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ORIGINAL RESEARCH

Tuning of meristem maturation rate increases yield in multiple *Triticum aestivum* cultivars

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Abstract

Breeding programs aim to improve crop yield and environmental stability for enhanced food security. The principal methodology in breeding for stable yield gain relies on the indirect selection of beneficial genetics by yield evaluation across diverse environmental conditions. This methodology requires substantial resources while delivering a slow pace of yield gain and environmental adaptation. Alternative methods are required to accelerate gain and adaptation, becoming even more imperative in a changing climate. New molecular tools and approaches can enable accelerated creation and deployment of multiple alleles of genes identified to control key traits. With the advent of tools that enable breeding by targeted allelic selection, identifying gene targets associated with an improved crop performance ideotype will become crucial. Previous studies have shown that altered photoperiod regimes increase yield in wheat (*Triticum aestivum*). In the current study, we have employed such treatments to study the resulting yield ideotype in five spring wheat cultivars. We found that the photoperiod treatment creates a yield ideotype arising from delayed spike establishment rates that are accompanied by increased early shoot expression of *TARGET OF EAT1* (*TaTOE1*) genes. Genes identified in this way could be used for ideotype-based improve crop performance through targeted allele creation and selection in relevant environments.

KEYWORDS
light treatment, meristem, wheat, yield components

1 | INTRODUCTION

Yield, defined as grain weight per unit area, results from the genetic makeup of the crop, the environment, and agronomic practices (Nakamichi, 2015). The reality of climate change reinforces the importance of considering the role of the environment and environmental responsiveness of the crop to sustain and improve yield performance (Henry, 2019). Technological efforts to address environmental factors or improve agronomic practices are critical (Anderson et al., 2005; Kirby, 1988; Tilman et al., 2002) but are limited by the genetic potential of the crop to yield and adapt. Adaptation of crops to diverse environments has been accomplished by indirect selection of photoperiod and temperature response loci. Genes underlying such loci have since been positionally cloned including rice GHD7, maize ZCN genes and wheat Ppd genes (Arjona et al., 2020; Castelletti et al., 2020; Hake & Ross-Ibarra, 2015; Sun et al., 2022).

Currently, the overriding strategy of breeding programs for large acre crops is to pursue yield and stability improvement via the indirect

selection of quantitative alleles in adapted backgrounds. Such programs treat yield across different environments as the primary selection trait (Alexander et al., 1984; Hawkesford et al., 2013; Wallace & Yan, 1998) and, more recently, have used machine learning approaches for the identification of the beneficial allelic combinations in the selected top-performing lines (Bernardo, 2020).

However, several reports indicate that yield can also be improved via the direct modification of individual traits (Eizenga et al., 2019; Jones et al., 2021; Li, Debernardi, et al., 2021). It has been demonstrated that modification of individual traits by direct selection of beneficial alleles or allelic combinations has led to major improvements in yield performance of modern crops. Selection of beneficial alleles that change plant height, flowering time, stem termination date, branch point number, seed number, panicle size, and fruit retention has been demonstrated to result in yield improvement (Bommert et al., 2013; Eshed & Lippman, 2019; Hedden, 2003; Je et al., 2016; Krieger et al., 2010; Lifschitz et al., 2014; Park, Jiang, et al., 2014; Rodríguez-Leal et al., 2017; Soyk et al., 2017; Zhang et al., 2020).

In addition, a recent study in spring wheat examining genetic components of yield gain identified specific alleles of the causal genes associated with QTL controlling traits responsible for the improved crop performance (Jones et al., 2021). The authors identified alleles of Q (APO1) and GW2 that have significant effects on yield components including tiller number, spikelet number per spike and kernel weight as a function of resource availability in plot environments. These examples underscore the opportunity to improve yield and crop adaptation to changing environments by targeted modification of specific traits via the direct selection of the beneficial alleles.

Current advances in molecular tools including gene editing enable many efficient strategies for generating and intentionally engineering a large number of novel alleles at individual loci (Hendelman et al., 2021; Rodríguez-Leal et al., 2017). The potential to create novel allelic series at rationally selected loci offers great opportunity for trait-based selection of the optimal allele. To enable these innovations, identifying the most crucial yield and crop stability trait components and genetic factors controlling them remains a key challenge for implementing crop improvement via a direct selection of the beneficial allelic combinations. Yield improvement in wheat through photoperiod treatment offers a case to illustrate how such trait components and genetic factors can be identified.

A classic series of physiological experiments in wheat have demonstrated that stage-specific application of photoperiod treatments can lead to increased yield performance (Guo et al., 2018; Rawson, 1970; Thorne et al., 1968). These studies have found that spring wheat plants grown under long days (LDs) (16 h light:8 h dark) flower and mature faster, develop fewer spikelets, and generally have more compact stature than plants grown under short days (SDs) (8 h light:16 h dark). It was shown that modulation of the timing and duration of photoperiod could effectively manipulate phenotypic diversity in traits such as spikelet number, seed number, and flag leaf area leading to superior yield per plant across multiple genetic backgrounds (Bonnett, 1936; Rawson, 1970; Thorne et al., 1968).

These previously described experimental systems provide a valuable avenue for studying yield trait relationships and identifying the genetic and molecular factors through which yield beneficial traits could be modified in an environment-independent manner. We used previously described "yield-positive" photoperiod manipulations to characterize differences in meristem development that underly trait changes and yield improvement. To gain additional insight into the molecular mechanisms underlying yield gain of the manipulated plants, we have monitored changes in the expression of known genes involved in photoperiod response and meristem development. We find that the yield improvement observed for photoperiod-treated plants is associated with a modified rate of inflorescence meristem maturation at the early stages of transition from vegetative to reproductive stage. We show that these changes correlate with higher expression levels of *TARGET OF EAT1* (*TaTOE1*) genes in immature wheat shoots.

We hypothesize that the experimental system presented here could be used to guide the genetic improvement of traits of interest through identification and modification of causal genes. Novel alleles created in this way may be screened for the desired trait intensity plus low sensitivity to environmental changes.

2 | MATERIALS AND METHODS

The five *Triticum aestivum* elite cultivars Blade, Samson, Faller, Glenn, and Howard were selected to represent diverse genetic populations (i.e., breeding programs) in North Dakota spring wheat. These cultivars were grown in two climate-controlled Conviron™ growth chambers set for a day temperature of 18°C to 20°C and night temperature of 16°C, a constant humidity of 50%, and a light intensity of 600 μE. One chamber was set for the LD photoperiod conditions (16 h light/8 h dark). The other chamber was set for the SD photoperiod conditions (8 h light/16 h dark). Plants were grown in the International Horticulture Technologies LLC Q-plug 40/80 growth medium in plug trays (product #WG10LP50SQBX) containing 50 plants per tray and irrigated twice a day with Jacks 15-5-15 fertilizer.

For data collection, sets of 100 plants from each cultivar were grown in the LD chamber and the SD chamber. Based on the results of our initial LD observations, another 100 plants from each cultivar were subjected to transient SD treatment. These plants were initiated in the LD growth chamber, transitioned to the SD growth chamber 10 days after germination and transitioned back to LD growth chamber 28 day after the first transfer.

