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Integrating genetic analysis and crop modeling: A major QTL can finely adjust photoperiod-sensitive sorghum flowering

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ABSTRACT

In West Africa Sudano-Sahelian zone, sorghum sensitivity to photoperiod is a major trait for flowering adjustment toward the end of the rainy season. This trait ensures that conditions for crop development are optimal. Improving the understanding of the genetic control of flowering time in sorghum is thus an important step toward breeding climate resilient varieties for meeting the challenge of climate smart agriculture. In the wake of green revolution, most sorghum breeders eliminated photoperiod sensitivity to develop early maturing varieties. The evidence is now that simultaneous improvement of production, yield stability and grain quality requires the development of photoperiod-sensitive varieties.

A segregating sorghum population derived from a cross between two photoperiod sensitive elite parents was evaluated in three different locations and five environments. CERES crop model was applied to decompose the flowering time of each genotype into basic vegetative phase, critical photoperiod and photoperiod sensitivity. Phenology and model derived variables were used for genetic analysis.

The three model parameters were controlled by specific genomic regions. A major QTL affecting critical photoperiod was identified, whereas only independent minor QTLs were found for basic vegetative phase and photoperiod sensitivity. Candidate gene analysis in the major QTL region allowed us to propose a candidate gene (*ELF3*) involved in the circadian clock as a key regulator of flowering time in photoperiod-sensitive sorghum. Our findings provide critical information supporting the development of photoperiod-sensitive genotypes specifically adapted to climate variability encountered in Sudano-Sahelian zone.

1. Introduction

Sorghum (*Sorghum bicolor* (L.) Moench) is a C4 grass grown for grain and biomass in a wide range of climatic and geographic conditions. In dryland systems, and particularly in West-Africa, this crop has a predominant role in food security for millions of rural families. Sorghum is a photoperiodic short-day plant (Garner and Allard, 1923) for which flowering occurs when day length becomes shorter than a critical photoperiod. Flowering time is a major ecologic and agronomic trait as it controls sorghum adaptation to environments by adjusting vegetative and reproductive growth phases to local biotic and abiotic constraints.

Photoperiod-sensitive sorghum landraces that are cultivated in Africa can be seen as the result of a long massal selection conducted by African farmers that contributed to fine-tune their adaptation to specific environmental and management conditions. The Sudano-Sahelian climate is characterized by a very high within and across year rainfall variability. Most sorghum varieties in West Africa are photoperiod sensitive and flower within 20 days preceding the average ending date of the rainy season regardless of the sowing date (Kouressy et al., 2008a, 2008b). Photoperiod sensitivity improves simultaneously (i) biomass production by optimizing the duration of the vegetative period, (ii) between year yield stability by mitigating the impact of drought (preventing late flowering) and avoiding midge and bird attacks (grouping flowering) and (iii) grain quality by limiting mold

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development (preventing early flowering) (Kouressy et al., 2008b).

Sorghum breeding programs eliminated photoperiod-sensitivity from elite grain sorghum germplasm mainly to develop varieties with a broader geographical adaptation (Stephens et al., 1967; Chantereau et al., 2001; Swaminathan, 2006). However, in West-Africa, the selection for early maturing varieties has often proven to be an inadequate goal as the problem is not the growing season short duration, but the variability of beginning and ending of seasons in both time and space. Furthermore, forecasted increase in climate variability supports development of new breeding strategies enhancing crop adaptation. Nowadays, development of high yielding photoperiod-sensitive varieties adapted to the Sudano-Sahelian climate becomes a priority of dryland cereals breeding programs in West-Africa (Kouressy et al., 1998; Vaksmann et al., 2008). In addition, photoperiod sensitivity, recently drew breeders attention to develop late-flowering sorghum (Murphy et al., 2014) or to increase biomass yield for biofuels production (Olson et al., 2012).

The genetic basis of flowering time has been extensively studied in sorghum through linkage analysis and association mapping studies summarized by Mace and Jordan (2011); Mace et al. (2013). From these studies, it may be concluded that flowering is controlled by several major maturity genes and modulated by a relatively large number of loci with small effects (Mace et al., 2013). However, most of these analyses were based on populations derived from photoperiod insensitive parents or from sensitive by insensitive crossings, neglecting populations developed from photoperiod sensitive parents.

Among the main known flowering pathways (i.e. photoperiod, autonomous, vernalization, gibberellin and plant age: Mouradov et al. (2002); Boss et al. (2004); Fornara et al. (2010); Wang (2014); Hyun et al. (2017)), temperature and photoperiod are identified as the main regulators. For short day plants, such as sorghum, flowering is delayed by synthesis of repressors when day lengths exceed a critical photoperiod.

To date, six major maturity genes (Ma_1-Ma_6) have been described in sorghum (Quinby, 1967; Rooney and Aydin, 1999; Morgan and Finlayson, 2000; Brady, 2006; Mullet et al., 2016). Generally tropical types are dominant at these loci (late-flowering) and recessive alleles (early-flowering) are used for temperate zone adaptation (House, 1985). Among the first four loci, Ma_1 causes the largest delay in flowering time in long days (Murphy et al., 2011). Both Ma_2 and Ma_4 have been shown to be temperature sensitive (Quinby, 1966; Major et al., 1990). Three of these genes have been cloned and the description of their interactions allowed the development of a global pathway model (Murphy et al., 2014; Yang et al., 2014). Positional cloning studies enabled to demonstrate that Ma_1 encodes *pseudoresponse regulator protein* (*SbPRR37*), a flowering repressor (Murphy et al., 2011), Ma_3 gene was shown to be *phytochrome B*, a plant photoreceptor (Childs et al., 1997), and Ma_6 has been identified as *Grain Number, Plant Height and Heading Date 7* (*SbGHD7*), a floral repressor regulated by the circadian clock and light signaling (Murphy et al., 2014). Another phytochrome gene, *PhyC*, was proposed as a candidate gene for Ma_5 based on sequence alignment and allelic variation (Yang et al., 2014). It has been then proposed that in long day conditions, Ma_3 regulates Ma_6 and Ma_1 who repress the expression of the grass floral integrator *Early heading date 1* (*Ehd1*) which usually activates floral inductors (homologs of the *Flowering Locus T/Centroradialis* (*CN*), *SbCN8*, *SbCN12* and *SbCN15*) leading to delayed flowering. In these conditions, floral induction is also dependent of the circadian clock output. In short days, expressions of the floral repressors Ma_1 and Ma_6 are reduced resulting in floral initiation with the condition that the plants have satisfied other requirements for flowering (Murphy et al., 2014; Yang et al., 2014).

In photoperiod-sensitive sorghum varieties, maturity and morphology are strongly impacted by the sowing date and hence difficult to predict. Crop models are commonly applied to assist plant breeding by integrating physiological and biochemical understanding, along with agronomic practices, environment and genetic information (Messina et al., 2006). Modeling, mainly based on the sorghum CERES model, has been used in sorghum to predict the effect of photoperiod on crop development (Ritchie and Alagarswamy, 1989).

The objective of the current study was to analyze the genetic architecture of flowering time in photoperiod sensitive sorghum. In addition to direct measurements of flowering time, eco-physiological modeling was used to shed a new light on flowering time QTLs and their use in plant breeding programs.

