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Short title:

***Ppd-H1* controls leaf size in barley**

Title:

Photoperiod-H1 (Ppd-H1) locus controls leaf size

One sentence summary:

Photoperiod-H1 controls leaf size by influencing the rate of leaf development in barley.

Authors:

Benedikt Digel[1a,b,c], Elahe Tavakol[1de], Gabriele Verderio[1d], Alessandro Tondelli[f], Xin Xu[g], Luigi Cattivelli[f], Laura Rossini[xdh], Maria von Korff[xa,b,c]

a Max Planck Institute for Plant Breeding Research, D-50829, Cologne, Germany;

b Institute of Plant Genetics, Heinrich-Heine-University, 40225 Düsseldorf, Germany;

c Cluster of Excellence on Plant Sciences "From Complex Traits towards Synthetic Modules" 40225 Düsseldorf, Germany;

d Università degli Studi di Milano – DiSAA, Via Celoria 2, 20133 Milan, Italy;

e Shiraz University, Department of Crop Production and Plant Breeding, College of Agriculture, Shiraz, Iran;

f Council for Agricultural Research and Economics (CREA), Genomics Research Centre, 29017 Fiorenzuola d'Arda, Italy;

g Hubei Provincial Key Laboratory for Protection and Application of Special Plants in Wu ling Area of China, Key Laboratory of State Ethnic Affairs Commission for Biologica Technology, College of Life Science, South-Central University for Nationalities, Wuhan 430074, China;

h Parco Tecnologico Padano, Via Einstein, Loc. Cascina Codazza, 26900 Lodi, Italy;

1 - authors contributed equally to the paper

x – corresponding authors

Footnotes:

Author's contributions:

B.D., E.T., G.V., L.R. and M.K. planned and designed the research. B.D., E.T., G.V., A.T. and X.X. performed the research, conducted the field work, collected and analysed the data. B.D., E.T., G.V., A.T., L.C., L.R. and M.K. interpreted the data and wrote the manuscript.

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Corresponding authors:

Laura Rossini (laura.rossini@unimi.it), Maria von Korff (korff@mpipz.mpg.de)

ABSTRACT

Leaf size is a major determinant of plant photosynthetic activity and biomass, however, it is poorly understood how leaf size is genetically controlled in cereal crop plants like barley (*Hordeum vulgare*).

We conducted a genome wide association analysis (GWAS) for flowering time, leaf width and length in a diverse panel of European winter cultivars grown in the field and genotyped with a SNP array. The GWAS identified *PHOTOPERIOD-H1* (*Ppd-H1*) as a candidate gene underlying the major QTL for flowering time and leaf size in the barley population. Microscopic phenotyping of three independent introgression lines (ILs) confirmed the effect of *Ppd-H1* on leaf size. Differences in the duration of leaf growth and consequent variation in leaf cell number were responsible for the leaf size differences between the *Ppd-H1* variants. The *Ppd-H1* dependent induction of the *BARLEY MADS BOX* genes *BM3* and *BM8* in the leaf correlated with a reduction in leaf size and leaf number.

Our results indicate that leaf size is controlled by *Ppd-H1* and photoperiod dependent progression of plant development. The coordination of leaf growth with flowering may be part of a reproductive strategy to optimize resource allocation to the developing inflorescences and seeds.

INTRODUCTION

Leaf size is a major determinant of plant photosynthetic activity and performance and contributes to yield in crops (Zhang *et al*., 2015). The leaf of cereal crops is strap-shaped and organized in two main regions: the proximal sheath encloses the stem, while the distal blade projects out of the stem axis to optimize light interception and photosynthesis. The blade/sheath boundary is marked by the ligule and two auricles, epidermal structures that hold the stem. Leaf growth in grasses is initiated by the division of cells at the base of the leaf (Esau 1977; Kemp 1980). Leaves grow in a linear process as cells are displaced in parallel longitudinal files by the continuous production and expansion of cells (MacAdam *et al*., 1989). This creates a clearly defined spatial pattern of cell development along the longitudinal axis with a basal division zone, where meristematic cells divide and elongate, and a distal elongation-only zone, where cells undergo postmitotic elongation (Skinner & Nelson 1995). The location where cells stop expanding marks the end of the leaf growth zone and the initiation of the differentiation zone. Leaves are initiated at the flanks of the shoot apical meristem (SAM) in a regular spatial pattern, so-called phyllotaxy and the time interval between the emergence of two successive leaves on a culm is called phyllochron (Wilhelm & McMaster 1995).

The final size of leaves is tightly controlled by genetic factors that coordinate cell proliferation and cell expansion. Mutant screens in rice and maize have identified a number of genes required for leaf development, for which loss-of-function mutations result in extreme mutant phenotypes (Scanlon *et al*. 2003; Chuck *et al*. 2007; Fujino *et al*. 2008; Qi *et al*. 2008; Zhang *et al*. 2009). Genes, encoding transcription factors such as KNOTTED-LIKE HOMEOBOX (KNOX) factors, proteins involved in hormone biosynthesis and response and miRNAs have been shown to play a role in leaf organogenesis across different species including maize and the model dicot plant *Arabidopsis thaliana* (Hay & Tsiantis 2010; Gonzalez & Inzé 2015; Sluis & Hake 2015).

Large genetic variation in leaf size has been identified in natural populations of rice and maize (Tian *et al*., 2011; Li *et al*., 2012; Yang *et al*., 2015; Zhang *et al*., 2015). QTL (quantitative traits loci) studies in both species revealed a complex genetic basis for leaf size variation (Peng *et al*., 2007; Farooq *et al*., 2010; Jiang *et al*., 2010; Tian *et al*., 2011; Wang *et al*., 2011). The majority of the identified QTLs did not coincide with any of the major known leaf development genes as identified in mutant screens (Scanlon *et al*., 2015). Consequently, different genes might underlie leaf size variation between and within species.

While natural differences in leaf size have been well characterised in rice and maize, natural variation in leaf size and its genetic basis are still poorly understood in temperate cereal crop plants such as barley (*Hordeum vulgare* ssp. vulgare). Barley is characterised by two major growth types as determined by natural variation at the two vernalisation genes *Vrn-H1* and *Vrn-H2* (Yan *et al*., 2003, 2004; Trevaskis *et al*., 2006). Winter types accelerate flowering after a prolonged period of cold (vernalisation), whereas spring barley does not respond to vernalisation. Winter barley usually shows a strong promotion of flowering in response to long days (Turner *et al*., 2005). Photoperiod response, rapid flowering under long days is determined by natural variation of the *PHOTOPERIOD-H1* (*Ppd-H1)* gene (Turner *et al*., 2005). The wild-type allele is prevalent in winter barley, while a natural mutation in the conserved CCT domain of *Ppd-H1* causes a delay in flowering under LDs and is predominant in spring barley from cultivation areas with long growing seasons (Turner *et al.*, 2005; von Korff *et al.*, 2006, 2010; Jones *et al.*, 2008; Wang *et al.*, 2010). While the genetic basis of flowering time variation in response to vernalisation and photoperiod is well characterised in barley, it is not known if variation in reproductive development affects leaf growth and size.

The aim of this study was to identify genomic regions and genes controlling natural variation in leaf size in a diverse collection of winter barley cultivars. By combining a genome-wide association analysis and detailed phenotyping of introgression lines, we establish a novel link between reproductive development and leaf size in barley.

RESULTS

Phenotypic variation in the field experiments

To characterise natural variation in leaf size and its correlation to variation in reproductive development, we examined time to flowering (FD), leaf width (LW) and length (LL) in a diverse collection of winter barley cultivars grown in the field at two different locations in Italy and Iran (Table 1). In both locations, large phenotypic variances were observed for FD, LW and LL. In Italy, plants flowered between 202 and 230 days after sowing (DAS) with a mean of 209 DAS. In Iran, the number of days from sowing to flowering varied from a minimum of 175 DAS to a maximum of 192 DAS with a mean of 181 DAS. LW was on average 17.8 mm in Italy with a minimum of 12.7 mm and a maximum of 24.5 mm. In Iran, LW varied between 8.3 and 19.3 mm with an average of 13.0 mm. LL, only scored in Iran, varied between 130 and 236 mm, with a mean of 177 mm.

FD, LL and LW showed high heritability values of 89%, 96% and 82%, respectively. The analysis of variance demonstrated that the genotype accounted for 82%, 80% and 31% of the total phenotypic variance for FD, LL and LW, respectively (Table S1). Consequently, the genetic components accounted for a large proportion of the total phenotypic variation for each trait. Positive correlations were found between FD and LW (0.32, p-value=0.0001) and between FD and LL (0.34, p-value=0.0001). A correlation coefficient of 0.77 (p-value < $2x10^{-16}$) was observed between LW and LL. Taken together, our analysis revealed a high genetic variation for leaf size parameters and these were positively correlated with time to flowering across both locations.

