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Full Length Article

Short-day Photoperiod Effects on Plant Growth, Flower Bud Differentiation, and Yield Formation in Adzuki Bean (*Vigna angularis*)

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Abstract

Adzuki bean, a typical short-day plant (SDP) has high value of pharmaceutical and health care. This study investigated the SD photoperiod effects on plant morphological traits, physiological parameters, flower bud differentiation characterization and yield formation. For the purpose, a subset of SD photoperiod treatments was set up in a SD sensitive cultivar *Tangshanhongxiaodou*. The results indicated that the SD photoperiod affected largely the plant growth traits, decreased the duration from flowering to seed-filling stage which can modify the plant dry mass allocations. The SD photoperiod treatments increased the contents of chlorophyll and soluble protein at late growth stages, the net photosynthetic rate (P_n) and transpiration rate (T_r) also increased at the three growth stages. The GA_{1+3} content reduced and the ABA content increased under SD photoperiod treatments. Under SD photoperiod treatments, the flower bud differentiation processes were promoted. The SD photoperiod treatments reduced the yield components and yield, but not affected significantly the yield components and yield under SD-12 h treatment compared with SD-8 h treatment. Experimental results of present study conclude that SD-12 h treatment can be shortened and without penalty on yield components and yield in North China and similar ecological region, which fit for breeding and cultivation technique practice improvement of adzuki bean.

Keywords: Dry mass allocation; Floret differentiation; Morphological; Physiological; SD photoperiod; Yield

Introduction

Photoperiod is one of the most important environmental factors which affect the plant growth and development. After response to the photoperiod stimuli, plants undergo a series of biological processes and enter the flower bud differentiation phase (Garner and Allard, 1920; Wu *et al*., 2006). As one of the important crops in Northern region of China, adzuki bean is a typical short-day plant (SDP) species and strongly photoperiod sensitive during stages of seedling emergence to flowering. Under varied photoperiod conditions, the adzuki bean plants exhibited dramatically variations in plant growth and development, such as to change the growth period, modify the plant morphological feature, plant height, branch number, node number of main stem, and adjust the stalk weight (Shanmugasundaram, 1979). Moreover, post-flowering photoperiod also exerts effects on the node numbers of soybean and increased when the plants are treated by long-day photoperiod after flowering (Kantolic and Slafer, 2007; Han *et al*., 2006).

Plant leaves can receive the environmental factor signaling initiated by SD photoperiod. On the other hand, photoperiod also play an important role in regulating plant growth and development through their photosynthetic function. It has been reported that photosynthetic rate (P_n) in *Glycine soja* plants had higher values under the long-day photoperiod treatment than the SD photoperiod (Zhou and Zhao, 2002). In addition, the SD photoperiod treatment also decreases the chlorophyll content (Wang, 2003). Under SD photoperiod treatment, the sucrose and protein in plant leaves can promote the meristem to differentiate florets (Bernier *et al*., 1993). Thus far, many investigations have confirmed that gibberellin (GA) and abscisic acid (ABA) act as the internal signals to control the plant growth phase transformation between the growth to development stage. It was found that swiftly change into the floret initiation from the vegetative growth in an early maturity soybean cultivar Dongnong 36 under SD photoperiod treatment, is largely attributed to its dramatically reduction of ABA and zeatin riboside (ZR) contents of leaves (Wang *et al*., 2008). In alfalfa, SD photoperiod treatment also changed the ABA content in leaves which further affect the plant development

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process (Wu, 2004). Other pytohormornes GA_{1+3} are up-regulated by the LD photoperiod treatment and the ratio of GA_{1+3}/ABA increased when compared with plants under the SD photoperiod treatment (Han *et al*., 1996). These findings suggest that subset of physiological processes is modified by the sunshine duration which determines the photoperiod characterization.

For a long time, the dark time contrast to the day time is found to be involved in the plant response to photoperiod. Physiological studies revealed that the length of dark period plays a major role in promoting the plant reproductive development under SD photoperiod treatments (Thomas and Raper, 1977; Thomas and Vince, 1997). For example, the flowering time of a soybean variety referred to Ransom was promoted under the SD photoperiod and delayed under the LD photoperiod, may be largely related to the prolonged dark duration effects in controlling growth phase transformation (Washburn and Thomas, 2000). Previously, the apical flower primordium has been investigated by using a variety of *Zigongdongdou* (Li *et al*., 2005). Under SD photoperiod treatment, the flowering time of *Zigongdongdou* was promoted drastically and contrasting to the flowering time of this variety delayed by the LD photoperiod (Wu, 2000).