During the growth cycle, all plants were assessed at defined time points for phenological state according to Zadoks scale (Zadoks et al., 1974). At the end of the cycle, 20 plants from the middle rows of each tray (to avoid edge effects) were used for trait scoring and statistical analysis. Statistical analyses and graphical visualizations were conducted with the R-software platform using ggplot2 and dplyr packages.

A subset of the plants from each variety in each treatment group was dissected at defined time points during the growth cycle to

visualize meristematic development. Images of the immature inflorescences, flowers, and meristematic tissues were acquired with Leica M205 FA stereomicroscope and imaging software.

Subsets of the LD-grown and the transiently SD-treated plants were used to investigate transcriptional changes. Primary tillers were sampled to enable combined assay of expression in meristematic and nonmeristematic tissues (Figure S3). Whole seedlings (in early stages) and main shoot tissue (at the later stages) from three individual plants at each treatment and for each variety were sampled at 7 time points. Samples were collected from LD-grown plants from all five wheat cultivars at seven and 10 days after sowing. At the end of day 10, half of the LD initiated plants were transferred to SD conditions for transient SD treatment, as previously. Tissue was sampled from LD plants at 11, 13, 21, and 38 days after sowing and, correspondingly, from the SD-treated plants at 19 h, 2 days, 10 days, and 18 days after initiation of SD treatment. Plant tissue was frozen in liquid nitrogen and used for total RNA extraction using the standard TRIZOL-based protocol (Pattemore, 2014). Subsequently, extracted RNA was treated with the Turbo DNA-free system (Ambion) to eliminate any contaminating DNA. Purified DNA-free RNA was used in equal amounts by concentration for each sample analyzed. RNA samples were analyzed by custom Quantigene 2.0 Plex assay with probes representing 117 unique wheat unigenes (Table S1) using supplies from the manufacturer. Analysis was performed according to standard Luminex methodology (Thermo Fisher Scientific, http://assets.thermofisher.com/TFS-Assets/BID/Reference-Materials/MAN0017862_quantigene-plex-gene-expression-assay-user-guide.pdf). Data analysis included background subtraction, and the log2 transformed the MFI as stated in the product guide and similar published work (Armstrong et al., 2013).

3 | RESULTS

3.1 | Establishing a framework for precise determination of photoperiodic trait effects in wheat

First, we established a simplified SD treatment protocol to more precisely characterize meristem development. Preliminarily, to develop the simplified SD treatment protocol, we examined the timing of developmental progression in wheat plants from representative commercial spring wheat lines grown under standard LD conditions. Analysis of meristematic progression in the five selected commercial spring wheat lines demonstrated that, during the first week after sowing, the apical vegetative meristem gradually expands (Figure 1a,b). By 10–12 days after sowing, the apical vegetative meristem reaches the initial stage of reproductive development (single ridge) characterized by appearance of visible bracts on the apical spike primordium (Bonnett, 1936; Feng et al., 2017) (Figure 1c). From that point on, the apical meristems of the primary tillers begin to develop axillary spikelet branches in alternating phyllotaxis (Figure 1d). This process continues until the formation of the terminal spikelet at the tip of the spike at between 20 and 30 days after initiation of the reproductive spike (Figure 1d, insert). Each spikelet bears up to 10 florets (Figure 1e); however, on average, only two to three florets form fully developed carpels (Figure 1f) capable of being pollinated and form viable seed.

Based on our observation of the timing for completion of vegetative meristem expansion and transition to reproductive development, we determined that SD treatment should be applied in our protocol prior to single ridge formation (Figure 1c). Instructed by our

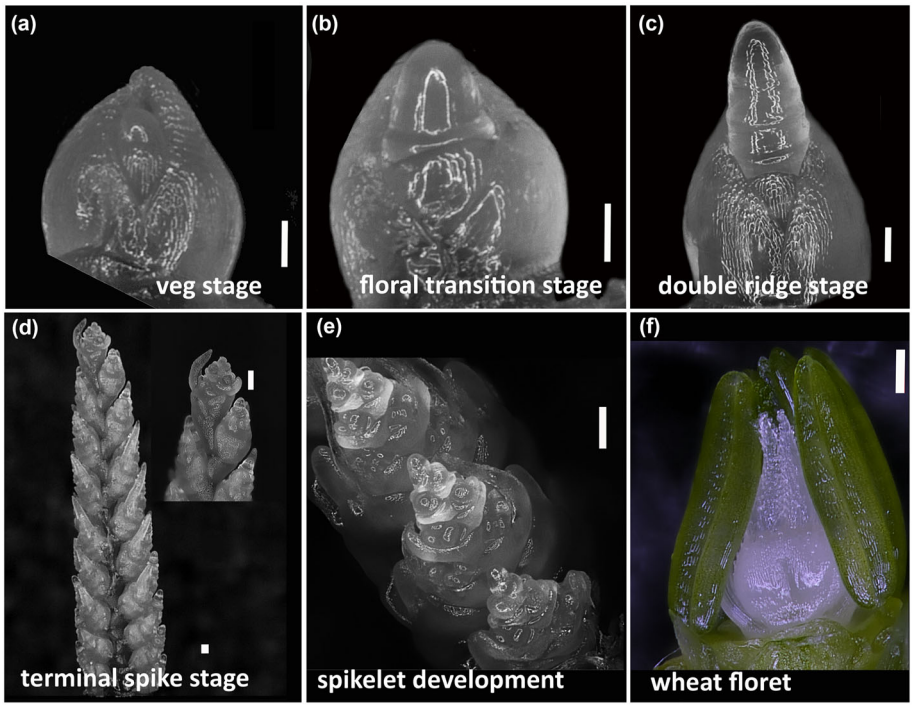

FIGURE 1 Meristem patterns throughout plant development. (a) Progression of meristem development in long day (LD)-grown spring wheat starts with the apical vegetative meristem, (b) gradually growing in size during the first 10 days after germination. (c) At about 14 days after germination, the apical meristem develops the first bracts marking an initiation of the reproductive spike—this stage is also called single ridge. (e) Subsequently, at the axillary of the bracts, spikelet meristems are formed, the spikelet branches initiate glumes, and, at the axillary of glumes, florets are formed. (d) At about 31 days after germination, the apical spike is terminated with a terminal spikelet. (f) Spikelet branches develop up to 10 immature florets. False color indicates ovary (purple) and glume (green). On average, only about two to three florets per spikelet develop mature floral organs, stamens, and carpels. Bars in (a)–(f) represent 100 μm.

characterization and previous research (Bonnett, 1936; Feng et al., 2017), we chose to apply transient SD photoperiod treatment at 10 days after sowing, when spikelet development initiates in LD conditions (Figure 1b) in order to influence meristem development and yield from inception. This simplified SD treatment is maintained for 28 days, until the initiation of the terminal spikelet, when reproductive fates are fully determined (Figure 1d). We established an experimental framework in which all varieties are exposed to the transient SD treatment, constant SD, or constant LD conditions in parallel for controlled comparison (Figure 2a). For this investigation, varieties were grown in parallel under these three regimes throughout the whole life cycle, and phenology stages were scored according to the Zadoks cereal development scale (Zadoks et al., 1974).

