily of cytochrome P450 enzymes (Mascher et al. 2014). Although the genes for *mnd1* and *gra-a* mutations have not been identified, their phenotypes are similar to those of rice mutants defective in the biosynthesis or signalling of strigolactones, a class of plant hormones that repress shoot branching (Ishikawa et al. 2005; Zou et al. 2006; Arite et al. 2007; Waters et al. 2017). Characterization of these mutants may be useful for the study of the strigolactone pathway in barley.

Noteworthy is a recent study reporting the first characterization of a strigolactone-related gene in barley, *HvD14*, encoding an alpha/beta hydrolase highly related to the rice strigolactone receptor (Marzec et al. 2016).

GWAS and QTL analyses of tillering in barley

Analysis of tiller number in barley revealed the presence of significant genetic variation in both germplasm collections and bi-parental populations (Abeledo et al. 2004; Borràs et al. 2009; Alqudah and Schnurbusch 2013; Alqudah et al. 2016). A considerable effect of row type on tiller number was demonstrated under various growth conditions (Alqudah and Schnurbusch 2013). Consistent with this finding, tiller number was shown to be affected by the allelic status of the *VRS1* gene (Liller et al. 2015).

Genetic variation in reproductive development may also cause variation in tillering. Many studies, including natural and biparental populations, have identified QTLs or marker associations for tillering in close proximity to genes responsible for flowering time and vernalization (Karsai et al. 1999; Borràs et al. 2009; Alqudah et al. 2016; Ogrodowicz et al. 2017). Increased tillering in barley was commonly correlated to strong vernalization requirement and reduced photoperiod sensitivity (Karsai et al. 1999; Wang et al. 2010). The major vernalization genes *Vrn-H1* and *Vrn-H2* and the photoperiod response gene *Ppd-H1* were shown to be significant in tiller production (Karsai et al. 1999; von Korff et al. 2006; Wang et al. 2010). It is likely that *Ppd-H1*, *Vrn-H1*, and *Vrn-H2* regulate tillering via controlling *FT*, the florigen gene acting in the apical meristem to enhance the transition from vegetative to reproductive growth (Corbesier et al. 2007; Tamaki et al. 2007).

A recent GWAS study using a 9 k gene-based SNP chip (Comadran et al. 2012) has shown that grouping accessions according to photoperiod sensitivity (*Ppd-H1* vs *ppd-H1*) and row type (*VRS1* vs *vrs1*) allows detection of novel QTLs for tiller number (Alqudah et al. 2016). Another GWAS study on 97 two-rowed spring barley lines also detected several QTLs for tillering at different developmental stages (Neumann et al. 2017).

Novel phenotyping approaches for tillering

Generally, tiller number is scored manually by counting the shoots from a single plant, commonly at harvest time as an end-of-life trait. However, this method is time-consuming and laborious. There is strong interest in developing automated plant phenotyping methods allowing dynamic measurements throughout plant development and in response to environmental conditions. However, to the best of our knowledge, few methods have been introduced for automated measurement of tiller number.

Boyle et al. (2016) developed an estimator of tiller number and applied it to wheat in experiments at the UK National Plant Phenomics Centre (NPPC), a facility that offers different types of imaging modalities under controlled environments. This method uses ribbon detection approaches to identify and count tillers, based on visible light images, applying *ad hoc* filters to distinguish them from leaves. Generally, multiple images are taken every day for each plant and the average of the approximate data obtained from each view angle is the best-estimate of tiller count per plant, for a specific day.

Another method proposed by Głąb et al. (2015) to count tiller number in grass species includes three main steps: (i) bunches preparation for analysis; (ii) imaging; and (iii) computer analysis of the image. At the initial step, the bunches of grass need to be cut, keeping 5 cm of aboveground straws. The observation area is next cleaned by removing the shoots after cutting and coloring the cut culms with white acrylic paint. The resulting white coloring helps to obtain contrasted images to separate the target features from the background. In the second step, images of grass bunches are taken from a 150 cm distance. In the third step, digital images are processed with Aphelion Dev 4.2.0 software for analysis. Image analysis can be further divided into the following four major steps/functions for filtering, segmentation, measurements and object separation, respectively (Wojnar and Majorek 1994; Głąb et al. 2015).

In the first step, the *ImgColorToRGB* function divides the raw images into three visible color bands, that is, red (R), green (G) and blue (B). Then this RGB image is further converted to grey images, depending on the blue band. Next, the *ImgMaximumContrastThreshold* function operates by automatically selecting a threshold to maximize the average contrast of edges detected in the image by the threshold value. In the segmentation step, the objects of interest (i.e., painted culm cross-sections) turn red, keeping the background a black color. The *ImgOpen* function is used to eliminate smaller objects which are less than 200 pixels, so that

the tiller number can be counted. Finally, the *ObjCompute* function calculates measurements (including shape parameters) for different spatial objects. A limitation of this method is that it is destructive and mostly applicable at the end of the plant life.

As grass species differ for their tillering behavior, validation and optimization of these methods would probably be required to apply them to barley.

