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SHORT REPORT



Variation in photosensitivity of flowering in the world soybean mini-core collections (*GmWMC*)

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ABSTRACT

Photosensitivity of flowering is the main yield limiting factor for soybean production in tropical areas. Our objective was to evaluate the variation of photosensitivity in the world soybean mini-core collections (*GmWMC*) under controlled environment. Ten and 13 h were selected as short- and long- photoperiods. The days from emergence to first flower open (DEF) were 20–49 days under 13 h, whereas 20–31 days under 10 h photoperiods. The variation in DEF under short photoperiod might be caused by juvenile growth phase or post-inductive phase, because 10 h was the photoperiod which induction phase of most genotypes were minimized. Index of photosensitivity of flowering (IPF) varied from 0.00 to 0.47 and correlated positively with DEF under short photoperiod. However, some genotypes were found having higher IPF but shorter DEF, or lower IPF but longer DEF. Results provided the valuable information for soybean production in tropical areas.

Abbreviations: DEF: days from emergence to first flower open; IPF: index of photosensitivity of flowering; JGP: juvenile growth phase; *GmWMC*: world soybean mini-core collections.

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Introduction

Soybean (*Glycine max* (L.) Merr.) originated in temperate regions between 32° and 40° N latitude in China (Li et al., 2008). Nowadays, it is grown widely throughout tropical, subtropical, and temperate regions as one of the world's most important economic crops for its high oil and protein concentration. However, soybean seed yield is highly responsive to environmental changes and it is extremely low in tropical areas compared to temperate areas. The main reason of low-seed yield in tropical areas could be insufficient vegetative growth caused by early flowering. Early flowering is generally brought by short photoperiod and high temperature in soybean (Board & Hall, 1984). To find adaptable genotypes to tropical areas, the better knowledge about the genotypic variation in photosensitivity of flowering will be notable option. Furthermore, long juvenile growth phase (JGP) would also facilitate yield production, since it could give enough vegetative mass regardless of short photoperiod in tropical areas.

It is generally accepted that soybean is a typical short-day crop. It has also been recognized that photosensitivity of soybean genotypes controls the plant size, and thereby affects vegetative mass and yield potentiality (Shanmugasundaram & Tsou, 1978). As a consequence,

photosensitivity is a key factor for determining latitudinal adaption. Lu et al. (1967) reported that the variation in photosensitivity of soybean genotypes adapted to different season.

Although Garner and Allard (1920) have found that the flowering in soybean plants respond to photoperiod, there are a large number of studies on the photosensitivity of flowering in soybean; for example, Criswell and Hume (1972) tested 111 soybean genotypes (maturity Group 00) with four photoperiods (12, 22, 23 and 24 h); Huxley et al. (1974) evaluated four soybean genotypes under 11:40 and 13:20 h photoperiod; Shanmugasundaram (1979) examined 40 genotypes under 16 h and 10 h photoperiod; and Niwa (1985) tested seven soybean genotypes with four photoperiod (12, 12:40, 13:20 and 14 h). They all reported a wide variation between the genotypes; however, there was no specific method to evaluate photosensitivity standardly. Therefore, exact photosensitivity determination is very difficult for large number of genotypes, because the effective photoperiod differs among the genotypes.

Soybean cultivation on a large scale was difficult in low-latitude areas due to the lack of potential genotypes until the end of 1960. Afterwards, this barrier was overcome with the induction of long JGP genotypes

(Neumaier & James, 1993). Incorporation of the long JGP into soybean germplasm adapted to one location may help the transfer of advantageous traits to another location. Moreover, JGP gives guidance to choose an adaptable genotype for a specific latitude belt and supports soybean growers with more management adjustability in response to climatic conditions and crop rotation schemes. In order to produce a genotype with certain vegetative growth that will be suited in tropical areas, either high photosensitivity or long JGP would be considered. However, the relations between photosensitivity and JGP are not well known.

Because photosensitivity could play a prominent role in expanding soybean adaptation areas, the present study aimed to evaluate the variation in photosensitivity using a wide range of genotypic background. The results of this study will provide useful information to increase soybean production in low-latitude areas and assist in conserving and utilizing soybean germplasm effectively.