Previous research confirms that photoperiod affect significantly the yield components and yield. Photoperiod have affected greatly the yield of soybeans (Karmakar *et al*., 1994), the number of pods and seed number increased (Guiamet and Nakayama, 1984a) but 100-seed-weight decreased, the yield basically unchanged or improved (Cure *et al*., 1982; Guiamet and Nakayama, 1984b). In this study, by using a late maturity variety referred to *Tangshanhongxiaodou*, we investigated the SD photoperiod effects on plant morphological traits, physiological parameters, flower bud differentiation characterization and yield formation in adzuki bean. Our results can provide theoretical basis for variety breeding and cultivation practice improvement in adzuki bean.

Materials and Methods

Plant Materials and Experimental Design

The experiment was conducted at the teaching experimental station of Agricultural University of Hebei, China (38°38′ N, 115°E) during the growth seasons 2013 and 2014. *Tangshanhongxiaodou*, a adzuki bean late maturing and photoperiod sensitive variety, was used as the material (seeds were provided kindly by the Research Institute of Grain and Oil Crops, Academy of Agricultural and Forestry Sciences of Hebei, China). The experiment was performed in a split-plot experiment design with three replicates, with the photoperiod duration used as main plot and treatment time as the sub-plot. During the two growth seasons, the seeds were sown manually in the plot 5 m×1 m on June 24. The soil type was loamy and 400 g compound fertilizer as regular basal fertilizer. At first leaf expansion stage, seven photoperiod treatments were set up by sheltering the seedlings with opaque cloth during the daytime. These treatments included natural photoperiod (NPD), the control with NPD, NPD-SD-12 h-3 WKS-NPD treated by three weeks under 12 h photoperiod, NPD-SD-12 h-2 WKS-NPD treated by two weeks under 12 h photoperiod, NPD-SD-12 h-1 WK-NPD treated by one week under 12 h photoperiod, NPD-SD-8 h-3 WKS-NPD treated by three weeks under 8 h photoperiod, NPD-SD-8 h-2 WKS-NPD treated by two weeks under 8 h photoperiod, and NPD-SD-8 h-1 WKS-NPD treated by one week under 8 h photoperiod. Of these photoperiod treatments, the eight hour photoperiod was initiated at 9:00 am and terminated at 5:00 pm whereas the twelve hour photoperiod duration from 7:00 am to 7:00 pm (Fig. 1).

Measurement of Plant Growth Traits

Nine plants with uniform growth in each plot were subjected to measure the plant growth traits after the photoperiod treatments. These growth traits assayed included plant height, stem diameter, leaf number and shoot dry weight per plant. The plant height was obtained by measuring the distance (cm) from the cotyledon node to the growing point. The stem diameter of plants was determined by using an electronic Vernier Caliper (United Precision Machine Precision Measurement Limited Company, Shenzhen, China). All leaves including main stem and branches were counted for the leaf number per plant. The shoot dry weight per plant was measured using the oven drying method.

Determination of Biomass Allocation

The plant biomass after photoperiod treatments was separated into four parts according to descriptions by Poorter and Nagel (2000) including (1) root dry mass (RD, root dry mass/total dry mass, $g.g^{-1}$) (2) stem dry mass (SD, stem dry mass/total dry mass, $g.g^{-1}$) (3) leaf dry mass (LD, leaf dry mass/total dry mass, $g.g^{-1}$) and (4) pod (including seeds) dry mass (PD, pod and seed dry mass/total dry mass, $g.g^{-1}$).

Measurement of Physiological Parameters

The second expansion compound leaves under growing point of main stem after the photoperiod treatments were sampled to assay the physiological parameters, such as the net photosynthetic rate (P_n) and transpiration rate (T_r), the contents of chlorophyll, soluble protein, and phytohormones. The (P_n) and (T_r) were measured from 9:30 am to 11:00 am by using a portable photosynthesis system (Li-6400, USA) based on the instructions provided by the manufactures. During the assay process, the temperature was 25±0.3°C and the radiation intensity was 1500 mol $m^{-2}s^{-1}$ (Fenta *et al*.,

2012). The chlorophyll contents were measured as described by Zhao (2000). The soluble protein content were determined by a Coomassie brilliant blue G-250 method to assay the OD value under 595 nm wavelengths by U-3900 (Read and Northcote, 1981). The phytohormone contents were assayed by using the enzyme linked immunosorbent assay (ELISA) as described by He (1992) in which the kits for detecting the phytohormones were provided kindly by the Chemical Control Research Group in China Agricultural University, Beijing.