IMPLICATIONS FOR BREEDING

Crop production is expected to increase in order to meet the food demands of the growing global population (Hunter et al. 2017). Furthermore, climate changes, such as strong winds, rising temperatures and heavy rainfall, have potential negative effects on crop production and food security (IPCC 2015; Ray et al. 2015). As a major food crop, barley has also experienced vulnerability to climate change, such as temperature increment (Ray et al. 2015; Rötter et al. 2015; Hunter et al. 2017). The Green Revolution brought agronomic and genetic advancements (Peng et al. 1999; Spielmeyer et al. 2002); however, new genotypes capable of performing under future climate changes and low agronomical inputs are still required in order to reduce environmental impacts (Dawson et al. 2015; Rockström et al. 2017).

The concept of "ideotype breeding" is an alternative/complementary breeding strategy to traditional selection for crop yield (Donald 1968). With the knowledge of the genetic and physiological mechanisms controlling plant performance, this concept aims at designing crops best adapted to target environments, through a combination of predefined traits. With the term "ideotype", literally "a form denoting an idea", breeders and scientists indicate a biological model with a defined and predictable behavior in a specific environment (Donald 1968; Martre et al. 2015). Ideotype breeding has been successfully applied, for example in rice (IRRI 1989; Peng et al. 2004), where it benefited from the integration of different approaches: (i) investigation of plant trait interactions and trade-offs in different agro-climatic conditions; (ii) high throughput sequencing, genome annotation and dense marker panels; (iii) availability of a congruous level of allelic diversity from a range of genetic resources (including mutants, landraces and crop wild relatives); and (iv) advanced phenotyping methods for accurate phenotypic evaluation (Donald 1968; Tao et al. 2017).

A plant ideotype is defined by model characters, which can be either morphological, physiological, agronomical or biochemical, contributing to crop yield and performance in a given environment (Kawano et al. 1966; Thorne 1966). Ideotype breeding can also be applied to develop dual-purpose crops, providing both grains and biomass for bioethanol fermentation, nickel from phyto-recovery and forage (Li et al. 2003a; Giunta et al. 2015; Townsend et al. 2017).

Designing a single ideotype for a given crop for a wide range of areas is restrictive since the fluctuations and changes in temperature, precipitation and soil composition will influence morphological and physiological plant features to different extents. Thus, development of an ideotype must take into account the target environment and consider future climate conditions based on simulation models (Rötter et al. 2015). Furthermore, crop modelling approaches are useful to predict the performance of different phenotypes for each crop/ecological area to support the design of appropriate breeding programs and crop management systems (Rasmusson 1991; Martre et al. 2015).

Choosing model characters for ideotype breeding

Many features can be taken as model characters that can influence the overall performance of the plant (Nadolska-Orczyk et al. 2017). In ideotype breeding, it is necessary also to consider the correlations among different traits, often resulting from pleiotropy, epistasis or linkage of the underlying loci, and compensatory physiological and developmental mechanisms (Chandler and Harding 2013; Rebolledo et al. 2013). As a successful example, Green Revolution cultivars, with their reduced plant stature, showed an increase in grain yield performance in intensive agriculture compared with traditional cultivars, and this was mainly due to the improved lodging resistance and enhanced nitrogen use efficiency (Gooding et al. 2012; Xu et al. 2017). In the following sections, we focus on the target traits already discussed, overviewing how the optimization of these traits can improve crop performance and yield (Zhu et al. 2010; Mathan et al. 2016; Wang et al. 2018).

Tillering

As each tiller has the potential to form a fertile inflorescence, the number of tillers is a critical

determinant of grain yield (Jia et al. 2011). However, tillering potential should be carefully balanced, as a reduced number of tillers will produce few panicles and loss of yield, whereas excessive number of tillers will result in unfertile tillers, diverting resources from developing spikes (Peng et al. 1994; Kennedy et al. 2017). Furthermore, high tillering generally has negative relationships with other traits related to biomass (e.g., plant height) and lodging resistance (e.g., stem diameter) (Tripathi et al. 2003; Kuczyńska et al. 2013). Finally, a crowded canopy will result in a humid micro-environment ideal for spreading of diseases (Mew 1991).

As a quantitative trait, tillering is very plastic and is determined by various factors, such as environment and local agronomic practices (del Moral and del Moral 1995; Zhong et al. 2003). However, several agronomic and genetic studies have indicated that the complexity of this trait can be dissected. For example, beside the abovementioned genes (see section on Genetics of barley tillering), the role of a vernalization requirement and photoperiod sensitivity on tiller development has been documented. These findings indicate that genes that influence the vernalization requirement and flowering can be manipulated by choosing appropriate alleles to reduce the plasticity of tillering.

In barley, Karsai et al. (2006) showed that, upon vernalization, winter-type varieties (*Vrn-H2*) produce, on average, more fertile tillers compared with the spring types, under long-photoperiod conditions. Moreover, winter barleys produce more tillers under long compared to short photoperiods (Karsai et al. 2006). Beside growth habit, row type has also been demonstrated to affect tillering. Two-rowed cultivars have, on average, a higher number of fertile tillers compared to six-rowed (Janoria Jabalpur 1989; del Moral and del Moral 1995).