Materials and methods

Experimental design and growth conditions

A preliminary experiment was conducted to choose an effective photoperiod for evaluating photosensitivity in the growth chamber at Saga University, Japan. The control photoperiods were 8–14 h (2 h intervals) at 28/22°C (day/night) temperature. Cool white fluorescent and incandescent lights (FPR96EX-D/A, Panasonic Co., Ltd., Japan) were used that produced $450 \mu\text{mol m}^{-2}\text{s}^{-1}$ photosynthetic photon flux density at about 1 m above the plants. Eight soybean genotypes (Table 1) were selected based on previous research by considering the variation of photosensitivity. Five seeds were sown in each pot (15 cm diameter and 20 cm height) filled with sand and vermiculite (1:1, volume/volume) as a growing medium. Two plants were allowed to grow in each pot for each genotype and replicated three times. Standard nutrient solution containing NH_4NO_3 (50 ppm), KH_2PO_4 (70 ppm), KH_2PO_4 (110 ppm), MgSO_4 (90 ppm), CaCl_2 (35 ppm), $\text{C}_{10}\text{H}_{12}\text{N}_2\text{O}_8\text{FeNa}$ (3.5 ppm), MnSO_4 (0.3 ppm), H_3BO_3 (0.06 ppm), ZnSO_4 (0.009 ppm), CuSO_4 (0.009 ppm), and MoO_3 (0.009 ppm) was applied two times per week (Zhao et al., 2014) and plants were watered as needed.

In the optimized photoperiodic conditions from a preliminary experiment, 82 genotypes of *GmWMC* provided by the NARO gene bank of Japan (Table 1) were tested under long (13 h) and short (10 h) photoperiods at 28°C. We have chosen 28°C which is nearly similar condition in tropical areas, since our previous experiment concluded that temperature may do not have a triggering effect on flowering initiation but affect soybean growth and development quantitatively (Islam et al., in press). The variations of photosensitivity were estimated in this experiment. The facilities and growth conditions were similar throughout all the experiment in this report.

Data collection

Dates of emergence (50% of plants with cotyledons above soil surface) and first flowering (50% of plants with one flower at any node, R1) were recorded in accordance with Fehr et al. (1971) throughout all the experiments.

Index of photosensitivity of flowering (IPF)

The photosensitivity is measured in various ways depend on the aim of the experiment. Shanmugasundaram (1982) used several photoperiods and established a sensitivity scoring system compared with flowering time among the photoperiods. Several researchers evaluated photosensitivity based on the delayed flowering with a long photoperiod (Fatichin et al., 2009; Sinclair & Hinson, 1992). However, in the present report, IPF in each genotype was calculated based on the following equation: $1 - \text{DEF}_{10\text{h}}/\text{DEF}_{13\text{h}}$, where $\text{DEF}_{10\text{h}}$ and $\text{DEF}_{13\text{h}}$ are the days from emergence to first flower open (DEF) under short- (10 h) and long- (13 h) photoperiods. This method was basically same with Sinclair and Hinson (1992) and Fatichin et al. (2009); however, the chosen photoperiods were different.

Statistical analysis

Single-factor analysis of variance (ANOVA) and Tukey's HSD (honest significant difference) test were used for the analysis of significance ($p < 0.05$) in eight selected

Table 1. Effect of different photoperiod on DEF at 28/22°C (day/night) temperature among eight selected soybean genotypes.

Photoperiod (h)	Genotypes							
	Fiskeby V	Nezumi Meta	Ke 32	Karasumame	L 2a	Hakuchikou	Sandek Sieng	Miss 33 Dixi
8	25 ± 0 b	25 ± 0 c	24 ± 0 ab	30 ± 0 d	25 ± 1 c	24 ± 0 ab	34 ± 1 b	35 ± 1 c
10	25 ± 0 b	26 ± 0 c	25 ± 0 a	33 ± 0 c	26 ± 0 c	25 ± 0 ab	35 ± 1 b	38 ± 0 b
12	27 ± 1 a	29 ± 1 b	25 ± 1 a	36 ± 0 b	30 ± 0 b	26 ± 1 a	45 ± 1 a	48 ± 0 a
14	27 ± 1 a	57 ± 1 a	26 ± 1 a	38 ± 1 a	35 ± 1 a	26 ± 1 a	No flowering	No flowering

Data expressed as mean values ± SD of three replication. In a column, means followed by same letter are not significantly different at $p < 0.05$ by Turkey Kramer test.

genotypes among the different photoperiod in Table 1. Additionally, the correlations with significant level were measured between IPF and DEF under short photoperiod in Figure 2.