2. Materials and methods

2.1. Plant materials

The mapping population was originally developed as part of a marker assisted recurrent selection program aiming at identifying QTLs for target traits and cumulate positive alleles in recurrent generations. A F_3 population was derived from the cross between Tiandougou and Lata3 sorghum lines in 2008. The two lines are elites respectively from IER (Institut d'Economie Rurale) and ICRISAT (International Crops Research Institute for the Semi-Arid Tropics) breeding programs. Target traits of the breeding project were grain yield and quality, as well as adaptation to local environment. Both parents are medium height (< 200 cm), well adapted to Sub-Saharian conditions and photoperiod sensitive. Furthermore, parents are interesting combiners based on their agronomic performances, Tiandougou for grain yield and Lata3 for grain quality. In normal sowing conditions (i.e. June), Tiandougou matures slightly later than Lata3 (127 and 120 days from sowing to grain physiological maturity respectively). Choosing two photoperiod sensitive parents enabled us to focus on fine regulation of maturity rather than photoperiod sensitivity suppression.

A single F_1 plant was selected and selfed to produce the F_2 generation. Four hundred individual F_2 plants were advanced to F_3 generation in off-season. Rows of 10 F_3 plants were sown in 2009 and a single F_3 plant was randomly selected in each row. Ten F4 plants per family were then sown in off-season, selfed and bulked leading to a total of 400 $F_{3:5}$ bulks seeds which were used for multiple agronomic phenotyping experiments. As the selfing cycle between the F4 plants and the F3:5 seed bulks reduced the level of heterozygosity in each family, only additive effects are provided in the genetic analyses.

2.2. Field phenotyping

The mapping population was phenotyped in three locations and five environments. Three IER stations, representative of different Malian agro-climatic zones, were used: Cinzana station (13°15′N, 5°58′E °N, 265 m; Sudano-sahelian savannah), Sotuba station (12°39′N, 7°56′E, 381 m, Sudano-sahelian savannah) and Farako station (11°13′N, 5°29′E, 375 m, Sudano-Guinean savannah). All sites (Fig. 1) have a monomodal pattern of rainfall in summer (May to November) accounting on average for 690 mm at Cinzana, 890 mm at Sotuba and 1060 mm at Farako. Average maximal (minimal) monthly temperatures were 35.6 °C (19.3 °C) at Cinzana, 34.7 °C (20.6 °C) at Sotuba and 33.7 °C (21.0 °C) at Farako.

In Sotuba research station, experiments were conducted at three sowing dates corresponding to different photoperiod conditions. The population was observed in long and intermediate day length (usual cropping season, sowing 19 June and 15 July 2011) and short day length (off-season, sowing 3 October 2011). Short day length observations were rather conducted in October than December to avoid cold temperatures that could interact with photoperiod sensitivity (Vaksmann et al., 1998). At Cinzana and Farako, only one sowing date was done, respectively 3 July and 19 June 2011. Maximum astronomical day length is 12.78 h at Cinzana, 12.75 h at Sotuba and 12.66 h at Farako increasing from South to North by 7 min.

An augmented experimental design including 29 blocks of 16 families was used. The 404 progenies (families) were randomly allocated

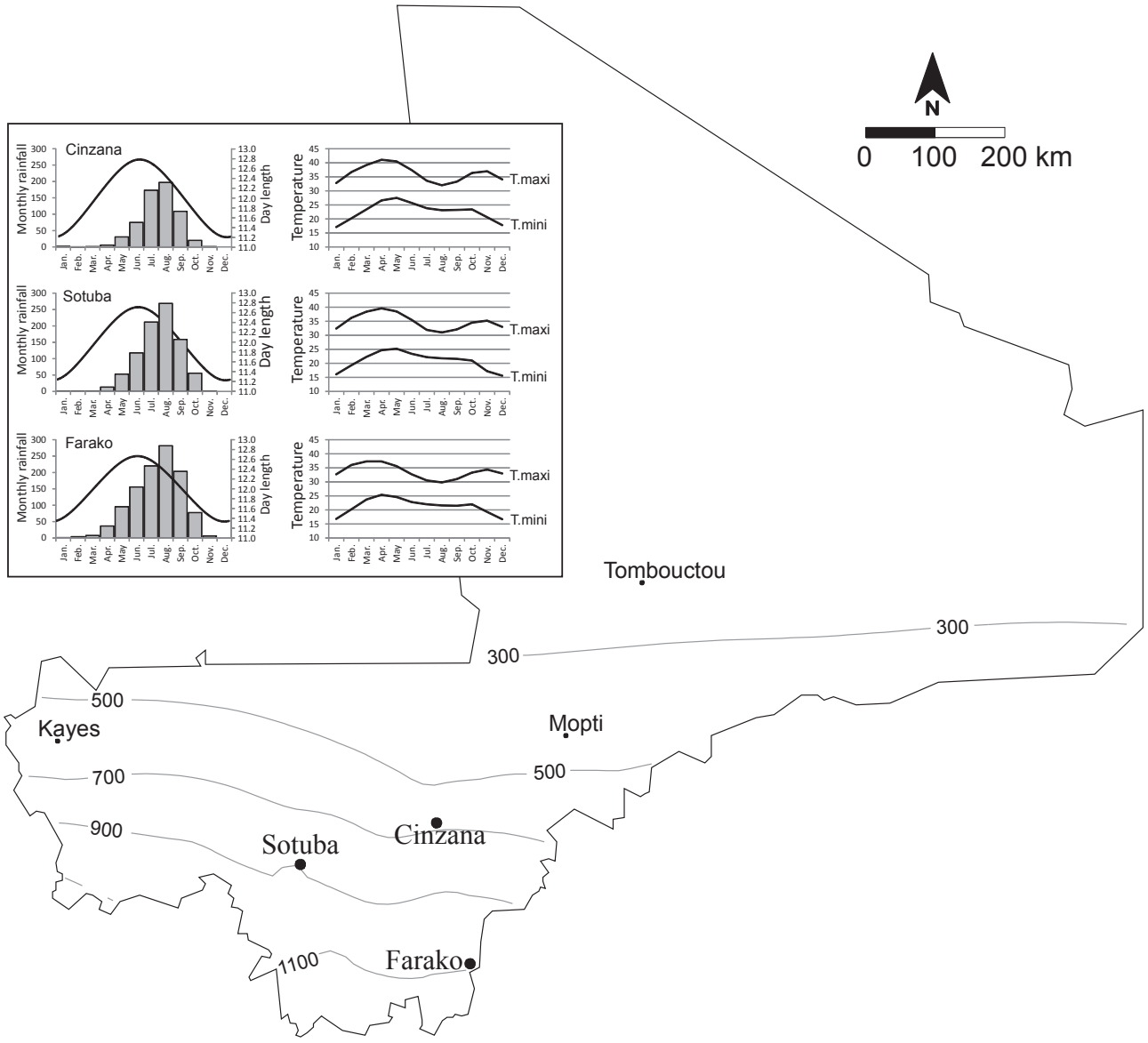

Fig. 1. Location of experimental sites in Mali compared with average annual rainfall (period 1981–2010). Evolution, for each of the three sites, of astronomical photoperiod (solid lines), average monthly rainfall (histogram), minimum (T.mini) and maximum (T.maxi) temperatures.

to the blocks with the two parents repeated within each block as check. In this way, test entries were included in the experiment only once and check entries allow testing block effects. The design was completed to 464 entries by adding supplementary replications of the parents. Each elementary plot consisted of 40 plants arranged in two rows of 4 m. Phenology was measured as the date when the flag-leaf's ligule was visible. This stage marks the end of leaf expansion and the beginning of anthesis about 10 days later (Kouressy et al., 2008a). Dates of flag-leaf ligulation were recorded when 50% of the plants in a plot had reached the stage. In sorghum, this observation is more accurate and repeatable than the scoring of the average flowering date commonly practiced in agronomic experiments (Tarumoto et al., 2003).