3.2 | Photoperiod treatments affect the dynamics and pattern of spring wheat phenology and meristem development

Despite genetic differences, all tested varieties had a similar response to the different photoperiod regimes. Plants grown in LD and plants subjected to transient SD treatment 10 days after sowing initially showed similar rates of developmental progression. However, towards the end of the SD treatment (30 days after sowing), a delay in phenological progression was detected (Figure 2b). This delay became more apparent after treated plants were returned to the LD environment. The SD-treated plants (Figure 2b, green lines) recovered from treatment with a slightly accelerated rate of stage-to-stage progression; however, they still reached physiological maturity (Zadoks 92 stage) 10–15 days later than the LD-grown plants of the same lines (Figure 2b, red lines). Plants grown in SD conditions had the slowest rates of maturation, reaching final maturity 30–40 days later than plants grown in the LD conditions.

In parallel with the phenological analysis, we dissected five plants from each line and photoperiod regime (a total of 75 plants) to characterize patterns of meristem maturation at 10, 13, 31, and 38 days after sowing (Figure 3). Similar to the phenology results, we found that photoperiod regimes, rather than genetic differences, had the greatest impact on meristem development. At 10 days after sowing, both LD- and SD-grown plants had two leaves fully emerged, but the meristems of the SD-germinated plants were much flatter than those of the LD-germinated plants (Figure 3a,b). At this point (10 days after sowing),

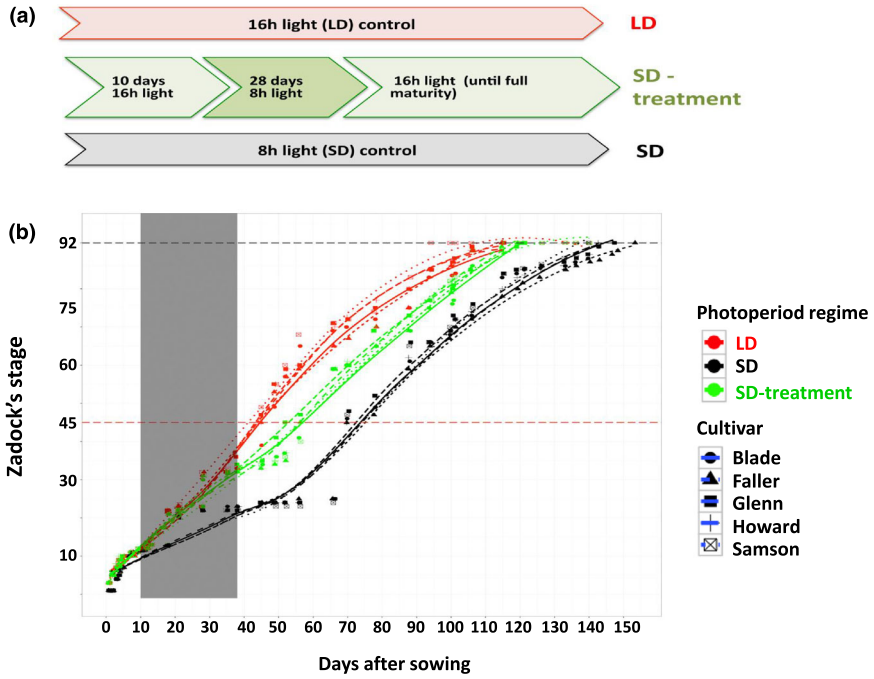

FIGURE 2 Summary of the three tested photoperiod regimes and rates of phenological progression detected in five *Triticum aestivum* varieties subjected to them. (a) Diagram depicting photoperiod regimes including constant long day (LD)- and short day (SD)-grown controls, plus a test set grown for first 10 days in LD, transferred to SD for 28 days, then returned to LD until full maturity (SD treated). Five spring wheat lines from genetically diverse pedigrees were grown in the three photoperiod regimes. Developmental stage of each line for each of the photoperiod regimes was scored at regular intervals according to the Zadoks stage scale until plants reached full physiological maturity (Zadoks 92 stage). (b) Developmental progression curves were modeled using best-fit ggplot2 statistical function. Line patterns and dot shapes indicate five different genetic backgrounds, red colored lines and dots indicate plants grown in constant LD environment, black color indicates plants grown in constant SD environment, and green color indicates plants subjected to transient SD treatment. SD treatment started at 10 days after sowing and was finished at 38 days after sowing (time period of the SD treatment is marked by the gray shade on the graph). Horizontal red dotted line highlights the stage of anthesis (Zadoks stage 45).

LD-grown plants were split into two groups where one group (50 plants per line) was left in LD and the other group was moved to the SD environment transiently. Analysis of meristematic patterns performed 3 days after transition to SD showed no significant differences between LD-grown and SD-treated plants (Figure 3c,d). However, we did detect much smaller vegetative shoot apical meristems (SAM) in plants grown continuously under the SD photoperiod (Figure 3e).

By 31 days after germination (21 days after initiation of the transient SD treatment), differences in meristematic development between the three photoperiod regimes were already dramatic. For example, transient SD-treated plants had fewer developed tillers than LD controls. LD-grown plants had formed most of the spikelet meristem initials but no terminal spikelet (Figure 3f), whereas SD-treated plants had formed multiple bracts with very few visible spikelet meristem initials (Figure 3g). Constant SD-grown plants had fewer visible leaves and tillers than both LD-grown and SD-treated plants, with the meristem just transitioning to reproductive development and forming a few significantly elongated bracts (Figure 3h). At 38 days after sowing (completion of transient SD treatment), we could detect only marginal phenological differences between constant LD- and transient SD-treated plants (Figure 3i,j, left panel). However, differences in the meristematic patterns were apparent as LD-grown plants had developed to terminal spikelet while spikelet meristem growth of the SD-treated plants had just started (Figure 3i,j, right panel). For reference, plants germinated and grown in SD showed both phenology and meristematic development that were at significantly less advanced stages of the spike development (Figure 3k). In summary, photoperiod treatment effects on gross morphology and meristem development are obvious, resulting in delayed meristem development and maturation delay for constant SD-grown plants and transient changes in meristem development resulting in intermediate delay in maturation for SD-treated plants.

3.3 | Duration of the spring wheat exposure to the SD positively correlates with increase in spikelet numbers and vegetative biomass but not with yield

We phenotyped plants at full physiological maturity (Zadoks 92) after monitoring phenological and meristematic progression for all varieties in the three photoperiod regimes and assessing the average time required for each line to reach maturity in each regime (Figure 2b).