Population structure, Linkage Disequilibrium and GWAS

To identify the genetic basis of leaf size variation in the winter barley cultivar collection, we analysed population structure and performed a genome wide association analysis with 2,532 iSELECT SNPs and three diagnostic markers in *Vrn-H1*, *Vrn-H2* and *Ppd-H1*. The principle component analysis indicated the existence of two major sub-populations, which separated the two-rowed and six-rowed barley cultivars (Fig. 1). The two-rowed barley cultivars showed a higher genetic diversity with a mean correlation coefficient of 0.39 as compared to the six-row barley genotypes mean genetic correlation coefficient of 0.48.

In order to verify the growth habit of cultivars in our germplasm set, all lines were genotyped with diagnostic markers for *Vrn-H1*, *Vrn-H2* and *Ppd-H1* (Table S2). The germplasm set revealed three different *Vrn-H1* haplotypes. The majority of cultivars were characterised by winter *Vrn-H1* alleles, with 117 cultivars (56 six-rowed and 61 two-rowed) carrying the full length *W-1A* allele and 14 cultivars (12 six-rowed and 2 two-rowed) carrying the winter allele *W-5C*, which is characterised by a deletion of 486 bp in the first intron (Cockram *et al*., 2009). Seven cultivars (5 six-rowed and 2 two-rowed) were characterised by the spring *Vrn-H1* allele (Cockram *et al*., 2009). A full deletion of the *Vrn-H2* locus, which is typical for spring barley, was identified in 5 out of 138 cultivars, including three carrying a winter *Vrn-H1* allele. The *Vrn-H1* and *Vrn-H2* spring alleles had a low frequency, but were equally distributed between the two-rowed and six-rowed varieties. Consequently, seven of the 138 genotypes were characterised as spring types, while five genotypes were identified as facultative cultivars which are characterised by a deletion of *Vrn-H2* and the winter allele at *Vrn-H1* (Fig. S1A) (von Zitzewitz *et al*., 2005). Genotyping with the diagnostic marker in the CCT domain of *Ppd-H1* showed that the mutated *ppd-H1* allele was present in approximately 25% of the winter barley lines and was preferentially detected in two-rowed genotypes (Table S2). However, barley genotypes with *Ppd-H1* or *ppd-H1* haplotypes did not form

separate clusters in the principle component analysis (Fig. S1B). In summary, only a low number of genotypes, two out of 138, carried spring alleles at *Vrn-H1* and *Vrn-H2*, while 25% of the germplasm set was characterised by a mutated *ppd-H1* allele which has been associated with late flowering under LDs (Turner *et al*. 2005).

The average linkage disequilibrium decay in the population was determined at 5.5 cM based on the r^2 between all intra-chromosomal pairs of loci (Fig. S2). The GWAS across both locations and for each location separately revealed two significant genomic regions on chromosome 2HS associated with FD, one region on 2HS for LL and two genomic regions on 2HS and 4HL for LW (Fig. 2, Fig. S3, Table 2). On chromosome 2HS, seven linked SNP markers at position 19.9 cM on the POPSEQ reference map (Mascher *et al*., 2013) were associated to FD, LW and LL (Table 2): SNP22, BK_12, BK_14, BK_15, BK_16, BOPA2_12_30871 and BOPA2_12_30872 designed on the genic sequence of *Ppd-H1*. All these seven markers were in complete linkage disequilibrium and included the diagnostic marker SNP22, which was proposed by Turner *et al*. (2005) to be responsible for flowering time variation under LDs (Table S2).

Genetic variation at *Ppd-H1* was associated with an average difference of two days in flowering time in the winter barley population. In addition, genetic variation at *Ppd-H1* caused an estimated variation of 8 mm in LL and of 1 mm in LW (Table 2). Variation at *Ppd-H1* accounted for 23%, 6% and 5% of the genetic variation for FD, LL and LW, respectively (Table S1). A second association on 2HS, at the position 58.78 cM close to the *HvCEN/EPS2* locus (Comadran *et al*., 2012) was identified for FD, but not LL or LW. Furthermore, for LW a significant association was found with the marker SCRI_RS_157866 at 110.2 cM on chromosome 4H which caused an average difference in LW of 0.7 mm. Variation at *Vrn-H1* and *Vrn-H2* was not associated with FD, LL or LW. In summary, variation at the photoperiod response gene *Ppd-H1* exhibited pleiotropic effects on FD, LL and LW in our barley germplasm collection under different field conditions.

Since a flowering time gene co-located with a QTL for leaf size, we recalculated the GWAS with FD as a covariate to test if leaf size was primarily controlled by overall plant development (Fig. S4). LW was still significantly influenced by the *Ppd-H1* locus and the marker SCRI_RS_157866 at 110.2 cM on chromosome 4H. However, the associations for LL fell below the significance threshold, possibly because LL was only measured in one environment.

Variation for leaf size in Ppd-H1 ILs

In order to further dissect the effect of natural variation at *Ppd-H1* on leaf size, LL and LW were analysed under LDs in three pairs of spring barley cultivars and their respective ILs (Fig. S5). The

spring barley genotypes and ILs differed for the SNPs associated with variation in FD, LW and LL in the barley germplasm collection: Scarlett, Triumph and Bowman were homozygous *ppd-H1* while respective ILs were homozygous *Ppd-H1* (Table S3).

The spring barley genotypes flowered significantly later than their respective ILs under LDs (Fig. S6). In addition, the spring barley cultivars exhibited a significant increase in LW and LL of the largest leaf as compared to their respective ILs under LDs (Fig. 3). Genetic differences in LL varied from average 121 mm between Scarlett and S42-IL107, to 113 mm between Bowman and BW281 and 42 mm between Triumph and Triumph-IL. Genetic differences in LW varied from on average 3.2 mm between Scarlett and S42-IL107, to 2.2 mm between Bowman and BW281 and 1.7 mm between Triumph and Triumph-IL. Differences in LL were larger and less variable between the ILs and recurrent parents, we therefore concentrated our further analyses on the effect of *Ppd-H1* on LL and leaf elongation rates. Leaf blade size was dependent on the leaf position on the main shoot in all genotypes. Successive leaves exhibited a continuous increase in LL with each node producing a leaf of gradually increasing length until a plateau was reached and, under LD conditions, leaf blade size declined again (Fig. 4, A and B; Fig. S7, A-D). Under LD conditions, the maximum leaf size was reached with leaves 5-6 in the spring barley cultivars and with leaves 4-5 in the ILs and was thus dependent on the total number of leaves per main culm (8-11 in spring barleys *vs.* 7-9 in ILs). Leaf blades were significantly longer in the spring barley cultivars as compared to their respective ILs starting from the third developing leaf in Scarlett/S42-IL107 and Bowman/BW281 and starting from the fifth to sixth leaf in Triumph/Triumph-IL under LDs (Fig. 4A; Fig. S7, A and C).

To further support our findings that variation at *Ppd-H1* controls leaf shape, we also examined LL under SDs. Since *Ppd-H1* is only functional and controls development under LDs, we predicted that the introgression lines would not differ from their parental lines in leaf shape under SDs. Under SDs, plants of all six genotypes did not flower, as the inflorescences of the main shoots were aborted before reaching the flowering stage and leaf emergence stopped before the flag leaf became visible (data not shown). In general, under SDs more leaves were produced on the main culm as compared to LDs. However, as expected for the LD dependent function of *Ppd-H1*, no differences in leaf size were detected between ILs and the respective recurrent parents under SD (Fig. 4B; Fig. S7, B and D).

In order to further understand how *Ppd-H1* affects leaf growth and size, we examined the phyllochron in the spring barley lines and ILs. Under LDs, the spring barley genotypes showed an increased phyllochron as compared to their respective ILs. A difference in phyllochron was observed for all leaves in S42-IL107/Scarlett or for leaves 4-8 in BW281/Bowman and leaves 6-11

in Triumph-IL/Triumph (Fig. 4C; Table 3; Fig. S7, E and F; Table S4). The rate of leaf emergence, and thus phyllochron, was constant for all leaves in the three ILs under LDs. In contrast, the phyllochron was dependent on the position of the leaf on the main shoot in the spring barley genotypes under LDs and in both, the spring barley cultivars and the ILs, under SDs (Table 3; Table S4).