2.3. Environmental parameter calculation

Thermal time after emergence was computed using an algorithm developed by Jones and Kiniry (1986), considering that growth speed increases as a linear function of temperature between a base and an optimal temperature, and then decreases linearly between optimal and maximal temperature. Cardinal temperatures were 11 °C for base temperature (Lafarge and Hammer, 2002), 34 °C for optimum temperature and 44 °C for maximum temperature (Abdulai et al., 2012). The resulting thermal time per day was used to calculate the progress of developmental processes. The Thermal Time from emergence to flag leaf ligulation (TTFL) was computed for each family and each sowing date and expressed in degree days (°Cd). Thermal time to panicle initiation (TTPI) was derived from TTFL using the linear formula proposed by Folliard et al. (2004). Thermal times to panicle initiation are given for Farako (TTPI-FK), Cinzana (TTPI-CZ) and the three sowing dates of Sotuba (TTPI-SB1, TTPI-SB2, TTPI-SB3) (Table 1).

Day length used is not astronomical day length but civil day length (sunrise to sunset plus civil twilight), which includes periods when the sun is 6° below the horizon to account for photoperiod effect during dawn and twilight (Aitken, 1974). To avoid confusion, in this paper, the term photoperiod will be used to express civil day length.

2.4. Statistical analyses

Phenotypic data were adjusted considering the augmented experimental design requirement using the DAU.test function (package

Table 1
Trait names, experimental sites, sorghum trait dictionary ID (http://www.cropontology.org/ontology/CO_324/Sorghum) and variables abbreviations for each studied variable. For the thermal time to panicle initiation variables, the table displays the date when the experiment was sown and the civil photoperiod conditions for each date at each site (h, hour).

Trait	Experimental site	Variable abbreviation	Sorghum Trait Dictionary ID	Sowing date	Photoperiod at sowing date (h)
Thermal Time to Panicle Initiation	Sotuba	TTPI-SB1	CO_324:0000704	19 June 2011	13.65
Thermal Time to Panicle Initiation	Sotuba	TTPI-SB2	CO_324:0000704	15 July 2011	13.57
Thermal Time to Panicle Initiation	Sotuba	TTPI-SB3	CO_324:0000704	3 October 2011	12.70
Thermal Time to Panicle Initiation	Cinzana	TTPI-CZ	CO_324:0000704	3 July 2011	13.66
Thermal Time to Panicle Initiation	Farako	TTPI-FK	CO_324:0000704	19 June 2011	13.55
Critical Photoperiod	Sotuba	P2O	CO_324:0000699	–	–
Basic Vegetative Phase	Sotuba	BVP	CO_324:0000695	–	–
Photoperiod Sensitivity	Sotuba	P2R	CO_324:0000708	–	–

'agricolae') in the R environment (R: The R Project for Statistical Computing). Normality of the variables was assessed using the Shapiro-Wilk normality test (shapiro.test function, package '*stats*').

2.5. Crop modeling

The varietal response to photoperiod was modeled using the sorghum linear CERES model (Major et al., 1975; Alagarswamy and Ritchie, 1991). This model (Fig. 2) is based on a linear adjustment between photoperiod and the length of the vegetative phase (Chantereau et al., 2001; Bangbol, 2013; Sanon et al., 2014). After emergence, the shortest thermal time required to reach panicle initiation is known as the Basic Vegetative Phase (BVP) (Major et al., 1990). During this phase, floral induction does not occur whatever the photoperiod conditions. The CERES model considers that below a critical photoperiod (P2O), the duration of the vegetative stage is constant and is equal to BVP. Above P2O, the duration of the vegetative stage increases as a linear function of photoperiod whose slope (P2R) defines photoperiod-sensitivity.

A modified CERES model version was used (Folliard et al., 2004). Photothermal time accumulation was replaced by a critical photoperiod threshold (varying on plant age) below which sorghum panicle initiation occurs. The three model parameters (P2O, P2R and BVP) were calculated using a method previously presented by Chantereau et al. (2001). For each family, the TTPI was plotted for the three sowing dates against the photoperiod at panicle initiation date (Fig. 2). In practice, BVP was calculated from the minimal duration of the vegetative phase observed at Sotuba in October sowing. The photoperiod sensitivity P2R was estimated as the slope of the line drawn between the points related to the sowing dates of June and July. The critical photoperiod P2O, corresponds to photoperiod at the intersection of this line and the BVP base line.

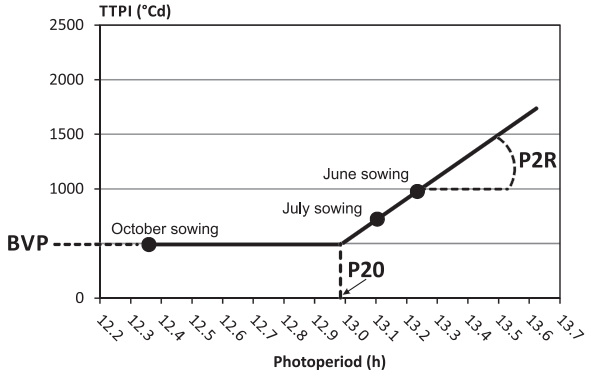

Fig. 2. Modelling of Thermal Time for Panicle Initiation (TTPI) according to CERES model. Three parameters, BVP, P2O and P2R, are derived from this modeling. Data from the parent Tiandougou were used to establish the figure.

2.6. Genetic analysis

For each of the 400 families, DNA was extracted from a bulk of 10 F4 plants using the MATAB method (Risterucci et al., 2000). Two hundred and twenty eight SNP markers were used. The information regarding these SNPs is accessible on the SNP genotyping service web page of the Integrated Breeding Platform.[2] SNP genotyping was outsourced to LGC Genomics (Teddington, UK).

The genetic map was built using Mapmaker (Lander et al., 1987). Linkage groups were determined using the "group" command with a LOD threshold of 3.0 and maximum distance of 50 cM. Loci were ordered in each group using the "order" command with the default parameters of the function. When several local orders were equally probable, the one in agreement with the expected order deduced from the physical positions of the markers was kept. The map distances for the final ordered linkage groups were computed using the Haldane mapping function.

QTL mapping was performed using R (R_Development_Core_Team, 2008) and the R-*qtl* package (Broman and Sen, 2009). The Multiple Interval Mapping method (MIM) was applied with a mapping step of 1 cM. To identify the multiple QTL model with maximal LOD score while controlling false positive rates, the *stepwiseqtl* function was applied that performs forward/backward model selection using a penalized likelihood approach to compare different model sizes, with penalties on QTL and pairwise interactions (Manichaikul et al., 2009). LOD penalties were derived for each trait from the result of 1000 permutations of a two-dimensional genome scan with a two-QTL model allowing covariates (functions *scantwo* and *calc.penalties*). The model optimizing the penalized LOD score criterion was fitted with the *fitqtl* function to get QTLs estimated effects. For each detected QTL, positions with maximum likelihood were identified (function *refineqtl*) before approximate 95% Bayesian credible intervals were calculated (function *bayesint*).