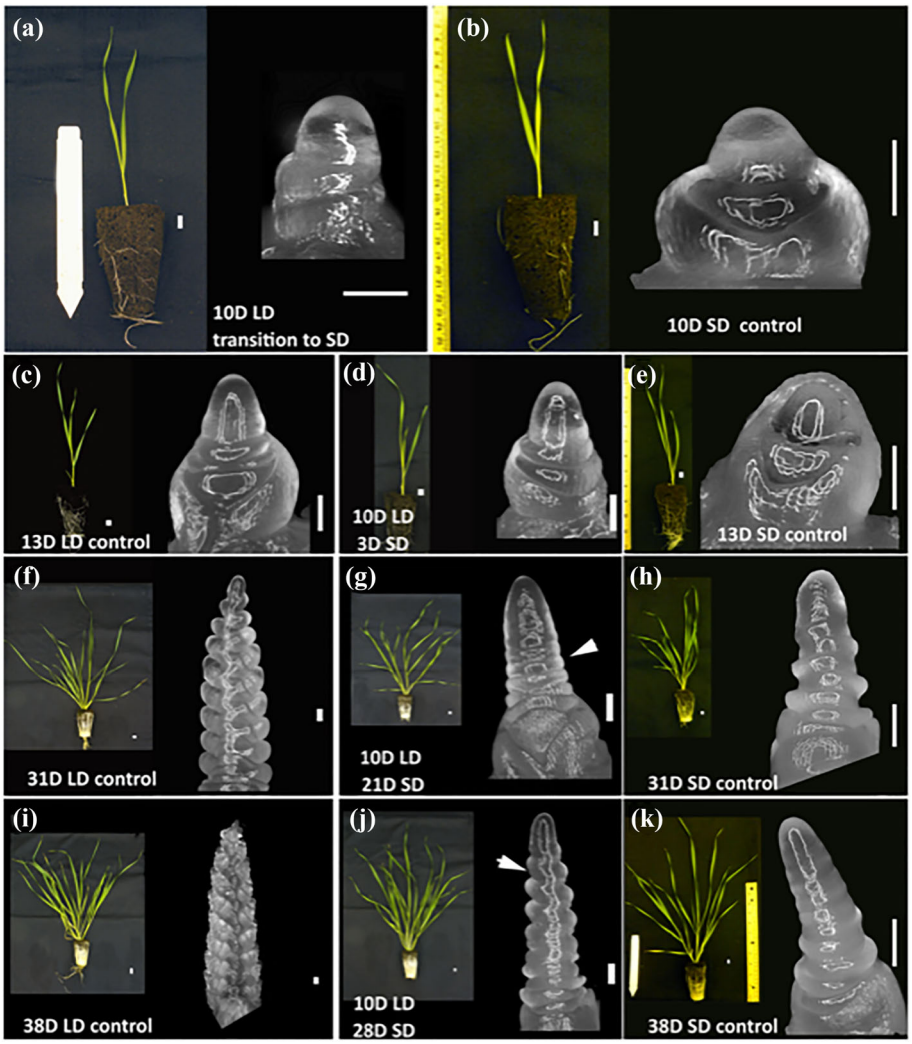

FIGURE 3 Visualization of the developmental dynamics under three photoperiod regimes detected on the whole plant level and apical meristem level in the Faller germplasm. Developmental dynamics detected on the whole plant level (phenology) (left panel) and of the meristem maturation patterns detected at the apical meristems of the primary tillers (right panels) of the (a,c,f,i) plants grown in LD photoperiod, (b,e,h,k) plants grown in SD photoperiod, and (d,g, j) plants grown in LD photoperiod for 10 days after sowing and then subjected to 28 days of the SD photoperiod treatment. White bars next to the meristem images indicate 100 μm, and white bars next to the whole plant images indicate 1 cm.

We measured eight morphology traits including spikelet number per plant, shoot biomass, length of the main spike, flag leaf size (length of the main spike and flag leaf size were assessed only qualitatively), leaf number on the main tiller, and tiller number per plant. We also collected four yield component traits: kernel number per plant, kernel weight per plant, calculated total grain weight, and harvest index per plant. Total grain weight per plant was used as a proxy metric to assess yield potential in this experiment.

The duration of the SD exposure was found to correlate positively with the time required for each variety to reach full physiological maturity (Figures 2b and 4b). Constant SD treatment also resulted in a greater increase in the number of reproductive and vegetative units and vegetative biomass than transient SD treatment. Irrespective of wheat variety, we observed SD-associated increases in spikelet numbers per plant, total vegetative biomass of the plant, length of the primary spike, size of the flag leaf (Figure 4a,c), leaf numbers on the main shoot, and tiller numbers (Figure S1A,B) that were greatest under constant SD.

However, for all tested varieties, the highest yield per plant was not detected in constant SD-treated plants even though these exhibited the largest biomass and highest spikelet numbers (Figure 4a–c). Instead, plants exposed to transient SD showed the greatest increase in yield, assessed as total grain weight (Figure 5a). Transient SD-induced changes in grain yield are associated with increased average kernel weight, not kernel number per plant (Figure 5b,c). Interestingly, kernel weight varied significantly between the tested varieties when exposed to transient SD. Transient SD-treated Faller, Glenn, and Howard cultivars show larger increases in kernel weight than Blade or Samson (Figure 5b). Conversely, constant SD treatment correlated with an increase in kernel number per plant but not single kernel weight or total grain weight (Figure 5a–c). In most of the lines excluding Glenn, observed biomass increase of the transient SD-treated plants relative to LD-grown plants did not lead to a decrease in harvest index. However, harvest index of the constant SD controls was significantly reduced in all tested lines (Figure 5d).

3.4 | Increased yield is associated with changes in expression of circadian and maturation genes

To gain a better understanding of the developmental changes observed in high yielding, SD-treated plants, we profiled relevant gene