Flower Bud Differentiation Observation and Recording

In order to understand the SD photoperiod effects on flower bud differentiation, the flower bud developments in positions of base, middle and top were examined based on observing the anatomical structures of the florets. For that, the tested flower bud were fixed and then sectioned by YD-202A Manual Rotary Microtome (Yidi Medical Equipment Limited Company, China). The longitudinal sections of the flower bud were imaged and recorded by a micro-photographic camera (Olympus DP70) after staining by hematoxylin-eosin. The differentiation phases were defined as described by Wang and Jin (1995) as follow seven stages: (1) pre-differentiation stage (2) inflorescence primordium (3) flower primordium (4) sepal primordium (5) petal primordium (6) stamen and carpel primordium (7) stamen and carpel structural differentiation stages.

Statistical Analysis

All data were statistically analyzed by using Excel 2003, DPS v2000, and SPSS17.0. The results are presented as mean ± Standard Error (S.E.) values and variance (ANOVA) was used for testing the differences between different treatments by the Duncan's new multiple range (DMR) test at=0.05 level. The pictures were treated by photoshop CS6 software.

Results

Plant Growth Behavior

Short-day photoperiod affected largely the plant growth traits, including the plant height, stem diameter, leaf number and shoot dry weight (Fig. 2A, B, C and D). And reduced much more with longer SD photoperiod treatment and shorter sunshine durations from flowering to seed-filling stage, furthermore, decreased mostly under SD-8 h treatment.

Biomass Allocation

Under the SD photoperiod treatments, more dry mass in adzuki bean plants was allocated to the roots and pods from the flowering to the seed-filling stage (Fig. 3). The SD-8 h and SD-12 h treatments allocated the dry mass to roots by 1.7 to 8% and to pods by 0.4 to 10.6%. By contrast,

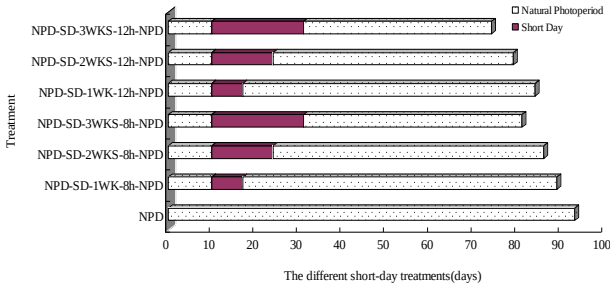

Fig. 1: Diagrammatic sketch of SD treatments. Each horizontal bar represent adzuki bean growth phase of the corresponding treatment. Red sections represent the period when plants were subjected under different SD treatments days and white point sections represent natural photoperiod

less dry mass was allocated to the stem and leaves under SD photoperiod treatments. In addition, earlier plant maturity was found under SD-12 h treatment than SD-8 h treatment.

***Chl* Content, *Chl a/b* Ratio and Soluble Protein Content**

The SD-12 h and SD-8 h treatments increased the contents of *Chl* and soluble protein in adzuki bean at the three growth stages, including flowering, podding and seed-filling. By contrast, the *Chl a/b* ratio decreased at these growth stages at same two SD photoperiod treatments (Fig. 4A, B and C).

Photosynthesis and Transpiration Rate

Under the SD photoperiod treatments, the net photosynthetic rate (P_n) increased at the three growth stages (flowering, podding and seed-filling) compared with the NPD. The plants under SD-8 h treatment exhibited the highest P_n (Fig. 5A). Similarly, SD photoperiod treatment exhibited higher contents of *Chl* and soluble protein. The SD-8 h treatment also elevated the transpiration rate (T_r) compared with NPD and the SD-12 h treatment (Fig. 5B).

Plant Hormone Contents

The GA_{1+3} content reduced from flowering to seed-filling stages under two SD photoperiod treatments. Among the treatments, the ones with SD-12 h treatment decreased much more in these phytohormone contents than with SD-8 h treatment (Fig. 6A). Similar results have been obtained on the ratio of GA_{1+3}/ABA under two SD photoperiod treatments (Fig. 6C). By contrast, the content of ABA was shown to be increased under the two SD photoperiod treatments compared with the NPD (Fig. 6B).

