Principles and practices **of the photothermal adaptability improvement in soya bean**

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Flowering plants can respond to the relative length of day and night, a phenomenon defined as 'photoperiodism' (Garner and Allard, 1920). Soya bean has been used as a model plant for photoperiodism studies because of its sensitivity to photoperiod and rich genetic diversity (Owen, 1927; Heinze *et al.*, 1942; Hendricks, 1958; Coulter and Hamner, 1964).

Increasing evidence demonstrates that photoperiod affects many aspects of soya bean growth and development such as leaf senescence, pod setting, seed filling, shoot and root growth, etiolation, and stress responses besides flowering and maturity (Han *et al.*, 2006; Covington and Harmer, 2007; James *et al.*, 2008; Song *et al.*, 2015; Nico *et al.*, 2016). On the other hand, as a thermophilic crop, soya bean growth and development are also susceptible to temperature changes (Setiyono *et al.*, 2007). Therefore, responses to both photoperiod and temperature affect the growth, development, and yield formation of soya bean cultivars.

Understanding the physiological characteristics, and molecular mechanisms of photothermal responses will not only contribute to thorough know-how of the varietal differences in the adaptation climatic conditions, but will also provide a theoretical basis and valuable guidance for germplasm introduction and the breeding of soya bean and other photothermal sensitive crops.

Photoperiod response in soya bean

Soya bean is a typical short-day (SD) plant, and its flowering and maturity are strictly regulated by photoperiod (Garner and Allard, 1920, 1923, 1933; Wang *et al.*, 1956). Floral bud initiation of photoperiod-sensitive soya bean cultivars can only be induced by SD treatment (Garner and Allard, 1923; Borthwick and Parker 1938, 1939). Leaves are photoperiodic signal receptors that perceive light signals to regulate the reproductive development of soya bean (Borthwick and Parker, 1938). The age effect of leaves on flowering induction increases with the development of young leaves until they reach full size (Borthwick and Parker, 1940).

Furthermore, its perception of the length of dark plays a critical role in the photoperiod response (Borthwick and Parker, 1938; Xu *et al.*, 2015). A short exposure to light during night (night break (NB)) inhibits growth and flowering in SD plants (Thomas and Vince-Prue, 1997). When the light was applied in the middle of a dark period, the effect of NB is the largest in soya bean (Xu *et al.*, 2015).

The effect of SD treatment can be partially or completely relieved by transient light treatment in the process of the dark period, and the effect of light discontinuity depends on the light quality of the last light (Parker *et al.*, 1946; Han *et al.*, 2006; Wu *et al.*, 2006). Red light (650nm) was the most effective in inhibiting flower bud differentiation, while far-red light (730nm) was ineffective (Parker *et al.*, 1946).

Moreover, when soya bean plants are subjected to SD treatment after emergence for some days and then transferred to long-day (LD) treatment, they can form flowers first and then revert to vegetative growth at the terminal shoot apex (Han *et al.*, 1998b; Washburn and Thomas, 2000). This phenomenon is called 'reversion of flowering' (Battey and Lyndon, 1990). Jiang *et al.* (2011) found that the effect of LD was a cumulative process and increased with the duration of LD treatment. As the length of LD treatment increased, the apical meristem could be reversed to produce vegetative organs. Therefore, the effect of SD can be partially or completely relieved by the continuous LD treatment in soya bean (Han *et al.*, 1998b; Wu *et al.*, 2006).

It was found that the photoperiodic response also existed in the post-flowering stages (Han *et al.*, 1995, 1996; Han and Wang, 1996). When the soya bean plants were subjected to LD treatment after flowering, the number of seeds increased with prolonged time of LD treatment (Morandi *et al.*, 1988; Han, 1996; Kantolic and Slafer, 2005; Jiang *et al.*, 2011). However, the photoperiod-sensitive cultivars resume vegetative growth with 'whole plant reversion' if the LD is over their critical photoperiod (Han *et al.*, 1998b; Jiang *et al.*,2011).

Soya beans are planted in a wide range of latitudes across the world, resulting from the rich diversity of variation in flowering and maturity time, whereas strict photoperiod sensitivity limits individual soya bean cultivars in a special latitudinal boundary (Cober and Morrison, 2010; Wong *et al.*, 2013). Large diversity in latitude preference results from variations in flowering genes and quantitative trait loci (QTLs) (Watanabe *et al.*, 2012; Wong *et al.*, 2013).

The extended photoperiod of high latitudes is suitable for soya bean cultivars that are less sensitive or insensitive to photoperiod because they flower and mature relatively early under such conditions (Upadhyay *et al.*, 1994). Vice versa, soya bean cultivars with different maturity groups (MGs) may have different photoperiodic responses and thus adapt to different day length conditions or latitudes.