In order to examine whether an increased phyllochron was associated with a decreased LER or a delayed termination of leaf elongation, i.e. leaf growth, we scored LER in Scarlett and S42-IL107 of all leaves on the main shoot under LDs and SDs (Fig. 5A; Fig. S8; Table S5). Genetic variation between Scarlett and the IL did not affect LER, but the duration of leaf growth as exemplified for leaf 5 in Fig. 5A. Under LDs, leaf growth terminated earlier in S42-IL107 than Scarlett, whereas under SDs no significant difference in the duration of leaf growth was observed between genotypes. However, leaf growth stopped earlier under LDs than SDs as observed from leaf 8 (Fig. S8). Under LDs, the delayed termination of leaf growth in the spring barley genotypes with the mutated *ppd-H1* allele were associated with a reduced interstomatal cell size and an increased number of cells per leaf along the proximal/distal axis (Fig. 5, B-D). Under SDs, leaf cell size was not affected by allelic variation at *Ppd-H1* (Fig. S9). This suggested that the effect of *Ppd-H1* on leaf size is based on differences in cell proliferation and possibly linked to its effects on floral transition and/or inflorescence development. Consistent with this view, we detected differences in the expression of the floral integrator homolog and targets of *Ppd-H1* in the leaf, *FLOWERING LOCUS* 1 (FT1), and the AP1/FUL-like genes *BM3*, *BM8* and *Vrn-H1* (Fig. 6). *FT1* expression increased with increasing leaf number under LDs and was significantly higher in the leaves of the ILs than in the spring barley lines. While *FT1* expression was higher in the IL in all leaves harvested during development as compared to Scarlett, expression of the AP1/FUL-like genes *BM3*, *BM8* and *Vrn-H1* was upregulated in the IL starting from leaf 2-3, when also the leaf size differences between genotypes became apparent.

Taken together, allelic variation at *Ppd-H1* had significant effects on LW, and in particular on LL under LDs, but not under SDs. Variation at *Ppd-H1* affected phyllochron and leaf elongation ceased later in Scarlett than in the introgression line. In contrast, LER was not affected by variation at *Ppd-H1*. Differences in cell number along the proximal/distal leaf axis between genotypes were only partially compensated by the increased cell length of the ILs with the photoperiod responsive *Ppd-H1* allele. Thus, variation at *Ppd-H1* affected LL by affecting the cell number, cell size and the duration of leaf blade elongation. In addition, leaf size differences correlated with the *Ppd-H1*-dependent expression difference of *BM*-like genes in the leaf.

DISCUSSION

Leaf size is an important agronomic trait, as it relates to radiation use efficiency and transpiration rate directly affecting photosynthesis and response to water limitations. Variation in these traits is of key importance for winter barley varieties cultivated in Mediterranean areas with terminal drought. The first goal of the present study was to explore natural genetic variation for leaf size in winter barley and identify genomic regions associated with leaf size variation in the field through an association mapping approach.

Most association studies in barley were carried out on panels of spring accessions or mixed panels of winter and spring accessions (Rostoks *et al*., 2006; Cockram *et al*., 2008; Stracke *et al*., 2009; Pasam *et al*., 2012; Tondelli *et al*., 2013). In this study, we used an autumn sown panel of winter cultivars where two-rowed and six-rowed types were equally represented, as reflected by analysis of population structure. A strong genetic differentiation between two- and six-rowed barley genotypes has already been detected in other studies (Rostoks *et al*., 2006; Cockram *et al*., 2010; Comadran *et al*., 2012; Pasam *et al*., 2012; Munoz-Amatriain *et al*., 2014) and derives from modern breeding practices: contemporary European spring and winter varieties descend from a small number of successful European landraces selected around 100 years ago (Fischbeck, 2003). In our panel, the two-rowed barley sub-group showed a relatively higher genetic diversity as compared to the six-rowed group. This may be due to the use of spring two-rowed varieties in breeding of winter two-rowed varieties potentially increasing genetic diversity (Fischbeck, 2003). Based on genotyping of *Vrn-H1* and *Vrn-H2*, seven (5 six-rowed and 2 two-rowed cultivars) of the 138 genotypes were characterised as spring types, while three genotypes were identified as facultative cultivars which are characterised by a deletion of *Vrn-H2* and the winter allele at *Vrn-H1* (von Zitzewitz *et al*., 2005). However, these cultivars clearly clustered with winter barley genotypes in a PCoA analysis of a comprehensive panel of spring and winter varieties (data not shown). A reduced vernalisation response in winter barley might offer advantages in autumn-sowing areas with mild winters, which are not as cold as those in more northern or continental climates (Casao *et al*., 2011). The mutated *ppd-H1* allele was present in approximately 25% of the winter barley lines and was preferentially detected in two-rowed genotypes used for malt production. This might be a consequence of the introgression of malting related traits from spring genotypes into winter cultivars. Whether the mutation in *Ppd-H1* has an impact on grain characteristics and, ultimately, on malting quality has yet to be demonstrated.

The association analysis demonstrated that under vernalising conditions, the *Ppd-H1* locus had the strongest effect on flowering time in our barley germplasm panel, with the recessive *ppd-H1* delaying flowering time and causing an increase in leaf size. While variation at the *Ppd-H1* locus affected both flowering time and leaf size, a second locus on 2H harbouring the floral repressor CENTRORADIALIS (*HvCEN)* (Comadran *et al*., 2012), was only associated with flowering time, but not leaf size. These results suggested that *Ppd-H1*, but not *HvCEN* influenced leaf size, possibly because these genes act at different developmental stages and in different tissues. While *Ppd-H1* is primarily expressed in the leaf where it controls photoperiod-dependent flowering, *TERMINAL FLOWER 1*, the Arabidopsis homolog of *HvCEN* acts as a repressor of floral development in the shoot apical meristem (Bradly *et al*., 1997; Ohshima *et al*., 1997).

The effects of the *Ppd-H1* locus on leaf size were confirmed in three pairs of ILs, where the *ppd-H1* allele increased leaf blade size under long, but not short days. Therefore, the effect of *Ppd-H1* on leaf growth was correlated with its long day-specific effect on reproductive development. Differences in leaf size were already evident at floral transition (three leaf stage in ILs), suggesting that processes linked to phase transition affected leaf size. Ontogenetic changes in leaf size and morphology (heteroblasty) have been associated with the transition from vegetative to reproductive development (Goebel 1900; Jones 1999). In Arabidopsis and grasses such as maize and rice, early flowering correlates with a reduction in leaf size suggesting that the fate of existing leaf primordia is changed with the transition to flowering (Poethig *et al*., 1990, 2010; Hempel & Feldman, 1994). The microRNAs, miR156 and miR157, and their direct targets, the SQUAMOSA PROMOTER BINDING PROTEIN (SBP/SPL) family of transcription factors have been identified as major regulators of vegetative phase change in a range of plants (Wu and Poethig, 2006, Chuck et al., 2007, Fu et al., 2012; Xie et al., 2012). A decrease in the expression of miR156 is linked to juvenile to adult transition and heteroblastic change in leaf shape resulting in two or multiple, discrete leaf types. However, in our experiments *Ppd-H1*-dependent differences in leaf size were rather cumulative and increased with leaf number on the main stem. While *Ppd-H1* does not have a strong effect on vegetative to reproductive phase change, it strongly controls inflorescence development and stem elongation (Digel et al. 2015). Differences in the rate of leaf emergence, in the duration of leaf growth and in the final leaf cell number suggested that *Ppd-H1* affected leaf size by influencing the rate of age-dependent progression of leaf development. Pleiotropic effects of flowering time regulators might be a consequence of changes in source-sink relationships triggered by the transition from vegetative to reproductive growth or inflorescence growth. On the other hand, flowering time genes may play dual roles to control and coordinate leaf development and phase