2.7. In silico mapping of candidate genes

Positions of genetic markers were retrieved from the *Sorghum bicolor* genome sequence assembly v3.1 (http://genome.jgi.doe.gov) using SNP flanking sequences and the Bowtie2 program (Langmead and Salzberg, 2012). The region flanking the Chromosome 3 major QTL was investigated for candidate genes. Markers flanking the QTL (SB03075 and SB03085) were considered as the confidence interval on the physical map and their positions on the chromosome (48,834,006 and 52,478,805 bp, respectively) were used to identify genes present in this interval. Using the version 3.1 of the Sorghum bicolor gene annotation available from Phytozome v11, 159 predicted genes were located within the QTL interval of which 120 had a best hit reported in Arabidopsis (Table S1). Protein sequences of the 39 genes with no available annotation were used to manually search for ortholog proteins using the NCBI protein BLAST program (https://blast.ncbi.nlm.nih.gov/Blast.

[2] https://www.integratedbreeding.net/482/communities/genomics-crop-info/crop-information/gcp-kaspar-snp-markers.

cgi). Out of these 39 genes, 15 predicted genes had a significant hit in rice that corresponded to expressed proteins with unknown function and no significant hit was found for any of the 24 remaining proteins. Consequently, the name of the best Arabidopsis hit was used for gene ontology categorization using the TAIR web tool for functional categorization (http://www.arabidopsis.org/to/bulk/go/index.jsp).

3. Results

3.1. Phenology study

The two parents exhibited differences for TTPI measurements and CERES model parameters. The photoperiod sensitivity of Lata3 was higher than that of Tiandougou (P2R = 2446 and 1275 °C days/h, respectively). These values can be considered as high photoperiod sensitivities and correspond respectively to increases by 150 and 80 days of the duration of the vegetative phase per hour of photoperiod increase. The critical photoperiod of lata3 (P2O = 13.25 h) was higher than that of Tiandougou (P2O = 12.99 h). In Sotuba, mean population TTPI value decreased from the first to the third sowing. Its values were respectively 709, 477, 306 °Cd from sowing dates 1–3. These values correspond respectively to 46, 33 and 22 days. The mean value of TTPI was 694 °Cd at Cinzana and 526 °Cd at Farako which corresponds to 45 and 39 days. The gap in days between Sotuba (46 days) and Farako (39 days) for the same first sowing date cannot be explained by the sowing date because trials were planted almost simultaneously. This difference could be explained by latitude influence since photoperiod in summer is slightly lower at Farako compared to Sotuba.

All the traits exhibited transgressive segregation in the population (Fig. 3). Transgression was particularly important for P2R values. Some families exceeded the value of 5000 °Cd/h for P2R. These extreme values are partly due to the CERES linear model as some families flower around the same time for June and July sowings. Consequently P2R values can become very high. Photoperiod conditions for BVP measurement in off-season are met because the actual photoperiod for October sowing panicle initiation (about 12.4 h) is below the measured minimum critical photoperiod (12.7 h). Thermal time for panicle initiation for the different locations and sowing dates were significantly correlated with each other (r varies from 0.72 to 0.83 with associated p-value < 0.001) (Fig. 4) except for BVP (TTPI-SB3) as photoperiod sensitivity was not expressed at third sowing date (short day length).

The BVP variable (TTPI-SB3) appeared to be independent of other variables. It was not significantly correlated with thermal time or other model parameters except for a weak relationship with P2O (r = 0.22, p-value = 0.001). P2O was significantly correlated to TTPI-SB1 and TTPI-SP2 (r from −0.6 to −0.9 with associated p-value < 0.001) and P2R was slightly correlated to TTPI-SB2 (r = −0.36, with associated p-value < 0.001).

Model parameters, P2O and P2R, were also moderately correlated with each other (r = 0.52, p-value < 0.001). Relationships between model parameters partly derive from their calculation procedure as the values of BVP and P2R are used to calculate P2O.

3.2. QTL detection

A total of 22 QTLs spanning eight chromosomes were detected for all the traits under study (Fig. 5). Sixteen QTLs were detected for Thermal Time to panicle initiation (TTPI) for sowings in normal growing season at Sotuba (TTPI-SB1, TTPI-SB2), Cinzana (TTPI-CZ) and Farako (TTPI-FK). Six QTLs were detected for model parameters (BVP, P2O, P2R) (Table 2).

A major region was identified at 74 cM on chromosome 3 where five QTLs exhibiting high LOD score values were detected for TTPI-SB1, TTPI-SB2, TTPI-CZ, TTPI-FK and P2O (LOD score values of 70.5, 80.4, 43.3, 48.1 and 59.1 respectively). The percentages of phenotypic variation explained by these QTLs ranged from 41% to 58.8%. At this position, the Tiandougou allele (additive effect) increased thermal time for panicle initiation (TTPI-SB1, TTPI-SB2, TTPI-CZ and TTPI-FK) from 62 to 72 °Cd (Table 2) corresponding to an increase in the duration of the vegetative phase from 3.5 to 4.3 days. At the same position, Tiandougou allele decreased P2O coefficient of 0.11 h (6 min and 36 s).

In addition to the major locus, several other QTLs with smaller effects were detected for all traits except P2O for which only the major QTL of chromosome 3 (74 cM) was significant. For TTPI-SB1, 6 QTLs were identified on chromosomes 2, 3, 4, 7, 8, and 10 explaining from 2.4% to 7.1% of phenotypic variance. The multiple QTL model, including an interaction term between the two QTLs on chromosomes 2 and 4, explained 63.9% of the total phenotypic variance for this trait. Two QTLs for TTPI-SB2 on chromosomes 2 and 10 were detected, explaining 2.8% and 2.2% of phenotypic variance respectively, and collocating with two QTLs for TTPI-SB1. Four and three QTLs were mapped for TTPI-CZ and TTPI-FK, respectively, corresponding to genomic regions already identified for TTPI-SB1 and TTPI-SB2. Three QTLs for P2R were detected on chromosomes 3, 7, and 9, explaining 5.8%, 5.6% and 3.7% of the phenotypic variance, respectively. For all of them, the Lata3 parent contributed positive alleles. Finally, two QTLs were detected for BVP, on chromosomes 6 and 9, explaining 4.8% and 5.7% of phenotypic variance and having positive contributions from Lata3 and Tiandougou, respectively.

With the exception of major effects QTLs located on chromosome 3, collocations between maturity QTLs and CERES model QTLs were limited. A QTL of TTPI on chromosome 6 colocalized with a P2R QTL but maturity QTLs on chromosome 2, 4, 8 and 10 did not colocalize with any CERES QTL. Similarly, the BVP QTLs on chromosomes 6 and 9 did not colocalize with any TTPI QTL.