Flowering Characteristics

SD photoperiod treatments reduced the days of adzuki bean from seedling to flowering and maturity stages. In comparison with NPD, the SD photoperiod treatment

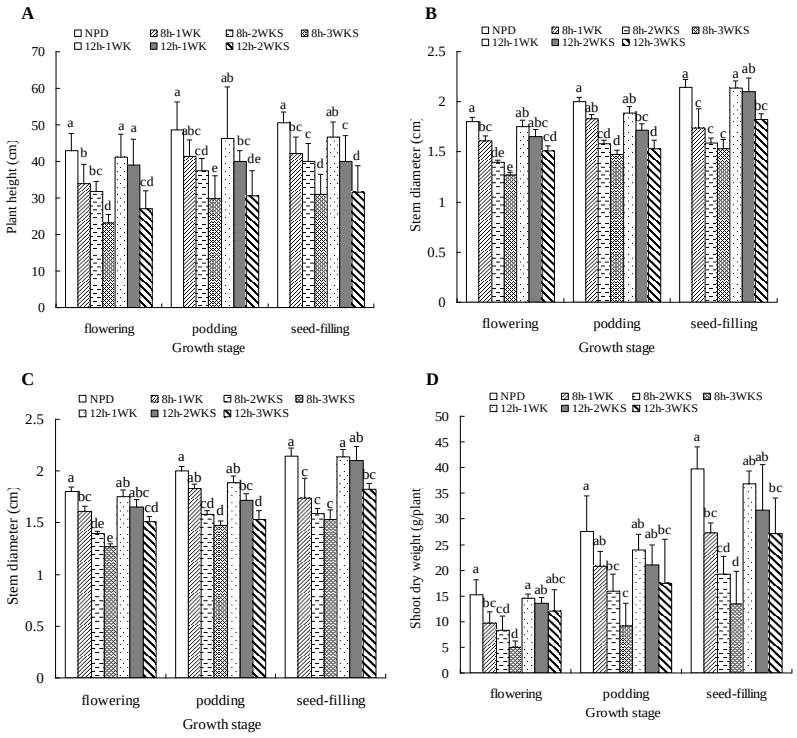

Fig. 2: Effects of the SD photoperiod treatments on plant height (A), stem diameter (B), leaf number (C) and shoot dry weight (D) in adzuki bean plants. Values represent mean ± S.E. (*n*= 9). The different lowercase letters over each bar indicate to be statistical significance at 0.05 level

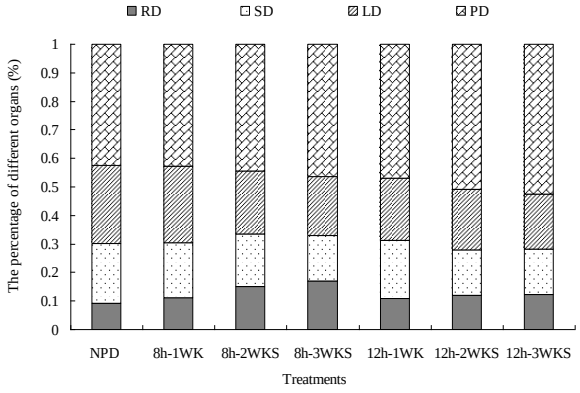

Fig. 3: Effects of the SD photoperiod treatments on dry mass allocation from flowering to the seed-filling stage. The biomass is assigned to root dry mass (RD) fraction, stem dry mass (SD) fraction, leaf dry mass (LD) fraction and pods dry mass (PD, including seed,) fraction. Values represent mean ± S.E. (*n*= 9)

with 12 h for 1, 2 and 3 weeks shortened the days from seedling to flowering by 9, 15 and 22 days. Similarly, the SD photoperiod treatment with 8 h for 1, 2 and 3 weeks shortened the days from seedling to flowering by 6, 11 and 19 days compared with NPD (Table 1). The flower promoting rate increased by 15.99, 26.19 and 38.02% in the former cases, and 10.70, 19.06 and 33.12% in the latter cases in comparison with NPD (Table 1).

The Flower Bud Differentiation Characterization

The SD photoperiod treatments promoted the flower bud differentiation process in adzuki bean plants (Fig. 7). Observations revealed that the flower bud differentiation at the lower parts of plants was as follows: when the plants in NPD were developed in the pre-differentiation stage, the plants in SD-8 h-1 WK treatment developed inflorescence primordium differentiation stage; the plants in SD-8 h-2 WKS treatment entered into flower primordium differentiation stage, whereas the plants in SD-8 h-3 WKS treatment were grown in petal primordium differentiation stage. Meanwhile, the plants in SD-12 h-1 WK treatment reached the development stage of squash growth cone; the plants in SD-12 h-2 WKS treatment entered the stage of sepal primordium differentiation whereas the plants in SD-12 h-3 WKS treatment started the stage of stamen and carpel primordium differentiation (Fig. 7A). Similar flower bud differentiation patterns were observed in the middle and top parts of plants (Fig. 7B and C).