Results and discussion

Flowering responses to a range of photoperiods

Table 1 shows the response of flowering to photoperiod from 8 to 14 h in selected 8 genotypes. The DEF were longer when the photoperiod was longer in all genotypes. However, DEF of three genotypes (Fiskeby v, Ke 32 and Hakuchikou) were almost constant against the changes in photoperiod. Furthermore, data also showed a negligible difference between 8 and 10 h in all genotypes, indicating the critical photoperiod for flowering stimulation. This result crucially suggested that 8 or 10 h photoperiod could minimize the differences in the effect of photoperiod on flowering in almost genotypes. Cober (2011) tested four genotypes, i.e. Parana, Paranagoiana, PI 159925, and X5063-39, with 3, 4, 5, 6, 8, and 12 h photoperiod at 25°C (day/night) temperature and reported that DEF were the shortest at 6 to 8 h photoperiod in all genotypes.

In addition, two genotypes (Sandek Sieng and Miss 33 Dixi) did not open flowers until 75 days after emergence at 14 h photoperiod, indicating that these two genotypes might have a critical photoperiod lower than 14 h or it takes an extremely long time for the flowers to open. These two genotypes originated from low-latitude area (Table 2), namely Sandek Sieng (Cambodia) and Miss 33 Dixi (Philippines).

Variation of photosensitivity

To evaluate photosensitivity comprehensively in all genotypes, we chose 10 and 13 h photoperiod. The earliest flowering time was observed at 8 or 10 h, but we chose 10 h for short photoperiod because it might be better for growth and development as well as 13 h for long photoperiod that is less than critical photoperiod because all genotypes opened the flower under this condition. Under these long- and short-photoperiodic conditions at 28°C, we tested the DEF of 82 *GmWMC* genotypes and evaluated their index of photosensitivity of flowering (IPF). DEF varied notably from 20 to 49 d with the 13 h photoperiod, whereas it was from 20 to 31 d with the 10 h photoperiod (Table 2). The reduction of DEF by 10 h were 0 to 22 d. Furthermore, IPF varied from 0.00 to 0.47 and incompletely related with the origin of genotypes in *GmWMC* (Table 2). The genotypes distributed overall the ranges, but showed two peaks at low IPF (0.06–0.10) and high IPF (0.31–0.45) (Figure 1). Our previous research showed that photosensitivity varied from –0.01 to 0.58 in *GmWMC* genotypes by changing sowing time at field (Islam et al., *in press*). However, the key problem with the previous research was that photoperiod and temperature changed daily. The range of photosensitivity for each genotype in the present study showed little discrepancies compared with previous study.

Genotypic variations in photosensitivity have been reported frequently. Huxley et al. (1974) found that DEF delayed 0 to 25 days by long photoperiod (13:20 h) versus short photoperiod (11:40 h) among 4 tested genotypes. Hartwig and Kiihl (1989) tested 11 genotypes under two sowing dates long- (15:15 h) and short- (13:30 h) photoperiod and reported that DEF

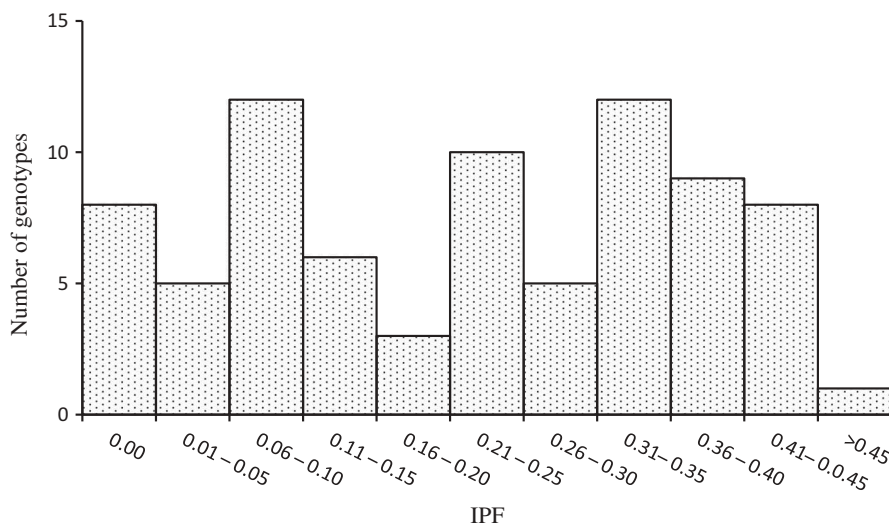


Figure 1. Distribution of the index of photosensitivity of flowering (IPF) among *GmWMC* genotypes.