3.3. Candidate gene selection by in silico mapping

Overall, 12 genomic regions were identified using QTL mapping for TTPI, P2R, P2O and BVP, representing more than 217 Mb of the sorghum genome. Only the region of the major QTLs locus on chromosome 3 involving the P2O, TTPI-CZ, TTPI-FK, TTPI-SB1 and TTPI-SB2 traits was investigated to identify possible candidate genes involved in the variation of these traits. This region, flanked by SB03075 and SB03085 markers, represented 3,644,799 bp and included 159 predicted genes of which 124 (78%) were annotated based on Arabidopsis in the Phytozome v11 database (Table S1). Gene ontologies (GO) analysis directed these genes to 14 main categories with the “cellular” and “metabolic processes” being the largest ones. The developmental process ontology, accounted for 22 annotations, representing 15 genes. Among those 15 genes, only two were involved in flowering regulation. The first one, Sobic.003G196300, homologous to AT3G24870, is involved in the “regulation of photoperiodism, flowering” ontology (GO:2000028) and is located at 2,054,278 bp from the LOD peak. The second one, Sobic.003G191700, homologous to AT2G25930 and corresponding to the *Early Flowering 3* gene (*Elf3*), is involved in the “entrainment of circadian clock” (GO:0009649), “photoperiodism, flowering” (GO:0048573), “circadian rythm” (GO:0007623) and “regulation of flower development” (GO:0009909) ontologies and is located at 1,191,464 bp from the LOD peak.

Using resequencing of sorghum accessions (McCormick et al., 2018), mutations with low or moderate effect on the protein were identified for Sobic.003G196300,[3] whereas two mutations having a high impact on the protein structure were identified for Sobic.003G191700[4]; one having a splicing effect (located on Chr03 at 51,271,899 bp) and the other having a frame shift effect (located on

[3] https://phytozome.jgi.doe.gov/pz/portal.html#!gene?search=1&crown=1&detail=%E2%80%89&method=0&searchText=transcriptid:37916424.

[4] https://phytozome.jgi.doe.gov/pz/portal.html#!gene?search=1&crown=1&detail=1&method=0&searchText=transcriptid:37917827.

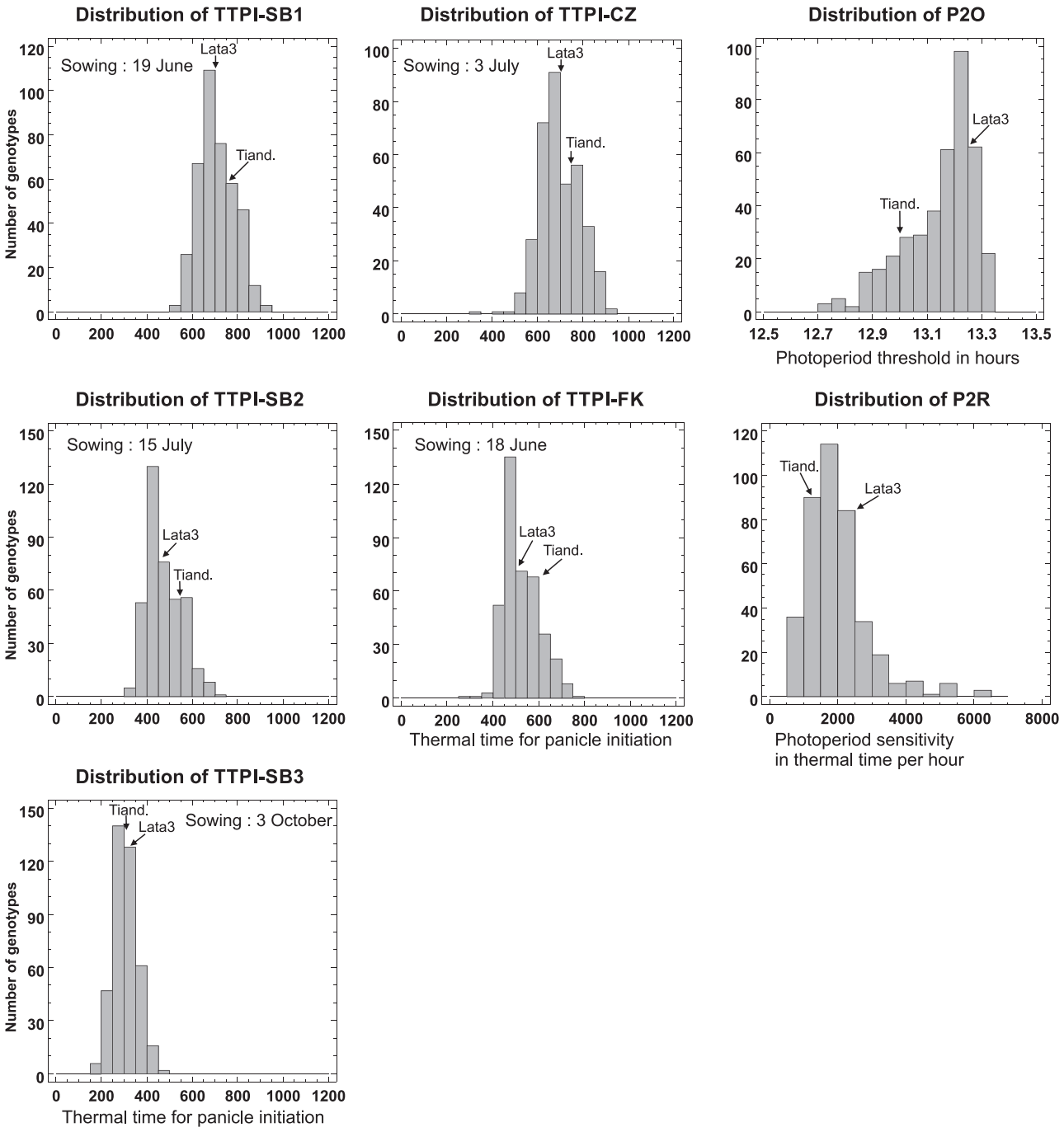

Fig. 3. Phenotypic distribution of Thermal Time from emergence to Panicle Initiation (TTPI) and model parameters (P2O, P2R). TTPI is given for Farako (TTPI-FK), Cinzana (TTPI-CZ) and the three sowing dates of Sotuba (TTPI-SB1, TTPI-SB2, TTPI-SB3). Model parameters are critical photoperiod (P2O) and photoperiod sensitivity (P2R). Basic vegetative phase distribution (BVP) is not displayed since BVP and TTPI-SB3 are identical. Arrows indicate average phenotypic values of the population parental lines, 'Tiandougou' and 'Lata3'.

Chr03 at 51,272,397 bp).

4. Discussion

4.1. A major QTL can finely adjust photoperiod-sensitive sorghum flowering

Most of the previous genetic studies focusing on flowering time in sorghum involved either highly contrasting parents for photoperiod sensitivity or photoperiod insensitive parents (Lin et al., 1995; Rooney and Aydin, 1999; Chantereau et al., 2001; Zou et al., 2012). These studies identified major genes alleles removing (or strongly reducing) photoperiod-sensitivity or associated with the temperature component of flowering (Mace et al., 2013). The above authors have not addressed genes related to fine regulation of photoperiod-sensitivity.