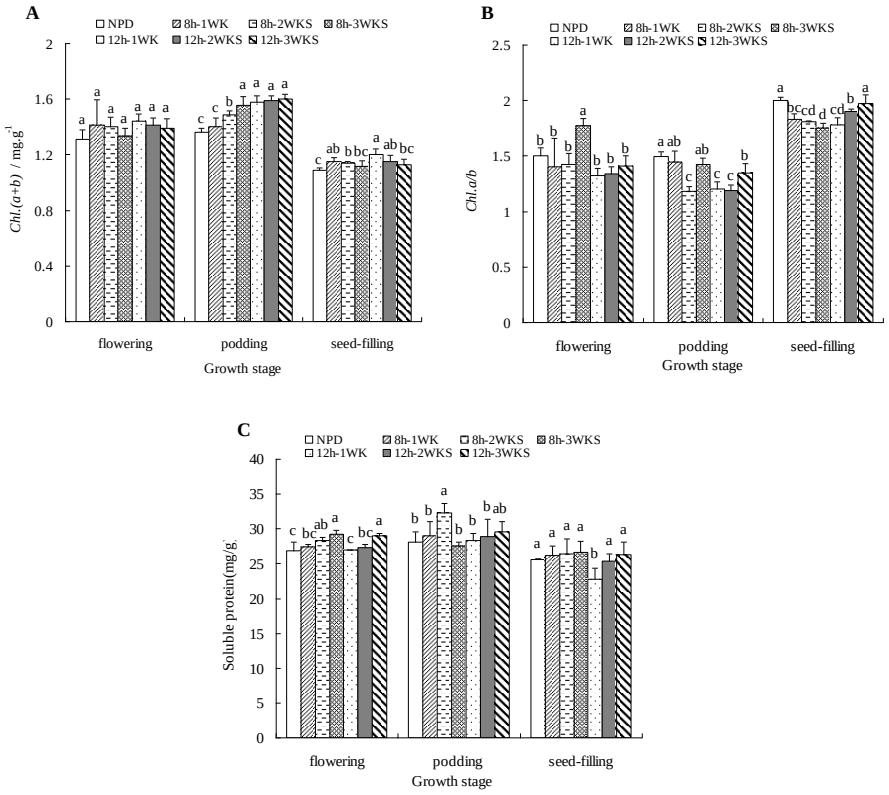

Fig. 4: Effects of the SD photoperiod treatments on *Chl* content (A), *Chl a/b* ratio (B) and soluble protein content (C). Values represent mean ± S.E. (*n*= 9). The different lowercase letters over each bar indicate to be statistical significance at 0.05 level

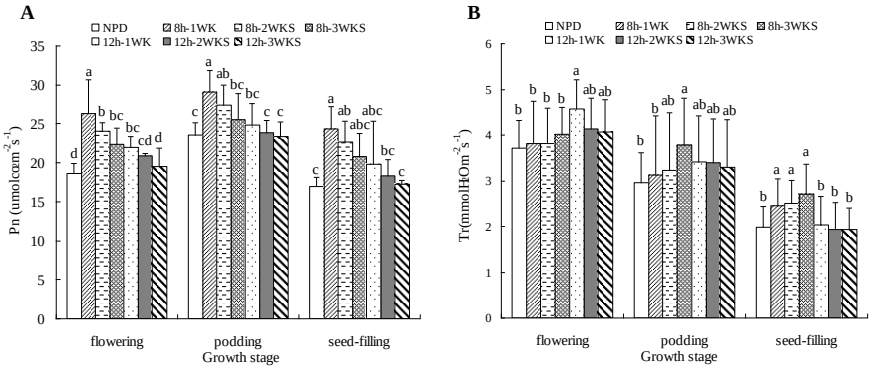

Fig. 5: Effects of the SD photoperiod treatments on net photosynthetic rate (P_n) (A) and transpiration rate (T_r) (B). Values represent mean ± S.E. (*n*= 9). The different lowercase letters over each bar indicate to be statistical significance at 0.05 level

Yield Components and Yield

In this study, the SD photoperiod treatments decreased the yield components and yield. Of these, the SD-8 h treatment decreased the pod numbers, pod weight and seed yield per plant by 36.4 to 63.9%. However, no obvious changes in the yield components and yield was observed under the SD-12 h treatment compared with NPD (Table 2).