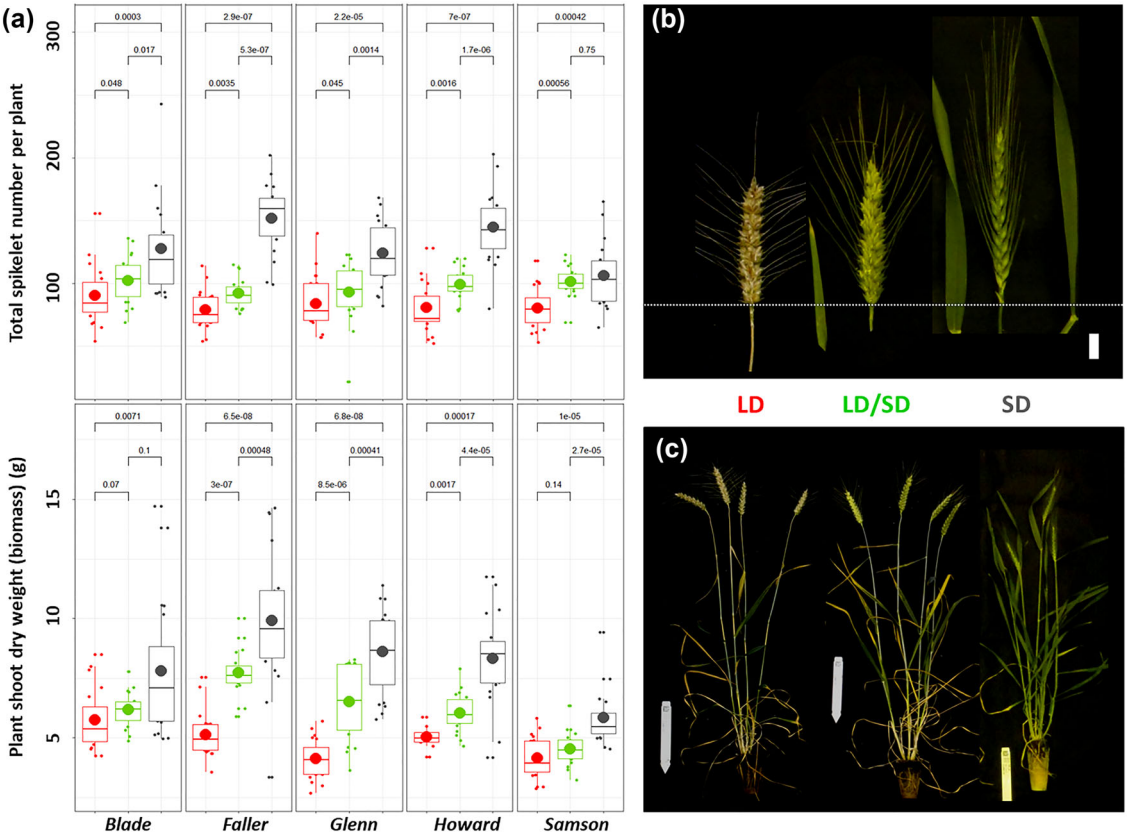

FIGURE 4 Impact of photoperiod regimes on total spikelet number and shoot dry weight across cultivars. (a) Box and dot plot chart summaries of the photoperiod regimes effect on total spikelet number per plant (top panel) and shoot dry weight (bottom panel) measured in five wheat cultivars. Colors represent photoperiod regimes (LD—red; SD—gray; SD treatment—green). Numbers above the square brackets on top of each chart represent Kruskal–Wallis *H* test *p* values, differences were considered significant when $p < .05$. (b) Representative image of plants from the Faller cultivar grown in three different photoperiod regimes at 90 days after sowing shows differences in relative maturity, length of the primary spike, size of the flag leaf, and total size of the plants (c). In (a), dots represent values of the individual plants; in (b), bar size is 1 cm; in (c), stake length is 15 cm.

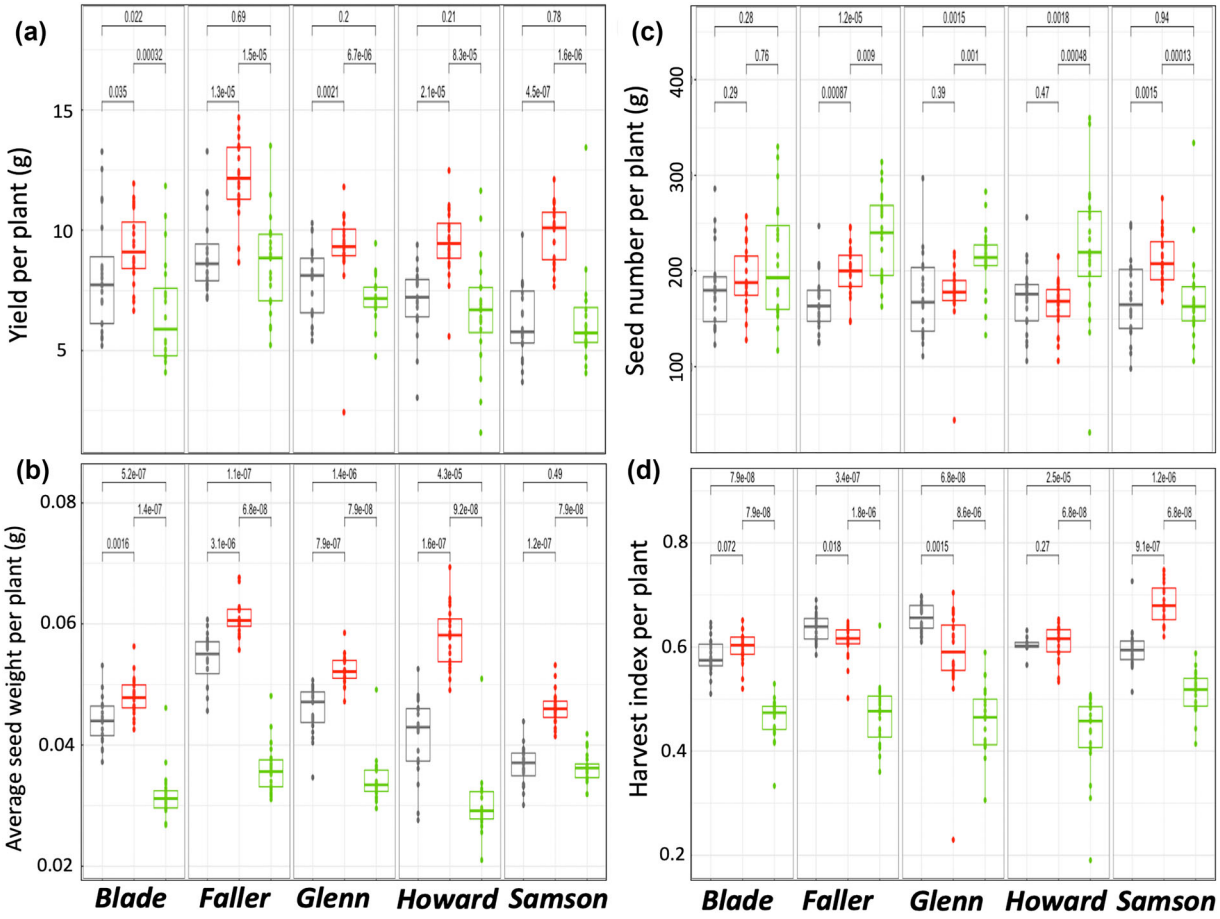

FIGURE 5 Impact of photoperiod regime on per plant yield and related traits. Box and dot plots summarizing effect of the photoperiod regime on the seed weight per plant used as a proxy to estimate (a) average yield per plant, (b) effect of the photoperiod regime on the average seed weight per plant, (c) seed number per plant, and (d) harvest index; red colors represent values measured for LD-grown plants; green values of the SD-treated plants; and gray, of the SD-grown plants. Numbers above the square brackets on top of each chart represent Kruskal–Wallis *H* test *p* values, differences were considered significant when $p < .05$. In (a)–(d), dots represent values of the individual plants.

expression dynamics in wheat meristems from primary tillers of plants undergoing the photoperiodic treatments studied here. For this purpose, we compared LD- and SD-treated expression levels of 116 wheat genes encoding key regulators. These genes included wheat homologs of well-characterized hormonal and developmental regulators in *Oryza sativa* and *Arabidopsis thaliana* (Higgins et al., 2010; Itoh & Izawa, 2011). Candidate *T. aestivum* homologs were identified by BLAST sequence comparison of *O. sativa* gene candidates to Wheat EST databases and the Wheat genome (Table S1; International Wheat Genome Sequencing Consortium [IWGSC] et al., 2018).