A major maturity QTL was detected on chromosome 3 (R2 up to 58.8%). This major QTL has only a medium effect on thermal time for panicle initiation (additive effect about 72 °Cd/4.3 days). One week change in time to maturity may not appear to be an important change. However, in practice, the main photoperiod-sensitivity effect is to group flowering at a precise date (Curtis, 1968). Therefore it is not the change in crop length cycle that matters, but the shift on (grouped) flowering date. Although P2O values seemed nearly similar between the two parents (15 min difference), this faint difference induces a variation in flowering date from 7 to 10 days which is sufficient to

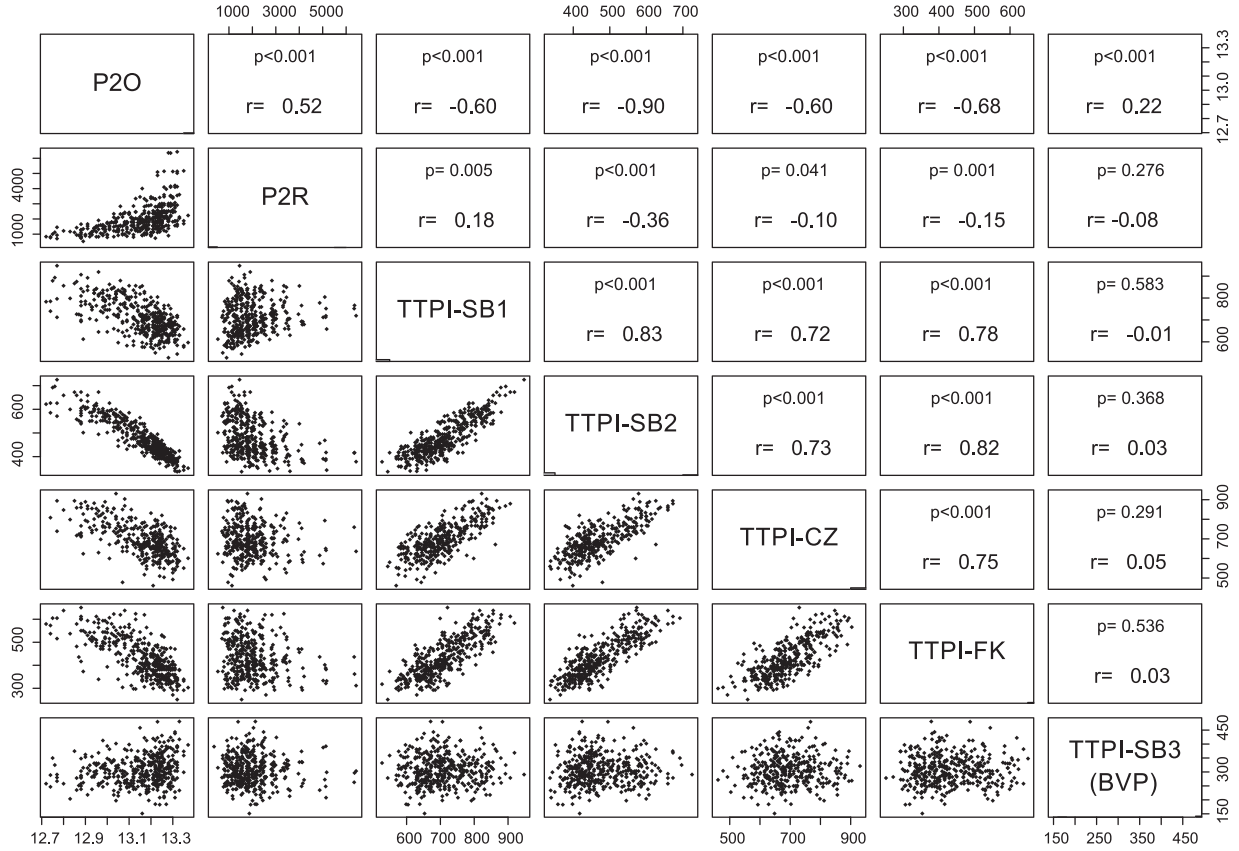

Fig. 4. Correlation matrix plot between variables. Thermal Time to Panicle Initiation at Cinzana (TTPI-CZ), Farako (TTPI-FK), Sotuba at 2 sowing dates (TTPI-SB1 and TTPI-SB2), Basic Vegetative Phase (BVP or TTPI-SB3), critical photoperiod (P2O) and photoperiod sensitivity (P2R). The figure displays in the upward half matrix correlation coefficients (r) between variables with associated *p*-values (p) and in the downward half matrix, scatter plot between variables.

finely adjust behavior and climate adaptation of new varieties.

QTLs weakness for photoperiod sensitivity (P2R) (explained variance ranging from 3.7 to 5.8%) suggests that the two parental varieties are rather less contrasted for this trait than for critical photoperiod (P2O). In previous studies, no QTL specifically related to the critical photoperiod were found either because parents were similar for this trait (Chantereau et al., 2001) or because the experiments were conducted in photoperiod conditions close to the population critical photoperiod (Bangbol, 2013).

4.2. Monitoring critical photoperiod for climate smart varieties in west africa

Since the late 1960s, sub Saharan Africa has experienced drought events of unprecedented severity in recorded history (Zeng, 2003). As a result of climate change, rain distribution variations can potentially affect the occurrence of drought, while changes in temperature can affect flowering time. Even if climate models are unclear in predicting the future distribution of African rainfall, an increase in climate variability and a succession of periods of drought and flooding are expected. Elite grain sorghum varieties developed by breeding programs have been mainly selected for photoperiod insensitivity and early flowering. However, this approach failed to produce efficient varieties due to the variability of environmental conditions in the sub-Saharan African context. Contrastingly, sorghum landraces are examples of adaptive selection to climate variability. In West Africa, the landraces adapted to the North (dry) zone have a high critical photoperiod (P2O), low photoperiod sensitivity (P2R) and flower earlier than the landraces adapted to the South (wet) zone characterized by a lower critical photoperiod and a higher photoperiod sensitivity (Sanon et al., 2014).

It is also considered that climate change, and in particular temperature increase, may lead to an increase of development rates resulting in a shorter life cycle and a decrease of photosynthesis and crop productivity (Craufurd and Wheeler, 2009; Ainsworth and Ort, 2010). In this context, photoperiod sensitivity appears as a key trait to face climate change since flowering depends mainly on photoperiod, an astronomical phenomenon that will remain unchanged regardless of climatic change.

The few studies that have investigated the variation of the critical photoperiod trait in sorghum varieties found values of P2O varying from 10.2 h to 17.5 h (Ritchie and Alagarswamy, 1989; Craufurd et al., 1999; Chantereau et al., 2001; El Mannai et al., 2011; Abdulai et al., 2012; Sanon et al., 2014). However, comparison with our P2O values is difficult because genetic coefficients of main development models are not stable with latitude, invalidating data obtained from multi-local experimentations (Abdulai et al., 2012; Kouakou et al., 2013). By studying latitude effect on sorghum phenology, Abdulai et al. (2012), under the same environmental conditions, showed that latitude effect on phenology between Cinzana, Sotuba and Farako were more important than portrayed by existing crop models.

In addition, the photoperiod calculation method varies according to studies (including or excluding dawn and dusk), which can result in up to one hour difference on calculated day length. However, the existence of varieties with low and high P2O values (late and early maturing varieties, respectively) suggests possible other alleles/genes controlling this trait whose identification will be key to improve sorghum adaptation to climate.