Temperature response in soya bean

Soya bean is a thermophilic crop of which growth and development are affected by temperature (Gaynor *et al.*, 2011). The ambient temperature of soil greatly

affects emergence of soya bean (Pan *et al.*, 1982, 1985). After emergence, soya bean development is accelerated with increasing temperature (between 16 and 27°C).

The optimum temperature range at the flowering stage of soya bean is 25 to 28°C (Van Schaik and Probst, 1958), but lower temperatures delayed flowering (Roberts and Struckmeyer, 1939). The night temperatures are more effective than the accompanying day temperatures in determining the nature of the response (Hamner and Bonner, 1938). Thus far, controlling the night temperature has been proven to be consistently effective in changing the influence of photoperiod (Roberts and Struckmeyer, 1939).

A result showed that increases in the temperature (ranging between 15,6 and 32,2°C) caused an increase in plant height and number of nodes (Van Schaik and Probst, 1958). In addition, pod numbers per plant were the greatest at 34°C/26°C (day/night), rather than at 30°C/22°C (day/night), followed by day/night of 38°C/30°C (Allen *et al.*, 2018).

In addition to the growth period and agronomic traits, soya bean quality is also affected by temperature. Low temperatures cause a significant reduction of oil content (Howell and Cartter, 1953, 1958). Song *et al.* (2016) found that the crude oil content of soya beans had a quadratic regression correlation with the mean daily temperature (MDT). In addition, a positive relationship between crude oil content and MDT was discovered when the daily temperature was < 19,7°C.

The content of crude protein was negatively correlated with diurnal temperature range (DTR) but was positively correlated with an accumulated temperature ≥ 15°C (AT15) and MDT. However, the major bioactive components of soya bean, such as total isoflavones, phospholipids, and total oligosaccharides, were negatively correlated with AT15 and MDT, but positively correlated with DTR (Song *et al.*, 2018).

Unlike photoperiod responses, the thermal response is still not well understood in plants, especially in soya bean. In Arabidopsis, genomic responses to photoperiod and temperature are different during flower induction (Balasubramanian *et al.*, 2006). In addition, high temperatures change the structure of DNA, RNA, and protein (Vu *et al.*, 2019). Meanwhile, chromatin remodelling is regulated by temperature (Wigge, 2013). However, similar phenomena are not reported in soya bean.

Effect of photothermal interaction

Photoperiod and temperature are two important ecological factors that affect soya bean growth, development, and adaptation (Cai *et al.*, 2020). An interaction between photoperiod and temperature takes place, with greater effect of photoperiod on thermal sensitivity under SD conditions than under LD conditions, and with greater effect of temperature on photoperiodic sensitivity under high temperature than low temperature conditions (Cober *et al.*, 2001; Wu *et al.*, 2015). SD and warm temperatures promote flowering, whereas LD and cool temperatures delay flowering (Han, 1996; Rahman *et al.*, 2006; Kantolic and Slafer, 2007).

High temperatures coupled with LD conditions are not conducive to the reproductive development of soya beans (Wu, 2000; Cober *et al.*, 2001). Based on the effect of photoperiod and temperature on soya beans, a model of photoperiod-temperature interaction is proposed (Han 2007). According to this model, photoperiod dominates the direction of development, meaning that SD promotes but LD inhibits the developmental process.

On the other hand, temperature determines the development rate, i.e. high temperature promotes flowering under SD conditions and suppresses flowering under LD conditions above the critical photoperiod. Mao *et al.* (2017) confirmed the interactive effect of photoperiod and temperature on soya bean flowering at the molecular level, which was consistent with the theory of the mentioned photoperiod-temperature interaction model.

Breeding strategy

Nearly 3 000 soya bean cultivars have been officially released in China up to 2019. However, only around 5% of them were widely grown in farmers' fields (Wang *et al.*, 2015). Understanding the evolution of the widely grown cultivars will help improve soya bean adaptability.

The demand for soya bean is increasing rapidly with the growth of the population. Therefore, the expansion of soya bean cultivation regions worldwide is imminent. The photothermal characteristics of soya bean are crucial factors in determining the expansion of the planting region.

Up to now, many genes related to photothermal characteristics have been discovered in model plants and breakthroughs have also been made in the flowering pathway of soya bean. These approaches pave the way for improving the adaptability of soya bean to diverse photothermal environments.

Based on the thorough 'ecotyping' of the major widely-adapted soya bean cultivars as platforms, we can integrate molecular technologies with conventional breeding methods to breed superior and adaptable soya bean cultivars, thereby expanding the planting area of soya beans in order to meet the increasing demands for soya bean globally.

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