A panel of probes was used to measure expression of 116 key regulatory genes (Table S1). Expression values (Table S3) from these probes were analyzed by one-way ANOVA to detect genes whose expression changed significantly as a result of photoperiod treatment (Table S2). From the total set of 116 probes, 12 genes showed significant SD treatment-induced changes in expression. Detailed analysis of the expression dynamics for each of these 12 genes identified only six that showed significant expression differences across a majority of wheat varieties during the treatment. These six genes all had similar response dynamics to the SD treatment, independent of cultivar (Figure S4). Notably, SD treatment led to a shift in morning levels of the wheat GIGANTEA (GI) homolog (TraesCS3A01G116300) (Figure 6a) and higher morning levels of wheat TOE1-like homologs (TraesCS1A02G058400; TraesCS1B01G076300; TraesCS1D02G059200) (Figures 6b and S4). We also observed lower morning levels of TaTOC1 (TraesCS6D02G207100), TaAGL10 like (TraesCS2B02G200800), TaVRN1 (TraesCS5A02G391700) (Figure 7a–c), and TaAGL29 (TraesCS2B02G281000) genes (Figure S4).

In summary, all tested cultivars responded to SD treatment by modifying transcriptional levels of the key clock gene TaGI (Figure 6a), showed higher levels of the TaTOE1 (Figure 6b) and lower levels of the TaAGL10 (Figure 7b). Most of the lines had also shown a significant decline in the morning levels of the clock gene TaTOC1 (Figure 7a), vernalization control gene TaVRN1 (Figure 7c), and MADS-box gene TaAGL29 (Figure S4). Other treatment-induced changes in expression were likely associated with cultivar specific responses (Figure S4).

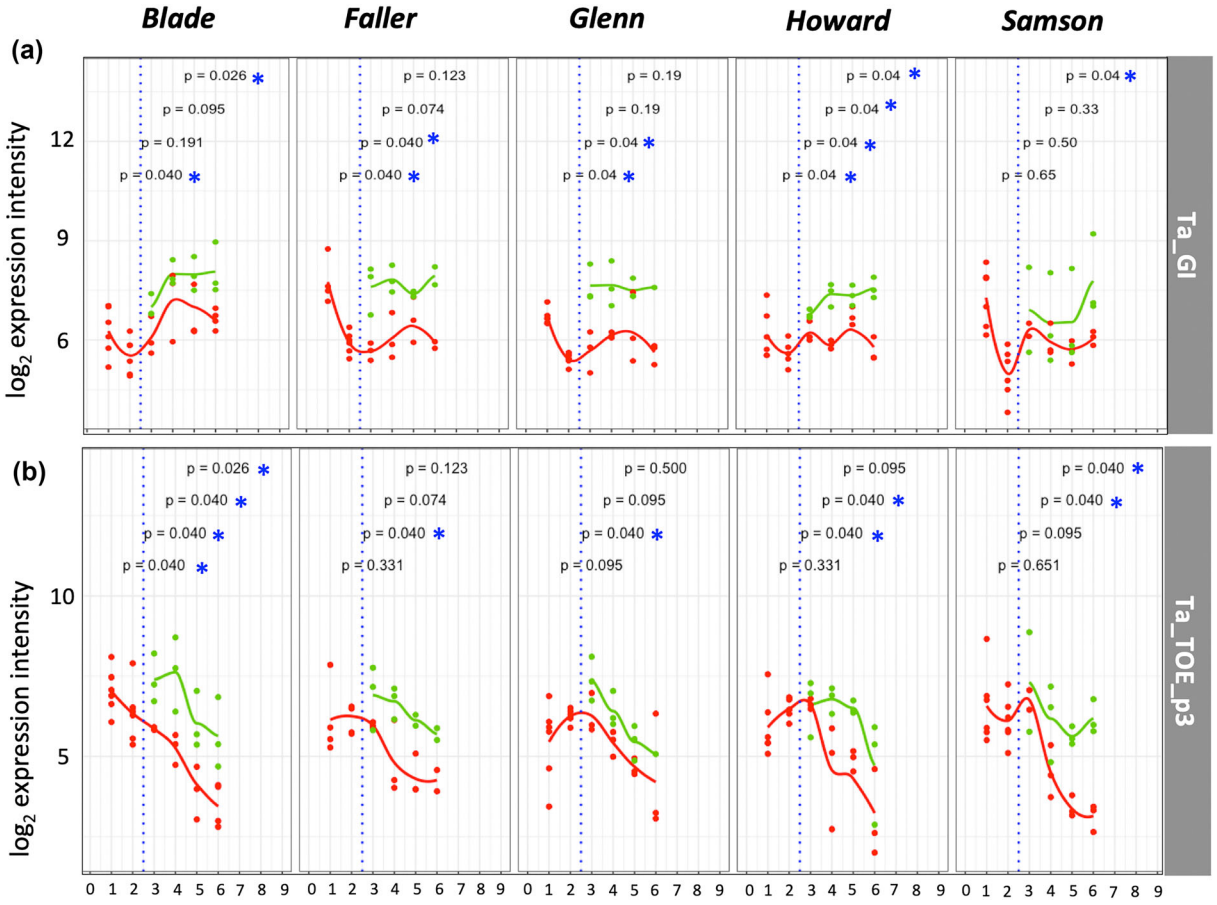

FIGURE 6 Expression changes in TaGI and TaTOE1 genes induced by photoperiod treatment in shoots sampled 2 h after dawn. Across all tested inbred lines, morning expression levels reported by the (a) Ta_GIGANTIA (TraesCS3A01G116300) probe and (b) Ta_AP2_TOE (TraesCS1A02G058400) probe were higher in SD-treated plants (green lines/dots) than in LD-grown controls (red lines/dots) In (a) and (b), *Y* axis indicates log2 expression intensity detected by the "Panomics" assay; *X* axis indicates time points after sowing. All plants were initiated at the LD conditions and sampled 7 days after seeding (Point 1) and then 10 days after sowing prior to transition of the treated group to SD conditions (Point 2). (Time point of treatment initiation is indicated by the vertical blue line). During SD treatment, sampling was performed at 11, 13, 21, and 38 days after sowing from both SD-treated and LD-grown plants (Time Points 3–6, respectively). *p* values above Time Points 3–6 indicate significance of the Student's *t*-test comparison between the LD-grown and SD-treated plants. Time points where differences of the expression levels were detected as significant marked by blue asterisks.