The major QTL for critical photoperiod allows the development of alternative breeding options based on improved variety selection for various environments. Until now, it was implicit that maturity and photoperiod sensitivity were closely linked and that early varieties were necessarily less photoperiod-sensitive (Clerget et al., 2007). Our results

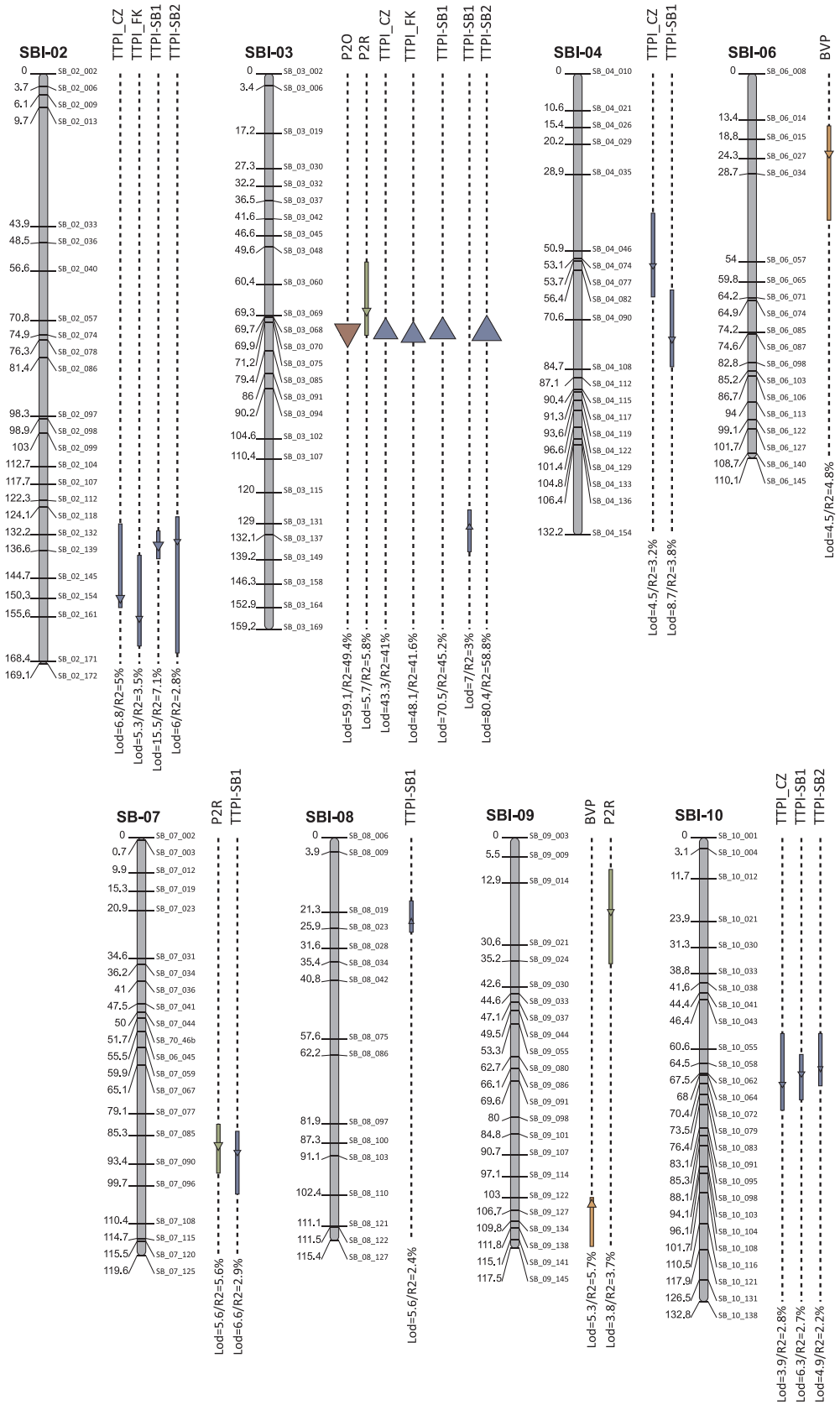

Fig. 5. QTL detected on the 'Tiandougou' × 'Lata3' genetic map for Thermal Time to Panicle Initiation at Cinzana (TTPI-CZ), Farako (TTPI-FK), Sotuba at 2 sowing dates (TTPI-SB1 and TTPI-SB2), Basic Vegetative Phase (BVP), critical photoperiod (P2O) and photoperiod sensitivity (P2R). Each QTL is represented by a line spanning the QTL confidence interval and a triangle located at the LOD peak with an area proportional to the R^2. Upward triangles represent a positive effect from 'Tiandougou' alleles and downward triangles a positive effect from 'Lata3' alleles.

Table 2
Parameters associated with the quantitative trait loci (QTL) detected in the Sorghum population by multiple QTL mapping (MQM) for phenological and model derived variables: Thermal Time to panicle initiation for the two sowing dates of Sotuba (TTPI-SB1, TTPI-SB2), for Cinzana (TTPI-CZ) and Farako (TTTPI-FK), Basic Vegetative Phase (BVP/TTPI-SB3), critical photoperiod (P2O) and photoperiod sensitivity (P2R).

Trait	CHR	LOD score	Position (cM)	95% Bayesian credible interval (cM)	Explained variance (%)	Total explained variance (%)	Additive effect	Closest marker	Flanking markers		Position on the Sorghum genome v3.1 (bp)		
									Left	Right	Closest marker	Left marker	Right marker
TTPI-SB1	2	15.5	135	131–139	7.1	63.9	−22.50	SB02139	SB02118	SB02145	69 504 054	65 052 311	70 854 896
	3	70.5	74	73–75	45.2		65.95	SB03075	SB03075	SB03085	48 834 006	48 834 006	52 478 805
	3	7.0	130	125–137	3.0		16.36	SB03131	SB03115	SB03149	64 831 343	60 950 542	68 814 938
	4	8.7	76	62–84	3.8		−9.54	SB04090	SB04082	SB04108	52 736 206	50 515 899	56 368 786
	7	6.6	90	84–102	2.9		−16.99	SB07090	SB07077	SB07108	59 613 944	57 506 979	62 863 131
	8	5.6	24	18–27	2.4		7.28	SB08023	SB08009	SB08028	3 669 490	1 302 298	4 374 962
	10	6.3	67.5	62–75	2.7		−13.82	SB10062	SB10055	SB10083	19 451 149	11 760 684	49 923 290
	2*4	4.3			*1.8		3.53	–	–	–	–	–	–
TTPI-SB2	2	6.0	134	127–166	2.8	61.4	−16.01	SB02132	SB02118	SB02171	67 990 256	65 052 311	76 894 769
	3	80.4	74	73–74	58.8		72.23	SB03075	SB03075	SB03085	48 834 006	48 834 006	52 478 805
	10	4.9	66	56–71	2.2		−12.37	SB10062	SB10043	SB10079	19 451 149	8 537 969	48 798 729
TTPI_CZ	2	6.8	150.3	129–153	5.0	48.6	−23.74	SB02154	SB02118	SB02161	73 056 016	65 052 311	74 394 509
	3	43.3	74	73–75	41.0		70.93	SB03075	SB03075	SB03085	48 834 006	48 834 006	52 478 805
	4	4.5	55	40–64	3.2		−18.25	SB04077	SB04035	SB04090	48 704 034	8 917 692	52 736 206
	10	3.9	70.4	56–78	2.8		−16.66	SB10072	SB10043	SB10091	46 110 670	8 537 969	52 084 453
TTPI_FK	2	5.3	156	138–164	3.5	44.4	−17.93	SB02161	SB02139	SB02171	74 394 509	69 504 054	76 894 769
	3	48.1	75	74–76	41.6		62.54	SB03075	SB03075	SB03085	48 834 006	48 834 006	52 478 805
P2O	3	59.1	74	73–75	49.4	49.4	−0.11	SB03075	SB03075	SB03085	48 834 006	48 834 006	52 478 805
P2R	3	5.7	68	54–75	5.8	15.6	−260.35	SB03069	SB03048	SB03085	42 474 125	11 243 730	52 478 805
	7	5.6	88	82–96	5.6		−244.78	SB07085	SB07077	SB07096	58 732 836	57 506 979	60 740 850
	9	3.8	21	9–36	3.7		−217.68	SB09014	SB09009	SB09030	2 423 487	1 508 004	6 175 775
BVP	6	4.5	23	15–42	4.8	10.0	−12.44	SB06027	SB06014	SB06057	32 521 645	3 465 631	46 043 053
TTPI-SB3	9	5.3	105	103–117	5.7		14.40	SB09127	SB09122	SB09145	55 954 750	55 056 523	58 738 356

*Interaction between the QTL on chr 2 and the QTL on chr 4 ($p < 0.01$).

show that changes in critical photoperiod make possible to modify the earliness without changing photoperiod sensitivity. This finding opens up new avenues for the development of early or late maturing varieties while preserving photoperiod sensitivity and therefore stability of crop production.