transitions at the shoot apical meristem, as indicated by studies in dicots. For example, a recent study demonstrated that natural variation of leaf shape in *Cardamine hirsuta* is controlled by the vernalisation gene *Flowering Locus C,* which is known to contribute to variation in flowering time in the *Brassicaceae* (Cartolano *et al*., 2015). In addition, *SINGLE FLOWER TRUSS* (*SFT*), the tomato ortholog of *FT*, affected flowering time, leaf maturation, and compound leaf complexity (Lifschitz *et al*., 2006; Shalit *et al*., 2009). These studies focused on species with compound leaves, whose shape and size arise from spatiotemporal regulation of morphogenetic activity within the leaf primordium as determined by prolonged expression of meristem-related gene functions (Sluis & Hake, 2015). However, to our knowledge, no link between specific flowering time regulators and leaf size had been reported in simple-leaf grasses. Interestingly, in our study the expression of *FT1*, and the putative downstream targets *Vrn-H1*, *BM3* and *BM8* in the leaf negatively correlated with the duration of leaf growth and final leaf blade size. In particular, the AP1/FUL like genes *BM3* and *BM8* were upregulated in the IL (*Ppd-H1*) compared to Scarlett (*ppd-H1*) starting from leaf three when also leaf size differences between genotypes became apparent. In *Arabidopsis*, FT and its targets, the AP1/FUL MADS box genes, are best known for their role in floral transition and floral development (Turck *et al*., 2008). However, studies in *Arabidopsis* have suggested that *FT* and the downstream *AP1/FUL* targets also control leaf size and shape (Teper-Bamnolker & Samach, 2005). Indeed, *FT* restricted leaf size via upregulation of the MADS box gene *FUL* and a *ful* loss-of-function mutation suppressed leaf size reduction caused by FT overexpression (Teper-Bamnolker & Samach, 2005). Similarly, variations in *BM* expression correlated with the genetic differences in the timing of leaf development, suggesting that duration of cell proliferation and leaf maturation were controlled by *Ppd-H1* and possibly downstream variation in the expression of *FT1* and *BM* genes. To our knowledge, our work provides the first link between specific flowering time genes and regulation of leaf growth in grasses, suggesting that monocots and dicots may share common genetic modules to coordinate leaf development and reproductive timing. This information will be important for the targeted manipulation and optimization of individual plant organs in plant breeding programs.

MATERIALS AND METHODS

Plant materials and phenotyping

A panel of 138 European winter barley cultivars (65 two-rowed and 73 six-rowed) released between 1921 and 2006 (Table S2) was evaluated at two experimental field stations in Fiorenzuola d'Arda,

Piacenza, Italy, (44°55'N and 9°53'E) and at the University of Shiraz, Iran (29°50'N and 52°46'E) during the growing season 2012-2013. The experimental fields were organized in a randomized complete block design with three replicates; each plot consisted of 4 rows of 2 m with 40 cm spacing between rows and 30 cm between plants within a row. Seeds were sown in mid-October and the beginning of November 2012 in Italy and Iran, respectively.

Flowering date (FD) was recorded when 60% of spikes were at the anthesis stage (Zadoks stage 68, Zadoks *et al*., 1974). Leaf blade width (LW) and length (LL) were measured on three to five mature plants/plot. For each plant, the longest and widest leaf of a culm was measured for a total of 3-5 culms per plant. LW was measured at the widest point of the blade and LL was measured from the ligule to the tip of the blade. In the experiment in Italy only LW was measured while in Iran both LW and LL were scored.

In order to confirm the effects of the major association with leaf size parameters at the candidate gene *Ppd-H1*, we analysed three pairs of barley near isogenic lines: spring cultivars with a mutated *ppd-H1* allele and derived backcross lines carrying introgressions of the dominant *Ppd-H1* allele. These spring barley genotypes were Scarlett, Bowman and Triumph and the derived introgression lines (ILs) were S42-IL107, BW281 and Triumph-IL, respectively. S42-IL107 and BW281 carry introgressions of the dominant *Ppd-H1* allele from wild barley (Schmalenbach *et al*., 2008; Druka *et al*., 2011). Triumph-IL is a BC4F2 selected IL derived from the Double Haploid (DH) population of a cross between Triumph and the winter barley cultivar Igri (Laurie *et al*., 1995) and was kindly provided by David Laurie (John Innes Centre, Norwich). The size of the introgression segments was determined by high-resolution genotyping using the Barley Oligo Pool arrays (Illumina Golden Gate) (Schmalenbach *et al*., 2011; Druka *et al*., 2011; Digel *et al*., 2015).

LL and LW of the largest leaf on the main shoot were scored in the three pairs of spring barley and ILs at full expansion by measuring the distance from the ligule to the tip of the fully elongated leaf blade and the widest point of the leaf, respectively, in 10-30 replicated plants grown under LD. In addition, plants of Scarlett/S42-IL107 were germinated in two independent experiments under short-day (SD) conditions (8h light/16h dark, PAR 270µM/m²s, 22°C/18°C) in a growth room, with 40 and 12 pots per genotype in the first and second experiment, respectively. After germination, half of the pots per genotype were transferred to long-day (LD) conditions (16h light/8h dark, PAR 270µM/m²s, 22°C/18°C) or cultivation was continued under SD. The number of leaves emerged from the main shoot (LEM) were recorded every two to three days under LD and every three to four days under SD. Leaves were scored as fully emerged as soon as the ligule was visible. If a leaf was not fully emerged, it was scored as 0.25, 0.5 or 0.75, relative to the length of the fully emerged leaf

blade of the preceding leaf. In addition, LL was determined for each leaf on the main culm in Scarlett/S42-IL107. The experiment was repeated for all six genotypes scoring heading date, LEM and LL of 5 replicated plants under SD and LD.

In parallel to scoring LEM, three plants per genotype were dissected and the developmental stage of the main shoot apex was determined according to the scale of Waddington *et al*. (1983), which is based on the morphogenesis of the shoot apex and carpels.

Phyllochron was calculated from the rate of leaf emergence (LEM) on the main culms as the inverse of the leaf emergence rate, i.e. the slope of the linear segments obtained for LEM from the regression models (see statistical analyses - Phenotype).

Furthermore, leaf elongation rates (LER) in Scarlett/S42-IL107 were obtained from one of the experiments. During leaf blade emergence from the leaf sheath, i.e. the ligule of the emerging leaf was not yet visible, LER was determined by measuring the length from the ligule of the preceding leaf to the leaf tip of the emerging leaf every two to three days under LD and every three to four days under SD. After leaf blade emergence, the measurement was continued from the ligule to the tip of the expanding leaf blade.

To determine leaf cell number and leaf cell size, five plants per genotype were germinated and grown under SD and LD, respectively. Cell length of 50 interstomatal cells of leaf 5 were determined at 33% and at 66% of the total leaf length, respectively, as described in Wenzel *et al*. (1997). Copies of the adaxial epidermal cell layer were transferred to microscopy slides by applying a solution of celluloseacetate (5% in acetone) to the leaf surface and transferring the solidified cellulose-layer to the slides using transparent duct tape. Cell length was determined on the copied epidermal surface using a light microscope (Nikon SMZ18). The number of interstomatal cells per leaf was estimated by: leaf length [mm] x 1000 / cell length [µm].

RNA extraction, cDNA synthesis and Real Time qRT-PCR

For Scarlett and S42-IL107 we harvested leaf samples from every leaf on the main shoot at the time of their complete emergence from the leaf sheath to analyse expression of *FLOWERING LOCUS T* (*FT1), Vernalisation-H1 (Vrn-H1), BARLEY MADS BOX 3 (BM3)* and *BM8* by quantitative RT-PCR (qRT-PCR) relative to the expression of the housekeeping gene *Actin*. Extraction of total RNA, reverse transcription and Real Time qRT-PCRs on cDNA samples using gene-specific primer pairs as listed in Table S6 were performed as described by Campoli *et al*. (2012). To estimate the concentrations of target transcripts in the cDNA samples dilution series of plasmids containing the

respective target gene amplicons were also subjected to qRT-PCR analysis. qRT-PCR assays were conducted on the LightCycler 480 (Roche; software version 1.5).

Genotyping

Genomic DNA was extracted from young leaves of the winter barley population using Qiagen DNeasy 96 or Tepnel Nucleoplex plant DNA extraction kits according to manufacturers' instructions (Qiagen, Hilden, Germany, or Tepnel Life Sciences PLC, Manchester, UK).

Genotyping was carried out at TraitGenetics (GmbH, Gatersleben, Germany) using a set of 7,864 high-confidence gene-based SNPs incorporated in the Illumina iSELECT Chip (Illumina Inc., Comadran *et al*., 2012). Genotype calling was performed as described in Comadran *et al*. (2012). A total of 6,810 SNPs were successfully assayed in the 138 winter barley genotypes. Filtering was carried out to only include 4,257 markers positioned in the POPSEQ map (Mascher *et al*., 2013) and to exclude SNPs with >5% missing data or <10% Minimum Allele Frequency (MAF). Finally, a total of 2,532 iSELECT SNPs which were mapped on the POPSEQ reference map (Mascher *et al*., 2013) were employed for all following analyses.

Among them, SNP markers BK_12, BK_14, BK_15, BK_16, BOPA2_12_30871 and BOPA2_12_30872 are located within the *Ppd-H1* genic sequence (Table S2). The population was also genotyped for functional variation at the two vernalisation genes *Vrn-H1*, *Vrn-H2* and at *Ppd-H1* using diagnostic markers as published in Cockram *et al*. (2009), Karsai *et al*. (2005) and Turner *et al*. (2005), respectively (Table S6). Functional variation at *VRN-H1 VRN-H2* and *Ppd-H1* was tested for association with trait variation without filtering for MAF together with the SNP panel.