Discussion

Photoperiod affected the plant growth and biomass allocation. Agronomic traits of soybean, such as plant height, the number of branches, node number, the number of leaves per plant and culm weight all decreased under SD photoperiod (Zhang, 1997), on contrary, all these traits increased under LD photoperiod (Thomas and Raper, 1983).

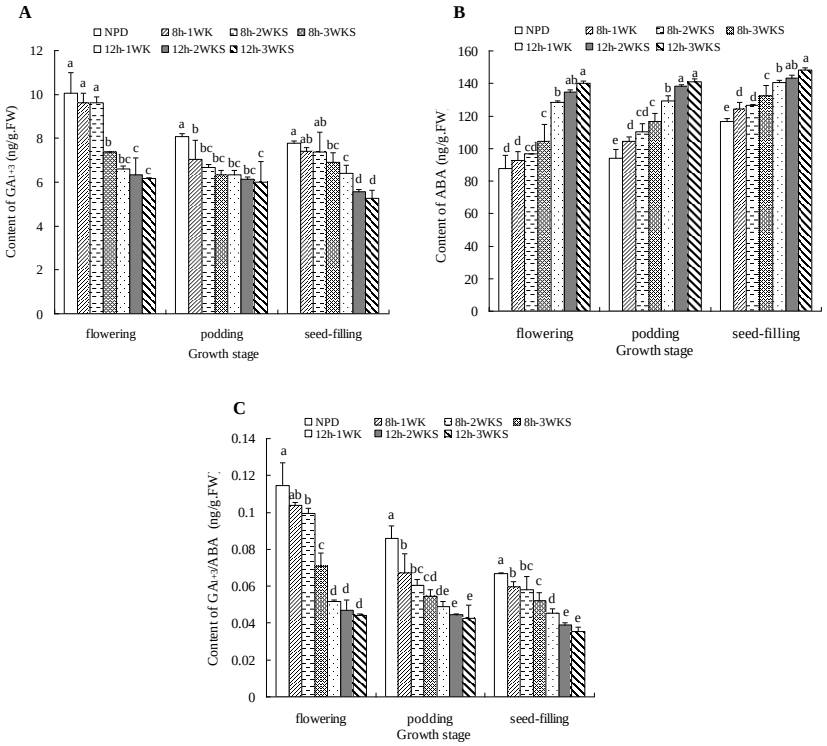

Fig. 6: Effects of the SD photoperiod treatments on content of GA_{1+3} (A), content of ABA (B), and ratio of GA_{1+3}/ABA(C). Values represent mean ± S.E. (*n*= 9). The different lowercase letters over each bar indicate to be statistical significance at 0.05 level