4 | DISCUSSION

4.1 | Transient SD treatment drives trait changes that create an optimal yield ideotype by changing meristem maturation patterns

In this study, we revisited the effect of photoperiod treatments to maximize yield performance of spring wheat cultivars in order to gain insight into associated trait and gene expression changes underlying yield improvement. For this purpose, we developed a simplified SD treatment protocol that induces higher yields compared with constant LD- or SD-grown controls. Previous reports suggested that improved yield performance of transiently SD-treated plants is linked to increased spikelet number compared with LD control (Guo et al., 2018; Rawson, 1970). However, we observed that the number of spikelet branches developed per wheat plant is correlated with duration of the plant's exposure to the SD conditions, not to yield. Thus, transient SD-treated plants have higher spikelet numbers than LD-grown controls but develop fewer spikelet branches than SD-grown controls (Figure 4a). These trait effects are associated with significantly higher per plant yields than achieved with constant SD or LD growth (Figure 5a).

Consistent with previous work, our observations suggest that SD conditions promote vegetative growth in wheat and delay final maturity (Rawson, 1970; Thorne et al., 1968). Wheat plants grown in SD throughout their life cycle show the greatest increase in traits related to late termination including flag leaf area, biomass, tiller, and leaf numbers (Figure 4a–c). Transient SD treatment performed during early stages of primary spike development leads to smaller increases in these traits (Figure 4a–c) which are thereby able to drive more biomass production without significant changes in harvest index (Figures 4a,c and 5d). Together, these observations

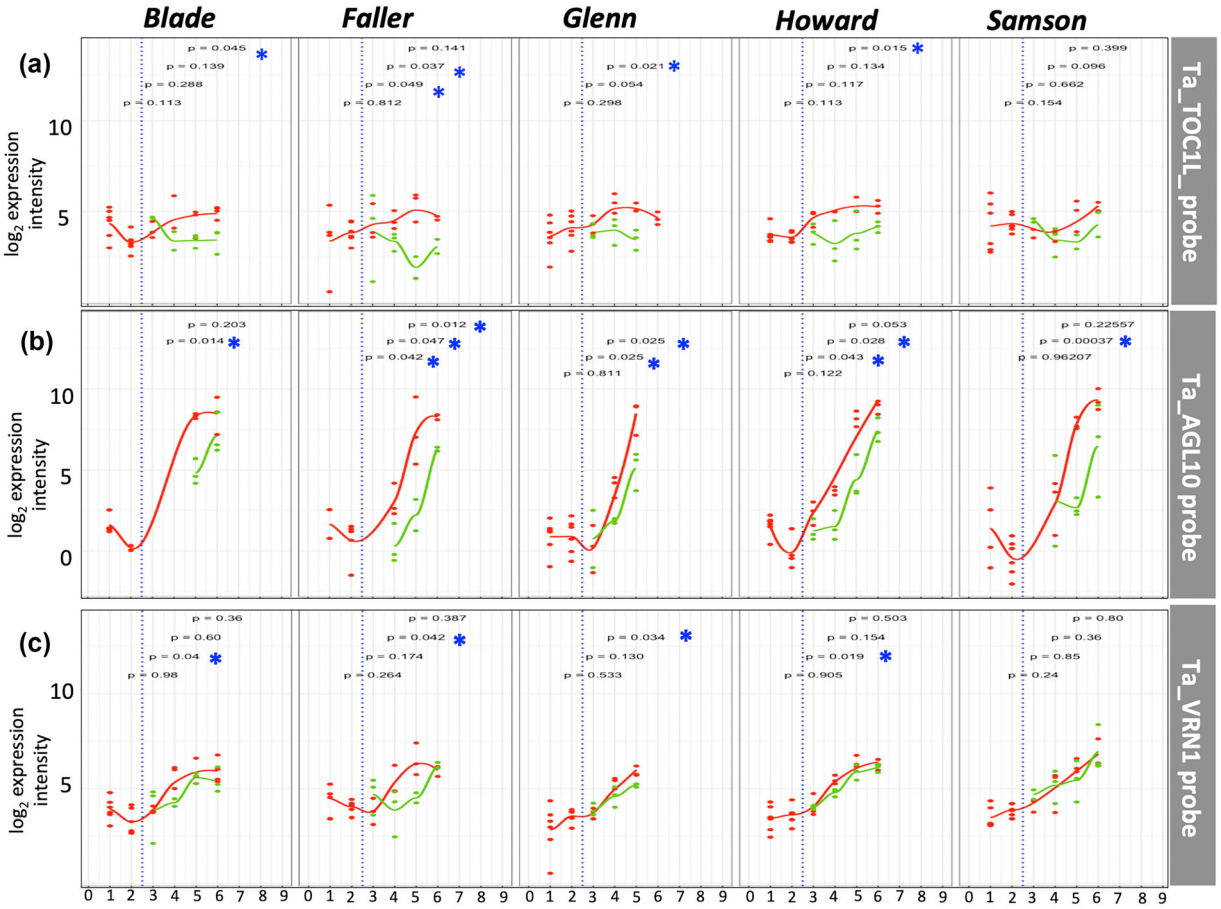

FIGURE 7 Expression changes in TaTOC1, TaAGL10, and TaVRN1 genes induced by photoperiod treatment in shoots sampled 2 h after dawn. Morning expression levels reported by the (a) Ta_TOC1 (TraesCS6D02G207100) probe and (c) Ta_VRN1 (TraesCS5A02G391700) probe were significantly down-regulated by the SD treatment in at least at one time point in all tested cultivars but Samson. Levels reported by the (b) Ta_AGL10 probe (TraesCS2B02G200800) were significantly down-regulated by the SD treatment at least at one time point during the treatment in all tested cultivars. In (a)–(c), red lines/dots (LD-grown shoots), green line/dots (SD-treated shoots); *Y* axis indicates log2 expression intensity detected by the "Panomics" assay; *X* axis indicates time points after sowing. *p* values above Time Points 3–6 indicate significance of the Student's *t*-test comparison between the LD-grown and SD-treated plants. Significant differences marked by blue asterisks.

suggest that transient SD-induced yield improvement is not linked to a change in any one trait but rather to the achievement of an optimal balance of changes in multiple traits that result in a higher yielding ideotype.

We note that yield for most crops, including wheat, has traditionally been modeled as the combinatorial outcome of so-called source and sink traits (Chang et al., 2017; Sonnewald & Fernie, 2018), with the notion that attaining the optimal balance of source (production) and sink (consumption) functions within the plant will result in superior yield output. Several studies in wheat have established positive correlations between sink traits (including spikelet number, kernel number per spike, and thousand-grain weight) and yield (Rawson, 1970; Slafer, 2003; Sreenivasulu & Schnurbusch, 2012). Source traits (including flag leaf area, stay green, spectral reflectance indices, and plant biomass) have also been positively correlated with yield (Gizaw et al., 2016; Johnson et al., 1990; Rebetzke et al., 2002). However, in many cases, the yield effect of source and sink trait modifications has been inconsistent across diverse environmental conditions and genetic backgrounds (Borrill et al., 2015; Chang et al., 2017; Sonnewald & Fernie, 2018; Wallace & Yan, 1998). In this study, we have extended beyond source and sink component traits to achieve trait-based yield improvement that accommodates diverse genetics and environments. This plant ideotype-based approach is more consistent with the need to create environmentally stable yield traits for a changing climate (Anderson et al., 2020).