Statistical analyses - Phenotype

All statistical analyses were performed using the R software version 3.1.1 (The R development Core Team, 2008). Variance components for FD, LW and LL including genotypes, replicates and locations (except for LL) as factors were calculated with a mixed linear model implemented by the "lmer" function from the lme4 package version 1.1.7, where genotypes, replicates and location were considered as random factors. Broad-sense heritability values were computed according to Knapp (Knapp *et al*., 1985): $h^2=\sigma^2g/(\sigma^2g+\sigma^2lg/n+\sigma^2e/n)$; where σ^2g is the genetic variance, σ^2lg is the genotype by location interaction variance, σ^2e is the error variance, and n is the number of locations. For LL, analysed only in one location, heritability was calculated as $h^2=\sigma^2g/(\sigma^2g+\sigma^2e)$. In addition, the "lm" function was used to conduct an analysis of variance based on a linear model

460 including locations (except for LL), genotypes and replicates. Finally, we partitioned the genotype
461 and genotype by location effects using *Ppd-H1* marker alleles.
462
463 Best Linear Unbiased Estimators (BLUEs) of FD, LW and LL were calculated as the phenotypic
464 values estimated for each genotype in a mixed linear model implemented by the "lmer" function,
465 where genotypes were set as fixed factor and location, location by genotype interactions and
466 replicates were considered as random factors (for LL the random factors were reduced to the
467 replicates). Pearson correlation analyses between FD and LW were calculated based on BLUEs
468 across environments and replicates. For correlations between LL and FD or LW, only BLUEs across
469 replicate measurements in Iran were calculated.
470 Leaf emergence (LEM) and leaf blade elongation (LER) over time were calculated with a piecewise
471 regression in the 'segmented' package (version 0.2-9.5, Muggeo 2003, 2008) implemented in the R
472 software. Bayesian information criterion (BIC) was used to decide on the number of breakpoints in
473 the final regression model. Point estimates and 95%-confidence intervals for the slopes of each
474 linear segment in the selected regression models were extracted using the slope function of the
475 'segmented'-package.
476
477 *Statistical analysis - Population structure, Linkage Disequilibrium and GWAS analyses*
478 The population structure of the panel was investigated by principal component analysis (PCA)
479 based on a correlation matrix derived from 2,532 iSELECT SNP markers, using the
480 PAleontologicalSTastical (PAST) software (Hammer *et al*., 2001).
481 In order to identify the intra-chromosomal linkage disequilibrium among markers, squared allele
482 frequency correlations (r^2) were calculated between pairs of loci using the TASSEL software
483 (Bradbury *et al*., 2007). Linkage disequilibrium decay was evaluated by plotting significant
484 ($p<0.001$) pair-wise r^2 values against genetic distances between each pair of loci and by fitting the
485 locally weighted scatterplot smoothing (LOESS) curve on the graph using the R software. A critical
486 r^2 value was estimated as the 95th percentile of r^2 values between pairs of unlinked loci (pairs of loci
487 on the same chromosome with >50 cM distance).
488 Genome wide association scans (GWAS) were performed based on BLUEs across environments
489 and replicates and based on BLUES for individual environments across replicates with the GAPIT
490 package version 2 (Lipka *et al*., 2012) implemented in the R software. To identify significant
491 marker trait associations a mixed linear model (MLM) described by the following formula was
492 used: phenotype= M+Q+K+e in which M and e denote the genotypes at the marker and residuals,

493 respectively. Q is a fixed factor due to population structure and K is a random factor due to co-
494 ancestry of individuals. Q was calculated as the first three components of the Principal Component
495 Analysis (PCA) (Fig. S10). The kinship matrix K represents similarities between genotypes and was
496 calculated based on the proportion of allele mismatches at each SNP between pairs of genotypes in
497 GAPIT with the Van Raden method (VanRaden, 2008). In a second mixed model we used FD as a
498 covariate to correct for flowering-time dependent changes in leaf size. The p-values of genotype-
499 phenotype associations were adjusted based on a false discovery rate (FDR) (Benjamini &
500 Hochberg, 1995) separately for each trait and a threshold value for significant associations was set
501 at 0.05. Manhattan plots displaying GWAS results were prepared with the qqman package (Turner,
502 2014) implemented in the R software.
503
504 ***SUPPLEMENTAL MATERIAL***

505 **Table S1:** Analysis of variance for flowering date (FD), leaf width (LW) and leaf length (LL).
506 **Table S2**: Genetic material and genotyping information
507 **Table S3:** Ppd-H1 haplotypes in the introgression lines
508 **Table S4:** Variation at *Ppd-H1* affects the phyllochron
509 **Table S5**: Variation at *Ppd-H1* does not affect the rate of leaf blade elongation
510 **Table S6**: Primers used for genotyping and Real Time qRT-PCR assays
511
512
513 **Figure S1**. Principal component analysis (PCA) plot based on the first two principal axes with
514 spring and facultative genotypes and *Ppd-H1* variants indicated in colour.

515 **Figure S2**. Intra-chromosomal LD decay of markers pairs over all chromosomes as a function of
516 genetic distance.

517 **Figure S3**. Manhattan plots of GWAS for flowering date (FD), leaf length (LL) and leaf width
518 (LW) calculated for Iran and Italy separately.

519 **Figure S4.** Manhattan plots of GWAS for leaf length (LL) and leaf width (LW) with flowering time
520 (FD) as a covariate.

521 **Figure S5.** Size and flanking markers of *Ppd-H1* introgressions in three independent introgression
522 lines.

523 **Figure S6**. Heading date is delayed in the presence of the mutated *ppd-H1* allele under LDs.

Figure S7. Leaf length and leaf emergence of Bowman/BW281 and Triumph/Triumph-IL.

Figure S8. Variation at *Ppd-H1* does not affect the rate of leaf elongation.

Figure S9. Leaf blade anatomy of the 5th leaf emerging from the main shoot of SD grown plants.

Figure S10. Variance explained by the first 10 principal components for the genetic diversity of the winter barley collection.

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TABLES

Table 1: Mean, minima, maxima and heritability of FD, LL and LW scored in Italy and Iran

Trait	Italy				Iran				h^2(%)
	Min	Max	Mean	St.Dev.	Min	Max	Mean	St.Dev.	
FD [days after sowing]	202	230	209	4.4	175	192	181	3.7	89%
LL [mm]	n.d.	n.d.	n.d.	n.d	130	236	177	18.7	96%
LW [mm]	12.7	24.5	17.8	2.1	8.3	19.3	13	2	81%

FD: flowering date; LL: leaf width; LW: leaf width; h^2: heritability; n.d.: not determined

542

543 **Table 2**: Summary of significant marker-trait associations identified by GWAS

LOCUS (*Candidate Gene*)	Chr	Position [cM]	MAF	FD			LL			LW		
				-log10 (p)	Δm [%]*	Effect** [days]	-log10 (p)	Δm [%]*	Effect** [mm]	-log10 (p)	Δm [%]*	Effect** [mm]
(*Ppd-H1*) SNP22 BK_12 BK_14 BK_15 BK_16 BOPA2_12_30871 BOPA2_12_30872***	2HS	19.9	0.27	7.5	38	2.1	4.5	39	8	6.4	25	1
(*HvCEN*) BOPA1_ConsensusGBS0008-1	2HS	58.78	0.19	4.2	27	1.7	/	/	/	/	/	/
SCRI_RS_157866	4HL	110.2	0.36	/	/	/	/	/	/	4.1	8	0.7

Chr: chromosome arm; cM: centiMorgan; FD: flowering date; LL: leaf length; LW: leaf width
*Difference between R^2 of the model with and without the marker; **Effect of minor allele; *** Markers designed on *Ppd-H1* gene

544

Table 3: Variation at *Ppd-H1* affects the phyllochron of Scarlett and S42-IL107

Photoperiod	Genotype	Leaf No.	Phyllochron[1] [days]	95%-CI
Long Day	Scarlett	1 - 6	4.5	4.3 - 4.7
		7 - 10	6.3	6.0 - 6.6
	S42-IL107	1 - 8	4.1	4.0 - 4.2
Short Day	Scarlett	1 - 9	5.7	5.5 - 5.8
		10 - 14	9.0	8.6 - 9.4
	S42-IL107	1 - 9	5.7	5.6 - 5.9
		10 - 14	10.6	9.9 - 11.2

[1] Phyllochron was calculated as the leaf emergence rate^{-1} from the slopes of the linear segments of the regression lines presented in Fig. 4C.