Genetic studies in wheat indicate that mutation in the *Tiller inhibition* (*Tin*) gene results in lower numbers of tillers but a higher ratio of productive tillers, to total tiller number, as well as larger spikes and grains (Moeller et al. 2014 and references therein; Hendriks et al. 2016). Duggan et al. (2005) proposed tiller reduction with the *tin* gene to improve production under terminal drought conditions, taking advantage of the reduction in non-productive tillers and a limited consumption of soil water before anthesis. However, results on performance of *tin* lines, under drought conditions, are somewhat contradictory (Mitchell et al. 2013).

An interesting example of tillering manipulation in a breeding program is represented by the rice New Plant Type (NPT), developed at the International Rice Research Institute (IRRI). Breeding of the NPT began early in the 1990s, with an aim of developing a new rice ideotype with improved characteristics (Peng et al. 2008; Khush 2013). The aim was to reduce the number of unproductive tillers, as the younger tillers make very little contribution to yield, but compete for nutrients (Peng et al. 2008). Due to the poor yield achieved in the first trial, tiller number was increased in a second generation of NPT rice lines; this was achieved by crossing the first generation NPT lines with elite Indica varieties.

In a four-field experiment, conducted in 2002/2003 in flooded fields, the second-generation NPT out-yielded the first-generation NPT (Peng et al. 2004). This yield increase was due to improved panicle number and grain-filling capacity. In a similar vein, the aim of the Chinese "super rice" breeding program was to combine alleles for establishment of rice lines with optimal architecture and number of tillers; this program resulted in a significant increase in grain yield (Qian et al. 2016; Wenfu et al. 2007).

Erect leaves and canopy architecture

Position, size and metabolic features of leaves are excellent targets for improving canopy architecture, to achieve higher photosynthesis rate in CO_2 rich environments that are expected in the coming decades (Horton 2000; Song et al. 2013; Ort et al. 2015). As an example, the "smart canopy" ideotype considers leaf position and morphology, proposing plants with erect leaves at the top of the canopy as a means to increase photosynthetic efficiency, in combination with biochemical traits (Innes and Blackwell 1983; Araus et al. 1993; Richards and Lukacs 2002; Ort et al. 2015). Several studies support the importance of leaf angle manipulation in different cereal crops (e.g., Gardener 1966; Zhang et al. 2017).

In barley, allelic variation in genes involved in the BR pathway provides opportunities for manipulating leaf angle. For example, *uzu* barleys are highly resistant to lodging and are productive in dense planting conditions, due to the short-culm trait and erect leaves (Dockter et al. 2014); for this reason, *uzu*-type barley was grown in 70% of Japanese barley fields in the 1930s. As mentioned above, some *uzu* alleles exhibit temperature-sensitivity, whereas others are more

stable (Dockter et al. 2014). In rice, Sakamoto et al. (2006) also reported that mutations in another BR pathway gene, *OsDWARF4*, affect canopy architecture, via leaf inclination, with positive effects on grain production. A rice canopy model elaborated by Long et al. (2006) defines cultivars with narrow leaf angle at the top of the canopy in order to reach elevated rates of CO_2 uptake. Among various morphological traits, the "super rice" ideotype defined angles for the three apical leaves as 5° for the flag leaf, 10° for the 2nd and 20° for the 3rd (Peng et al. 2008). In China, 34 "super rice" hybrid varieties were commercially released between 1998 and 2005 and sown on an area of 13.5 million hectares, increasing rice production by 6.7 million tons (Peng et al. 2008).

CONCLUSION AND PERSPECTIVES

Recently, crop modelling revealed its potential as a tool to support ideotype design for crop breeding (Li et al. 2012; Rötter et al. 2015; Gouache et al. 2017). Simulation testing within a series of environments through an ensemble of models was proposed as a promising way to investigate ideotype design and reduce uncertainties in the simulations (Wallach et al. 2016; Tao et al. 2017).

It is important to understand that the selected traits are not supposed to work individually, in agreement with the Gestalt rationale that "*the whole is more than the sum of its parts*" (Lim et al. 2007). In order to optimize interactions among plant traits, symmetries, contrasts and positive or negative correlations must be investigated in detail. In this respect, high throughput phenotyping technologies can play a major role to evaluate complex and unexplored traits on a breeding scale (Fiorani and Schurr 2013). At the same time, identification and preservation of allelic diversity, present in landraces, wild relatives and mutant collections, is important for efficient exploitation of genetic diversity (Tavakol et al. 2017; Szareski et al. 2018). This exploitation can be facilitated by state-of-the-art genomic tools, which can be employed for mapping of relevant genes (Figure 3) and systematic exploration of germplasm collections. Such approaches are being harnessed to better our understanding of the complex mechanisms linking shoot architecture and plant performance, with an objective to develop useful information to establish new crop ideotypes.

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