Our study suggests that transient SD-induced trait changes leading to yield improvement begin with altered meristem development. SD treatment changes meristem development within the first 10 days after application (Figure 3c,d,f,g). Our results suggest that manipulation of meristem maturation dynamics leads to changes in the balance between other yield-related trait components. Importantly, these observations imply that the optimization of yield could be achieved by manipulation of plant developmental dynamics rather than individual source and sink traits.

Interestingly, trait component analysis performed at harvest shows that SD treatment leads to improved yield mainly due to an increase in the average grain weight rather than kernel number (Figure 5a–c). Similar observations were reported in some early studies (Rawson, 1970). In SD-treated plants, both anthesis and grain fill period happened several weeks after the completion of the treatment, when SD-treated plants had been returned to the same conditions as LD controls. It has been suggested that increased grain weight in the SD-treated plants is related to flag leave size (Rawson, 1970). However, our data shows that the flag leaves of SD-treated plants were actually smaller than controls (Figure 4b), suggesting instead that early optimization of the developmental dynamics lead to subsequent trait changes, resulting in more efficient grain fill.

4.2 | Expression changes associated with meristem maturation rate reveal genetic targets for crop improvement

We have identified key underlying changes in gene expression that are associated with SD-induced developmental dynamics. We observed significant changes in diurnal expression of TaGI and TOE1-like members of the large wheat AP2 gene family (Riaz et al., 2021; Zhao et al., 2019). We found that in the morning hours TaGI levels are higher in the SD-treated plants across all the lines (Figure 6a), consistent with previous profiling of TaGI expression in the SD and LD-grown spring wheat (Zhao et al., 2005). Similar dynamics were detected for TaTOE1 transcripts (Figures 6b and S4), suggesting that in wheat, transient SD treatment could act via the GIGANTEA/AP2-TOE1/mir172 pathway (Jung et al., 2007). Consistent with our results, a recent study of doubled haploid populations identified the TOE1-like gene TaTOE1-B1 as one of the candidate genes for floral repression activity under a large effect SD response QTL in wheat (Zikhali et al., 2017).

In addition to changes in TaGI and TaTOE1 expression, we determined that SD treatment leads to slower accumulation of the TaAGL10 and TaAGL29 MADS-box transcription factors in developing shoots (Figures 7b and S4). Analysis of expression data generated by an independent study shows that transcripts associated with TaAGL10 and TaAGL29 ESTs have very low expression levels across different tissues prior to Zadoks 30 stage and are up-regulated at Zadoks 71 leaves, Zadoks 32–65 stems, and Zadoks 32–65 spikes (Choulet et al., 2014; https://wheat.pw.usda.gov/WheatExp). The same data reveal opposite dynamics for transcripts associated with TaTOE1 EST which are accumulated at higher levels in Zadoks 10 leaves and Zadoks 30 stems than at any other above-ground tissue at the later developmental stages. Together, our observations and these data suggest that TaAGL29/10 expression is associated with maturation of the wheat leaf and meristematic tissues whereas TaTOE1 expression is associated with early stages of the leaf and stem development. Transient SD treatment delays the progression of maturation in the treated wheat plants which results in slower rate of down-regulation of the TaTOE1 transcripts and delayed accumulation of the TaAGL29/10 transcripts. For TaTOE1 genes, such dynamics appears to be in line with the role of the gene described in other species (Jung et al., 2007; Poethig, 2013; Teotia & Tang, 2015). However, to this date, little is known about the role of the TaAGL29/10 genes. Future investigations of TaAGL29 and TaAGL10 expression patterns, in situ localization patters, mutant allele analysis and protein functional characterization would be required to provide a clearer explanation of their role in regulation of the wheat developmental dynamics. Future work could also address whether TaAGL29 and TaAGL10 interact with or through circadian clock pathway genes such as LUX ARRHYTHMO/PHYTOCLOCK 1, previously shown to modulate spike length and number in einkorn wheat (Gawroński et al., 2014). In addition, our results in wheat indicate that SD treatment after initiation of inflorescence leads to slower accumulation of TaVRN1 transcripts and correlates with delayed meristem maturation (Figures 3 and 7c). These results align with recent reports demonstrating that TaVRN1 is promoting reproductive transition and maturation of the wheat spike meristem (Li et al., 2019; Li, Zhou, et al., 2021). The classical photoperiod-sensitivity (Ppd) genes in wheat (Arjona et al., 2020) do not exhibit changes in expression under photoperiod treatments in this experiment.

In conclusion, results presented here demonstrate a strong link between photoperiod treatments capable of driving improved yield performance and the dynamics of inflorescence meristem maturation. Our detailed analysis of meristem development and gene expression in response to photoperiod treatments show that application of SD during wheat inflorescence establishment leads to deceleration of spike development and up-regulation of molecular factors associated with the vegetative phase, like TaTOE1 (Choulet et al., 2014; Jung et al., 2007; Poethig, 2013; Teotia & Tang, 2015), as well as down-regulation of factors like VRN1 that are linked to control of the transition from vegetative to reproductive development and the rate of spike maturation in cereals (Greenup et al., 2009; Hemming et al., 2008). Work in the past decade has highlighted the linkage between photoperiod responses and molecular networks responsible for the transition from vegetative to reproductive meristem fates (Lifschitz et al., 2014; Song et al., 2015; Teotia & Tang, 2015). However, the role of the same networks in reproductive development remains underinvestigated. Our results suggest similar mechanisms are involved in regulation of the vegetative to reproductive transition and the maturation dynamics after meristems change fate. We show that manipulation of these dynamics could lead to a plant ideotype with improved yield performance of spring wheat and potentially other crops. Comparable observations have been reported in tomato (Lifschitz et al., 2014; Park, Eshed, et al. 2014; Park, Jiang, et al., 2014). Fine-tuning of meristem maturation rate is an important target for future improvement of crop yield performance. Taken together with the recognition that varietal adaptation depends on selection for optimal photoperiod response, there is opportunity to link yield improvement with future adaptation to a changing climate through this approach. With the development of genome editing tools and the increasing ability to manipulate allelic variation of individual genes (Rodríguez-Leal et al., 2017; Soyk et al., 2017), we can take

advantage of our enhanced understanding of genetic elements that underly agronomic traits to design more productive, climate-resilient crops for the future (Henry, 2019).

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CONFLICT OF INTEREST

The authors are employees of Bayer Crop Science, a manufacturer of seeds.

AUTHOR CONTRIBUTIONS

A.G. and S.P. designed the hypothesis and experiment. A.G., T.Z., and D.Z. conducted the experiment. A.G., B.B-T., and T.S. analyzed the data and wrote the manuscript.

DATA AVAILABILITY STATEMENT

Marker and additional data sets are available in supplemental materials.

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SUPPORTING INFORMATION

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