FIGURE LEGENDS

Figure 1. Principal component analysis (PCA) plot of 138 barley cultivars based on the first two principal axes (component 1 = 12% and component 2 = 8%). Two-rowed barley cultivars are indicated in grey, and six-rowed cultivars in black.

Figure 2. Manhattan plots of GWAS for flowering date (FD), leaf length (LL) and leaf width (LW) in the barley cultivar collection. The -$\log_{10}$ (p-values) from the association scans are plotted against the SNP marker positions on each of the seven barley chromosomes. The dashed horizontal line indicates the genome-wide significance threshold at FDR < 0.05.

Figure 3. Size of the leaf blade is increased in spring barley lines with the mutated *ppd-H1* allele. **(A)** Maximal leaf blade length and **(B)** leaf blade width of the largest leaf in spring barley lines with a mutated *ppd-H1* allele (grey bars) and the derived ILs (white bars) carrying the dominant *Ppd-H1* under LD. Bars represent means with 95%-confidence intervals.

Figure 4. Leaf blade length and phyllochron of Scarlett and S42-IL107 grown under different photoperiods. Leaves emerging from the main shoot in Scarlett (grey bars) and S42-IL107 (white bars) under **(A)** long-day and **(B)** short-day conditions. Arrows indicate the longest leaf for Scarlett and S42-IL107. Bars represent means with 95%-confidence intervals. **(C)** Number of leaves emerging on the main shoot per time unit after germination in Scarlett (solid line, triangle) and S42-IL107 (dashed line, square) under LDs (black) and SDs (grey). Breakpoints of the regression model are indicated for the different genotypes and conditions above

570 the regression curves with their 95%-confidence intervals.
571
572 **Figure 5**. *Ppd-H1* affects the duration of leaf elongation, cell number, cell size and leaf length under LD
573 conditions. **(A)** leaf elongation rates were determined by measuring the leaf length every three days under
574 LDs in Scarlett (solid line, triangle) and S42-IL107 (dashed line, square) in the 5th leaf of the main shoot.
575 Breakpoints of the regression model and their 95%-confidence intervals are indicated for the different
576 genotypes and conditions above the regression curves. **(B)** cell length, **(C)** the estimated number of
577 interstomatal cells and **(D)** the final leaf length, respectively, of the 5th fully expanded leaf on the main shoot.
578 Barley genotypes with the mutated *ppd-H1* allele and the ILs with the photoperiod responsive *Ppd-H1* allele
579 are represented by grey and white bars, respectively. Bars represent means +/- 95%-confidence intervals
580 (n=5).
581
582 **Figure 6**. Expression patterns of *FT1* and *AP1/FUL-like* MADS box transcription factors in successive
583 barley leaves. Quantification of gene expression levels by quantitative Real Time PCR (qRT-PCR) in leaf
584 samples harvested from successive leaves emerging from the main shoot of Scarlett *(circle)* and S42-IL107
585 *(triangle)* plants grown under short-day *(grey)* and long-day *(black)* conditions. Expression levels are
586 demonstrated relative to the transcript abundance of the *Actin* housekeeping gene. Error bars represent
587 standard deviations over three biological and two technical replicates. Asterisks indicate significant
588 differences (P<0.05) in transcript abundance between S42-IL107 and Scarlett when plants were grown under
589 long-day conditions.

590 **Figure S1.** Principal component analysis (PCA) plot of 138 barley cultivars based on the first two principal
591 axes (component 1 = 12% and component 2 = 8%). A) Genotypes with a spring *Vrn-H1* allele or a deletion of
592 the *Vrn-H2* locus are indicated in red. B) Genotypes are coloured according to row-type and *Ppd-H1* allele.

593 **Figure S2**. Intra-chromosomal LD decay of markers pairs over all chromosomes as a function of genetic
594 distance. The fitted LOESS curve (black line) illustrates the LD decay, and the horizontal line represents the
595 critical r^2 value.

596 **Figure S3**. Manhattan plots of GWAS for flowering date (FD), leaf length (LL) and leaf width (LW) scored
597 in Iran (upper panel) and in Italy (lower panel) in the barley cultivar collection. The -$\log_{10}$ (p-values) from
598 the association scans are plotted against the SNP marker positions on each of the seven barley chromosomes.
599 The dashed horizontal line indicates the genome-wide significance threshold at FDR < 0.05.

600 **Figure S4.** Manhattan plots of GWAS for leaf length (LL) and leaf width (LW) with flowering time (FD) as
601 a covariate based on data of the barley cultivar collection scored in both locations. The -$\log_{10}$ (p-values) from
602 the association scans are plotted against the SNP marker positions on each of the seven barley chromosomes.
603 The dashed horizontal line indicates the genome-wide significance threshold at FDR < 0.05.

Figure S5. Size and flanking markers of *Ppd-H1* introgressions on chromosome 2H. Donor parents for the photoperiod-responsive *Ppd-H1* allele of the introgression lines and their respective spring barley background genotypes are indicated above each chart. Introgression lines were genotyped with the 9kiSelect chip from Illumina. Flanking marker positions of the introgressions are given relative to the POPSEQ map (Marscher et al., 2013).

Figure S6. Heading date is delayed in the presence of the mutated *ppd-H1* allele under LDs. Heading date of three LD grown spring barley genotypes with the mutated *ppd-H1* allele (grey bars) and introgression lines for the photoperiod responsive *Ppd-H1* allele (white bars). Bars indicate means with 95%-confidence intervals.

Figure S7. Leaf length and leaf emergence of Bowman/BW281 and Triumph/Triumph-IL. **(A-D)** Analysis of leaf length of every leaf on the main shoot of plants grown under **(A and C)** LD and **(B and D)** SD conditions. Leaf length and leaf emergence is shown for the genotpyes **(A and B)** Bowman/BW281 and **(C and D)** Triumph/Triumph-IL with the spring barleys and introgression lines being represented by grey and white bars, respectively. Arrows indicate the longest leaf per genotype. Bars represent means with 95%-confidence intervals. **(E and F)** Number of leaves emerging from the leaf sheath per time unit after germination in **(E)** Bowman/BW281 and **(F)** Triumph/Triumph IL, when spring barley genotypes (solid line, triangle) and introgression lines for the wild type *Ppd-H1* allele (dashed line, square) were grown under LDs (black) and SDs (grey). Breakpoints of the regression model and their 95%-confidence intervals are indicated for the different genotypes and conditions above the regression curves.

Figure S8. Variation at *Ppd-H1* does not affect the rate of leaf elongation. Leaf length was measured every three days under LDs (black) and every four days under SDs (grey) in Scarlett (solid line, triangle) and S42-IL107 (dashed line, square). Breakpoints of the regression model and their 95%-confidence intervals are indicated for the different genotypes and conditions above the regression curves.

Figure S9. Leaf blade anatomy of the 5th leaf emerging from the main shoot of SD grown plants. **(A)** Cell length, **(B)** estimated cell number and **(C)** final leaf blade length of spring barley genotypes with the mutated *ppd-H1* allele (grey bars) as compared to their respective ILs with the photoperiod responsive *Ppd-H1* allele (white bars). Bars represent means +/- 95%-confidence intervals (n=5).

Figure S10. Variance explained by the first 10 principal components for the genetic diversity of the winter barley collection.

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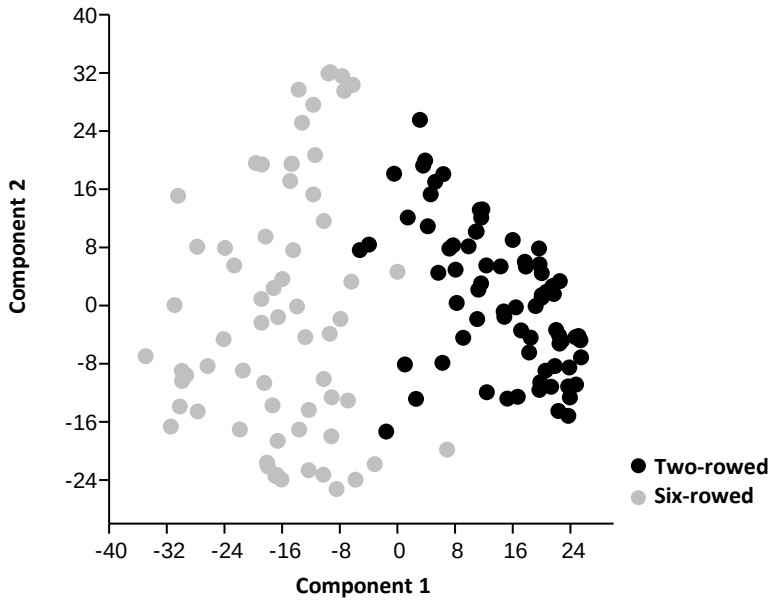

Figure 1. Principal component analysis (PCA) plot of 138 barley cultivars based on the first two principal axes (component 1 = 12% and component 2 = 8%). Two-rowed barley cultivars are indicated in black, and six-rowed cultivars in grey.

