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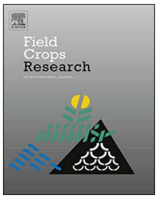

Integrating genetic analysis and crop modeling: A major QTL can finely adjust photoperiod-sensitive sorghum flowering

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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