4.3. Candidate gene search highlighted two genes involved in flowering time regulation

In the major QTL region controlling the critical photoperiod variability (chromosome 3, 74 cM), the gene ontology categorization approach (Ashburner et al., 2000) detected 15 genes corresponding to the "developmental process" class which is relevant to the flowering time process. Within these 15 genes, two were of particular interest since they are involved in photoperiodism and flowering in other species.

One of the two genes involved in flowering and located in the QTL region corresponds to Sobic.003G196300, which is similar to AT3G24870 (*ATEAF1B*). This gene has been shown to be necessary for proper timing of transition to flowering in *Arabidopsis* (Bieluszewski et al., 2015). Although, phenotypical analysis of *Arabidopsis* mutants showed decreased expression of the *Flowering Locus C* (*FLC*) that prevents flowering, and early flowering, the Bieluszewski et al. (2015) study was the only one to mention AT3G24870 in the context of flowering and provided only a few elements to support the photoperiodic control of flowering by this gene. Furthermore, this gene has never been shown to be involved in flowering in other species than Arabidopsis.

The second flowering gene identified in the Chromosome 3 critical photoperiod region is Sobic.003G191700 (Sb03g025560), one of the two sorghum orthologs of *Early Flowering 3* (*Elf3*) for which functional evidences support its implication in the regulation of circadian rhythms and photoperiodic flowering in both rice (Fu et al., 2009; Zhao et al., 2012; Yang et al., 2013) and *Arabidopsis* (Hicks et al., 1996; McWatters et al., 2000; Reed et al., 2000; Covington et al., 2001; Hicks et al., 2001; Liu et al., 2001; Kim et al., 2005; Yoshida et al., 2009). These studies considered that *Elf3* is a time taker that modulates resetting of the circadian clock and integrates both temperature and photoperiod signals. Furthermore, different independent *Elf3* alleles impacting flowering dynamics were identified in rice, two as QTLs, *early flowering 7* (*ef7*) (Saito et al., 2012) and *heading date 17* (*hd17*) (Matsubara et al., 2008; Matsubara et al., 2012), two insertion mutants (Zhao et al., 2012; Yang et al., 2013) and transgenic RNAi lines (Zhao et al., 2012). These results showed that *Elf3* is involved in photoperiod sensitivity in rice and that this gene is a key component of the circadian clock through its regulatory effect on several downstream genes.

Several sorghum orthologs of these "downstream genes" have been identified as major maturity genes. Under both short and long-day conditions, *Os-ELF3-1* promotes flowering by negatively regulating the floral repressor gene *Ghd7 (*Saito et al., 2012), which is the ortholog of Ma_6 in sorghum (Murphy et al., 2014). Zhao et al. (2012) proposed that *OsELF3-1* regulates light input into the clock by binding to *PHYTOCHROME B* (Ma_3 in sorghum) and thus forming a complex that regulates flowering. In addition, the same study showed that *PRR37*, also known as Ma_1 in sorghum (Murphy et al., 2011), is negatively regulated by *Os-ELF3-1* (Zhao et al., 2012).

It is also important to mention that the second sorghum ortholog of *ELF3* (Sobic.009G257300) is localized in the vicinity of the QTL interval for the Basic Vegetative Phase on the chromosome 9. These results are consistent with the rice results in which genetic analysis of a late heading-time mutant line has been used to demonstrate that the *OsELF3-2* gene (the second ortholog of *ELF3* in rice) conferred an extremely long Basic Vegetative Phase and increased photoperiod sensitivity under long photoperiod (Yuan et al., 2009). Furthermore, considering the regulation of *PRR37* by *Os-ELF3-1* (Zhao et al., 2012), it is interesting to underline that in our study the sorghum Ma_1 gene (Sobic.006G057866) is located within the QTL interval for the basic vegetative phase on chromosome 6, starting at 40,304,883 bp near the SB06034 marker (40,227,313 bp).

Circadian clock genes functions appear to be well conserved among species and they underlie QTL with positive effect on key agricultural traits, particularly flowering time but also yield and biomass production (Bendix et al., 2015). In rice, *OsELF3-2* mutant found application in programs to breed for rice suitable to low latitudes (Yuan et al., 2009). In barley, *ELF3* loci conferring reduced or non-existent responses to photoperiod have also been used to breed early maturity cultivars for short growing seasons at different latitudes in the world (Laurie et al., 1995; Faure et al., 2012; Zakhrabekova et al., 2012). The location of one of the *ELF3* sorghum ortholog (Sb03g025495) within a major QTL affecting the critical photoperiod (chromosome 3) in addition with the observed proximity of Sobic.009G257300 (the second ortholog of *ELF3*) with a QTL affecting the basic vegetative phase (chromosome 9) are consistent with the previous results reported in *Arabidopsis* (Liu et al., 2001; Kim et al., 2005), rice (Yuan et al., 2009) and barley (Laurie et al., 1995; Faure et al., 2012; Zakhrabekova et al., 2012).

Despite evidences found in the literature that were mentioned previously in the manuscript about the implication of *ELF3* in the control of flowering, further analyses of this locus in our population are needed to demonstrate that this gene is involved in trait variation. Sequencing of this locus in the parental lines appears to be the first step to assess the implication of this gene in the trait regulation. Based on sorghum accessions resequencing (McCormick et al., 2018), two mutations with high impact on the protein of the *ELF3* gene were identified in the sorghum diversity. Although this is not a proof that these mutations are present in our parental lines, this information opens interesting perspectives to deepen the genomic understanding of trait regulation by this candidate gene.

Furthermore, genetic analysis in multi-parental design and isogenic lines would be a good guide to precisely map the candidate gene position to support its role as well as to precise the effect of allelic variation.

5. Conclusions

This approach combining genetic analysis and crop modeling deepened the sound understanding of photoperiod-sensitivity. We demonstrated that it is possible to decompose flowering time into different physiological parameters, which are controlled by specific genomic regions.

The major QTL detected on chromosome 3, controlling critical photoperiod, collocate with an ortholog of the *ELF3* gene for which functional evidences have been provided in *Arabidopsis* and rice.

Plant modeling allowed a better ecophysiological understanding of the detected QTLs. But, in a medium to long-term perspective, the expectations linked to the use of the combined modeling and quantitative genetic approaches go far beyond. Integrating modeling and molecular genetics is expected to conceive breeding ideotypes according to climate change scenarios capitalizing on the prediction ability of ecophysiological modeling and on the precision and efficiency of marker assisted breeding.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.fcr.2018.02.007.

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