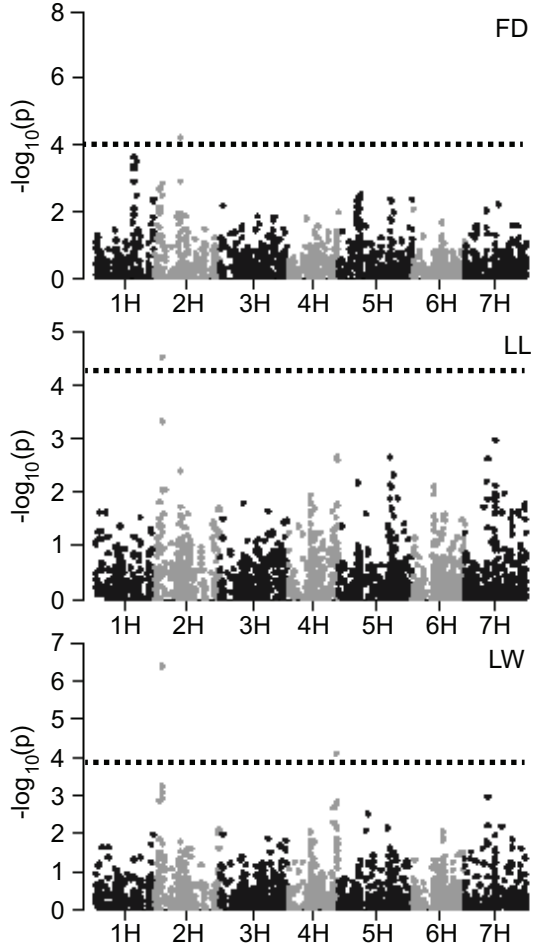

Figure 2. Manhattan plots of GWAS for flowering date (FD), leaf length (LL) and leaf width (LW) in the barley cultivar collection. The -$\log_{10}$ (p-values) from the association scans are plotted against the SNP marker positions on each of the seven barley chromosomes. The dashed horizontal line indicates the genome-wide significance threshold at FDR < 0.05.

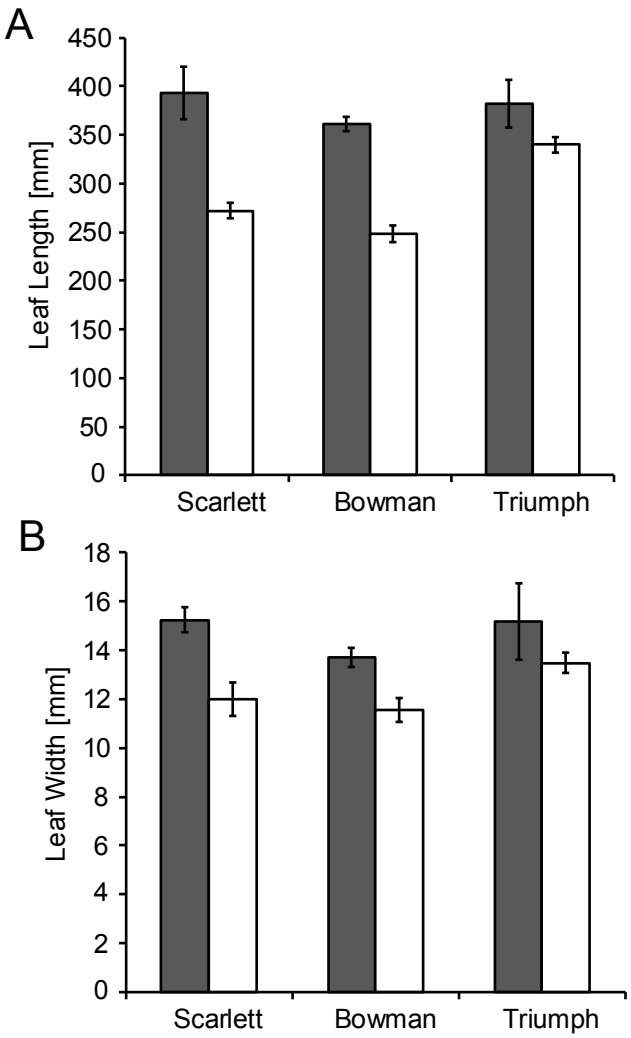

Figure 3. Size of the leaf blade is increased in spring barley lines with the mutated *ppd-H1* allele. **(A)** Maximal leaf blade length and **(B)** leaf blade width of the largest leaf in spring barley lines with a mutated *ppd-H1* allele (grey bars) and the derived ILs (white bars) carrying the dominant *Ppd-H1* under LD. Bars represent means with 95%-confidence intervals.

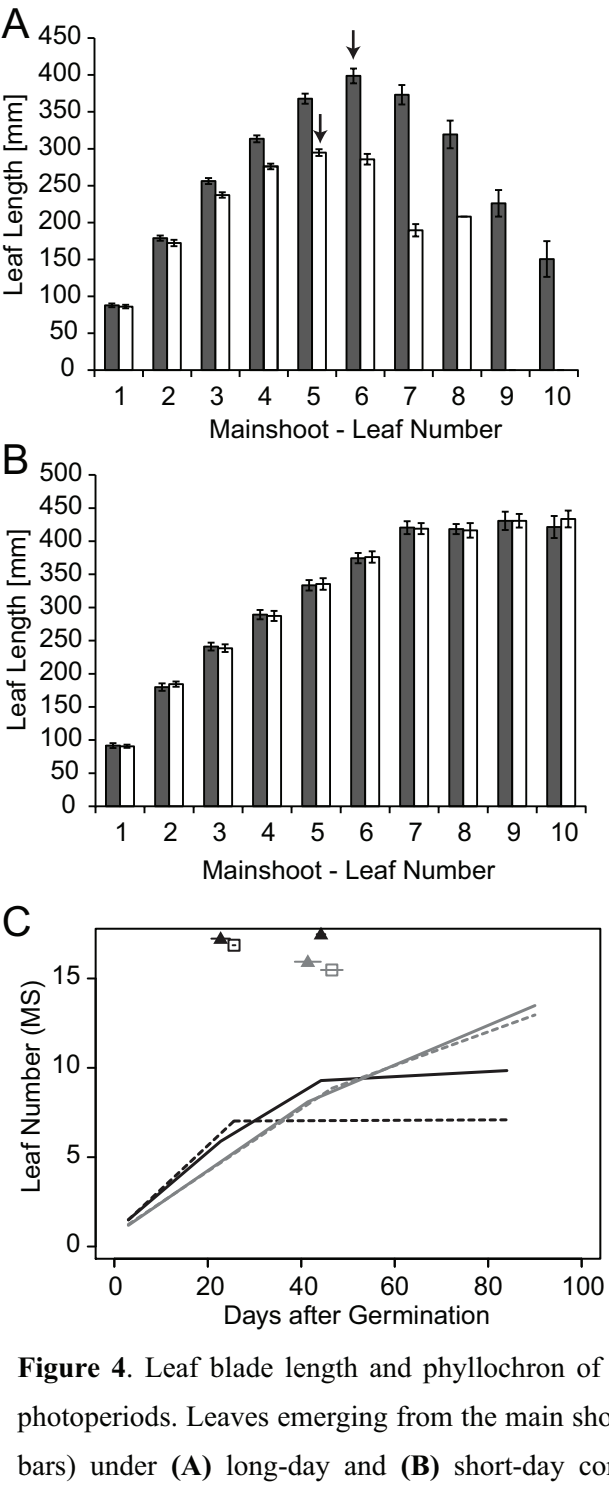

Figure 4. Leaf blade length and phyllochron of Scarlett and S42-IL107 grown under different photoperiods. Leaves emerging from the main shoot in Scarlett (grey bars) and S42-IL107 (white bars) under **(A)** long-day and **(B)** short-day conditions. Arrows indicate the longest leaf for Scarlett and S42-IL107. Bars represent means with 95%-confidence intervals. **(C)** Number of leaves emerging on the main shoot per time unit after germination in Scarlett (solid line, triangle) and S42-IL107 (dashed line, square) under LDs (black) and SDs (grey). Breakpoints of the regression model are indicated for the different genotypes and conditions above the regression curves with their 95%-confidence intervals.