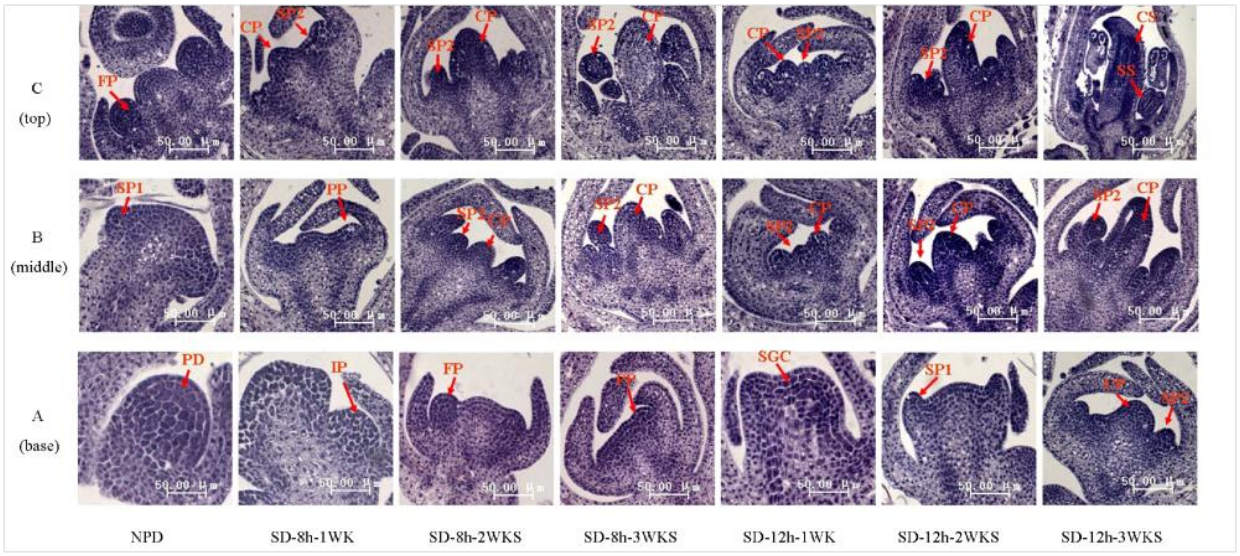

Fig. 7: Effects of the SD photoperiod treatments on flower bud different differentiation stages in adzuki bean plants
All plants were treated under SD-8 h and SD-12 h photoperiods with different times. (A) The flower bud differentiation processes at lower parts of plants after 15 days of SD photoperiod treatments. (B) The flower bud differentiation processes at middle parts of plants after 24 days of SD photoperiod treatments. (C) The flower bud differentiation processes at top parts of plants after 41 days of SD photoperiod treatments. Scale bars =50 um

Two SD photoperiod treatments decreased largely the plant height, stem diameter, leaf number and shoot dry weight (Fig. 2A, B, C and D). Moreover, adzuki bean plants allocated more dry mass to the roots and pods from the

Table 1: Effects of the SD photoperiod treatments on flowering characteristics

Treatments	Seeding- flowering stage (d)	Seeding-maturity stage (d)	Blossom early days (d)	SDHR (%)
NPD	57.83 a	86.33 a	0.00 e	0 e
SD-8h-1WK	51.67 b	81.63 b	6.20 d	10.70 d
SD-8h-2WKS	47.33 c	79.47 bc	11.17 c	19.06 c
SD-8h-3WKS	39.50 e	74.43 de	19.23 a	33.12 a
SD-12h-1WK	49.43 bc	77.40 cd	8.77 cd	15.99 cd
SD-12h-2WKS	43.40 d	72.33 e	15.13 b	26.19 b
SD-12h-3WKS	36.37 e	67.33 f	21.83 a	38.02 a

Different lowercase letters in the same row indicate to be statistical significance at 0.05 level

Table 2: Effects of the SD photoperiod treatments on seed yield and its components of adzuki bean

Treatments	Pod number (n/plant)	Pod weight (g/plant)	Seed yield (g/plant)	Seed number (n/pod)	Seed weight (g/pod)	Test plot yield (kg/5m²)
NPD	40.56±10.70 a	22.27±6.09 a	17.41±4.76 a	7.99±1.11 a	0.82±0.14 a	0.43±0.08 a
SD-8h-1WK	25.78±7.85 bc	12.71±4.61 bc	9.70±3.60 bcd	7.28±2.83 ab	0.64±0.11 bc	0.34±0.06 abc
SD-8h-2WKS	23.89±6.85 bc	10.88±3.07 c	8.84±2.24 cd	7.08±1.48 abc	0.64±0.13 bc	0.25±0.03 bcd
SD-8h-3WKS	20.22±8.50 c	8.55±4.13 c	6.29±3.28 d	6.44±1.93 c	0.54±0.15 c	0.16±0.07 d
SD-12h-1WK	37.44±16.97 a	20.59±7.99 a	16.38±6.45 a	7.83±1.66 a	0.74±0.06 ab	0.41±0.12 a
SD-12h-2WKS	33.11±7.59 ab	18.86±3.46 ab	14.67±4.37 ab	7.42±1.44 ab	0.68±0.17 bc	0.35±0.04 ab
SD-12h-3WKS	31.78±10.96 ab	17.64±9.50 ab	13.207.71 abc	6.78±1.66 bc	0.58±0.11 c	0.23±0.09 cd

Values represent mean ± S.E. (n= 9). The different lowercase letters in the same row indicate to be statistical significance at 0.05 level

flowering to the seed-filling stage (Fig. 3) and the plants matured earlier under SD-12 h photoperiod treatment than SD-8 h photoperiod. The former treatment showing early maturity was possibly related to other SD photoperiod effects in regulating the physiological process, such as the dry mass accumulation and the inner photosynthate translocation. It was found that the reduced photoperiod and extended SD treatment time could promote the transformation initiation from the growth to flower bud differentiation. These results indicated that SD photoperiod accelerated the plant growth and development with the SD duration-dependent manner as reported in earlier studies (Bose and Ghosh, 1975; Zhang *et al*., 2001; Fei *et al*., 2009).

Photoperiod not only affected the plant growth, but also physiological parameters. Shading can increase *Chl* content of Cercis canadensis but decreased *Chl a/b*, net photosynthetic (P_n) and transpiration rate (T_r) (Zhang *et al*., 2009). The *Chl*, soluble sugar and soluble protein content of adzuki bean were different, because of different growth period (Yin *et al*., 2008). Short-day photoperiod treatments increased the contents of *Chl* and soluble protein (Fig. 4A; 4C), but decreased *Chl a/b* ratio (Fig. 4B) at three growth stages. The reduced ratio of *Chl a/b* under the SD photoperiod treatment was possibly attributed to the varied effects of the SD photoperiod treatment on two *Chl* components, *Chl a* and *b*, in which the former component was dramatically down-regulated by SD photoperiod treatment compared with the latter component. The net photosynthetic (P_n) and transpiration rate (T_r) (Fig. 5A; 5B) were also increased and inconsistent with previous studies (He *et al*., 2001; Zhang *et al*., 2010; Li, 2012), this might be due to the difference in periods of shading or could be associated with the plant growth and development characterization in the adzuki bean plants in response to the photoperiod. Endogenous hormones play an important role in regulating the plant development and flowering process under varied photoperiods (Metzger, 1995). Among them, GA and ABA are two types of phytohormones involved in plant growth phase transformations from the vegetative to flower bud differentiation stages. GA_{1+3} content and GA_{1+3}/ABA were reduced and ABA increased under the two SD photoperiod treatments at three growth stages (Fig. 6A, B and C). These results indicate that the contents of GA and ABA were affected by photoperiod and suggested to be further involved in the plant biological processes relating to the growth stage transformation.

Photoperiod acts as one of the important factors in affecting the plant flowering initiation and determining the plant flowering time in the photoperiod sensitive plants (Davis, 2002). In this study, the days of adzuki bean from seedling to flowering stage and seedling to the maturity stage were reduced under two SD photoperiod treatments. Moreover, flower promoting rate was also increased and SD-12 h is higher (Table 1). That results revealed that the SD photoperiod treatment with 12 h displayed much more notable effects in promoting the plant flowering than the SD photoperiod treatment with 8 h is possibly associated with that relative longer photoperiods can provide more photosynthetic products to the shoot apex to help the flower bud differentiation (Battey and Tooke, 2002; Jack, 2004; Krizek and Fletcher, 2005). The corresponding biological mechanism underlying above phenomenon is needed to be further investigated. In addition, the flower bud differentiation process was promoted under SD-8 h and SD-12 h photoperiod, the latter process much more faster (Fig. 7). These findings clearly confirmed that the SD photoperiod treatments can promote the plant flower bud differentiation with a SD photoperiod treatment duration-dependent manner.

Previous studies have reported that photoperiod

treatments exert drastic impact on yield components and yield in legume species such as soybean, in addition to affecting the internode numbers, seed development and the reproductive organ growth (Adriana and Gustavo, 2007), and the floral induction, flower differentiation duration, and the pod growth behavior (Morandi *et al.,* 1988). The two SD photoperiod treatments decreased the yield components and yield but SD-12 h has little influence or no influence on yield (Table 2). Therefore, appropriate photoperiod can promote plant growth and development and finish the whole growth stage in a relative short time without penalty on yield in adzuki bean production in North China and similar ecological region.

Conclusion

That SD photoperiod affected largely the plant growth traits, decreased the duration from flowering to seed-filling stages and modified the plant dry mass allocations. The SD photoperiod treatments increased the contents of chlorophyll and soluble protein at late growth stages, the net photosynthetic rate (P_n) and transpiration rate (T_r). The GA_{1+3} content was reduced and the ABA content was increased under the two SD photoperiod treatments. These alterations in above phytohormones are suggested to be involved in regulating the plant growth stage transformation. The flower bud differentiation processes was promoted under SD photoperiod treatments. The SD photoperiod treatments reduced the yield components and yield, but not largely changed the yield components and yields under the SD-12 h treatment compared with NPD. These investigations confirmed that appropriate short-day photoperiod can improve the plant physiological parameters and promote plant growth and development that are possibly attributed to the modified biological processes such as the varied metabolism of GA and ABA.

Acknowledgments

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