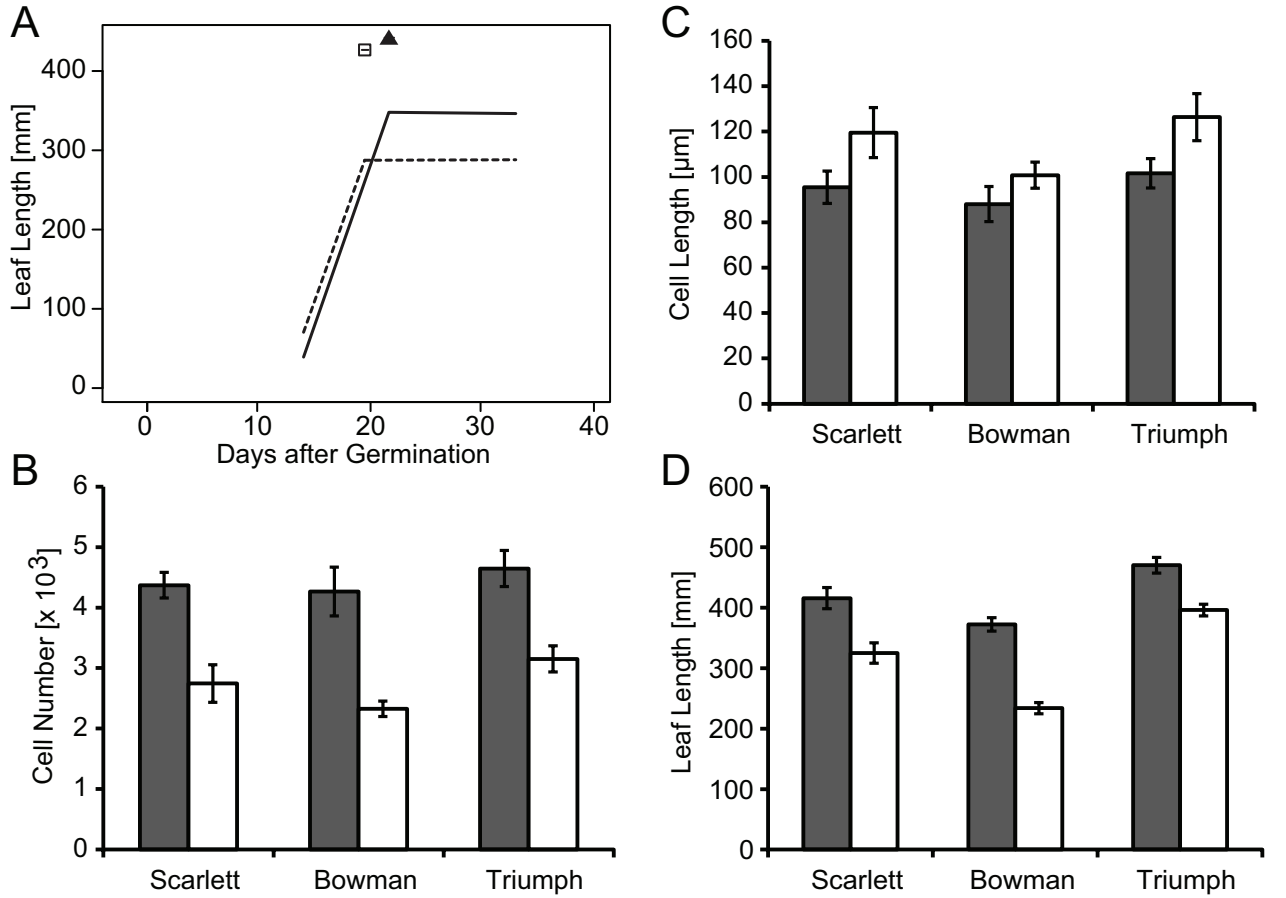

Figure 5. *Ppd-H1* affects the duration of leaf elongation, cell number, cell size and leaf length under LD conditions. **(A)** leaf elongation rates were determined by measuring the leaf length every three days under LDs in Scarlett (solid line, triangle) and S42-IL107 (dashed line, square) in the 5th leaf of the main shoot. Breakpoints of the regression model and their 95%-confidence intervals are indicated for the different genotypes and conditions above the regression curves. **(B)** cell length, **(C)** the estimated number of interstomatal cells and **(D)** the final leaf length, respectively, of the 5th fully expanded leaf on the main shoot. Barley genotypes with the mutated *ppd-H1* allele and the ILs with the photoperiod responsive *Ppd-H1* allele are represented by grey and white bars, respectively. Bars represent means +/- 95%-confidence intervals (n=5).

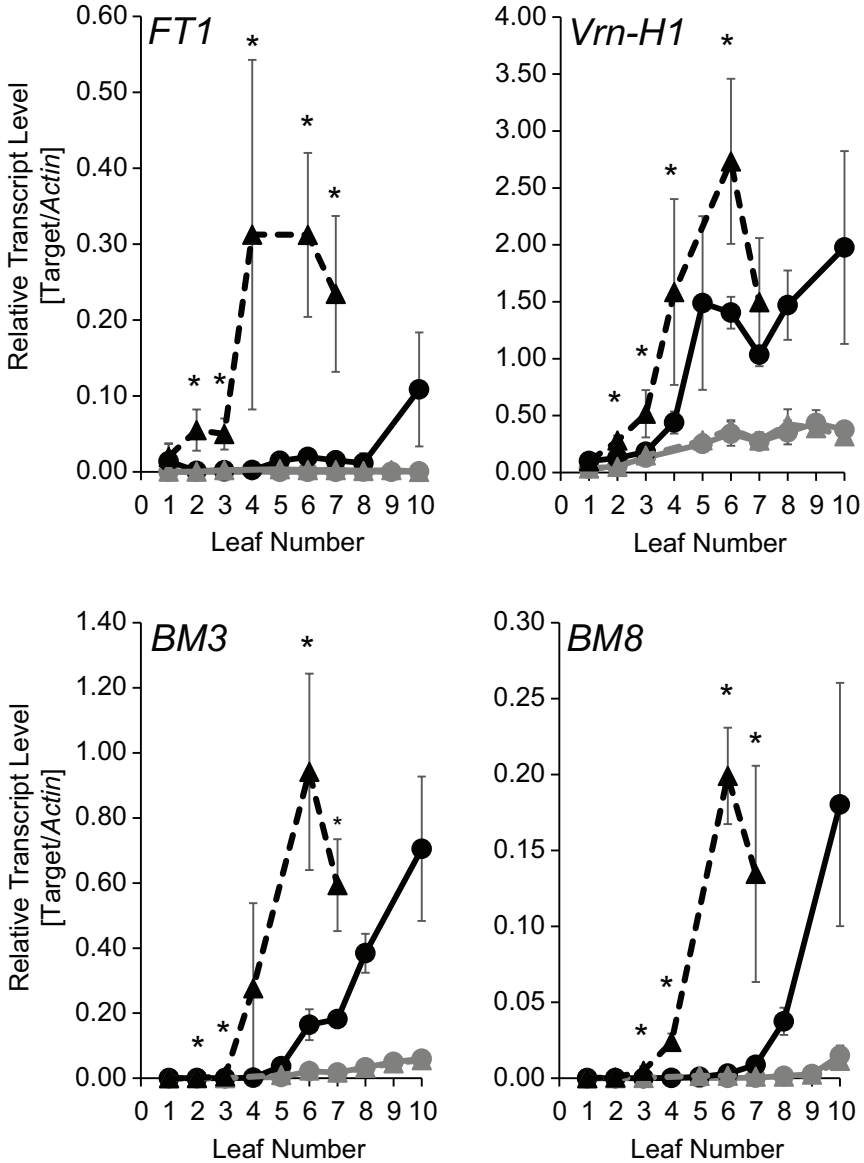

Figure 6. Expression patterns of *FT1* and *AP1/FUL-like* MADS box transcription factors in successive barley leaves. Quantification of gene expression levels by quantitative Real Time PCR (qRT-PCR) in leaf samples harvested from successive leaves emerging from the main shoot of Scarlett *(circle)* and S42-IL107 *(triangle)* plants grown under short-day *(grey)* and long-day *(black)* conditions. Expression levels are demonstrated relative to the transcript abundance of the *Actin* housekeeping gene. Error bars represent standard deviations over three biological and two technical replicates. Asterisks indicate significant differences ($P<0.05$) in transcript abundance between S42-IL107 and Scarlett when plants were grown under long-day conditions.

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