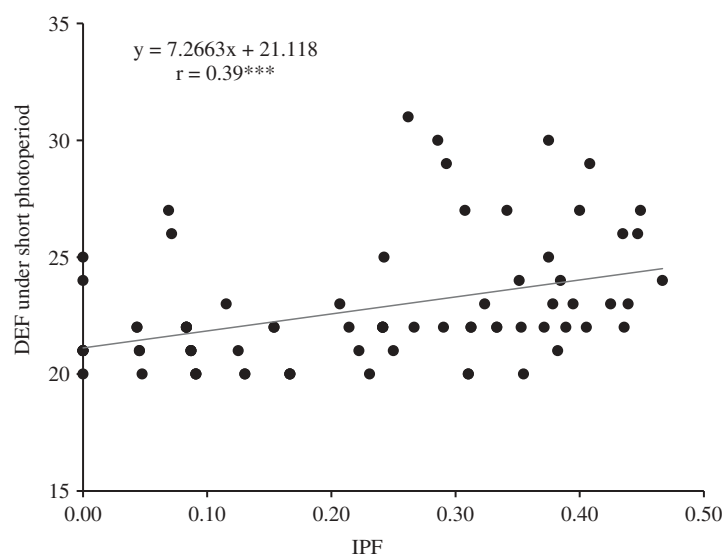


Figure 2. Relationship between index of photosensitivity of flowering (IPF) and the days from emergence to first flower open (DEF) under short photoperiod (10 h). *** denotes significant at $P < 0.001$.

Table 2. DEF and index of photosensitivity of flowering (IPF) in *GmWMC* genotypes.

ID number	Genotype	Origin	DEF _{10h} (d)	DEF _{13h} (d)	DEF _{13-10h} (d)	IPF
<i>GmWMC</i> 001	Fiskeby V	Sweden	21	21	0	0.00
<i>GmWMC</i> 006	Ks 1034	Malaysia	20	21	1	0.05
<i>GmWMC</i> 011	Seita	Rep.Korea	21	27	6	0.22
<i>GmWMC</i> 012	Manshuu	China	22	26	4	0.15
<i>GmWMC</i> 014	Kls 203	Rep. Korea	26	–	–	–
<i>GmWMC</i> 015	Chuuuhoku 2	Rep.Korea	20	23	3	0.13
<i>GmWMC</i> 018	Rigai Seitou	China	22	32	10	0.31
<i>GmWMC</i> 019	Chousenshu (Cha)	Korea	21	21	0	0.00
<i>GmWMC</i> 020	Pochal	Taiwan	22	28	6	0.21
<i>GmWMC</i> 022	Nezumi Meta	Korean Peninsula	21	34	13	0.38
<i>GmWMC</i> 024	Chieneum Kong	Rep.Korea	20	24	4	0.17
<i>GmWMC</i> 027	Kongnamul Kong	Rep.Korea	20	24	4	0.17
<i>GmWMC</i> 029	Shirosota	Korean Peninsula	22	23	1	0.04
<i>GmWMC</i> 035	Pekin Dai Outou	China	21	21	0	0.00
<i>GmWMC</i> 036	Masshokutou (Kou 502)	China	21	21	0	0.00
<i>GmWMC</i> 038	Ichiguuhou	China	23	38	15	0.39
<i>GmWMC</i> 042	Masshokutou (Kou 503)	China	21	21	0	0.00
<i>GmWMC</i> 045	Okjo	Rep.Korea	22	24	2	0.08
<i>GmWMC</i> 046	Ke 32	Philippines	20	20	0	0.00
<i>GmWMC</i> 048	Heamnam	Rep.Korea	22	32	10	0.31
<i>GmWMC</i> 066	Heukdaelip	Rep.Korea	22	23	1	0.04
<i>GmWMC</i> 070	Choyoutou	China	21	22	1	0.05
<i>GmWMC</i> 071	Pk 73-54	India	21	28	7	0.25
<i>GmWMC</i> 072	M 581	India	22	26	4	0.15
<i>GmWMC</i> 073	Uronkon	Korean Peninsula	21	23	2	0.09
<i>GmWMC</i> 075	Cheongye Myongtae	Rep.Korea	21	22	1	0.05
<i>GmWMC</i> 083	Keumdu	Rep.Korea	21	24	3	0.13
<i>GmWMC</i> 084	Peking	China	20	22	2	0.09
<i>GmWMC</i> 086	Anto Shoukokutou	China	20	22	2	0.09
<i>GmWMC</i> 089	Bongchunbaekjam	China	22	24	2	0.08
<i>GmWMC</i> 094	Jeokgak	Rep.Korea	22	29	7	0.24
<i>GmWMC</i> 103	Senyoutou	China	25	40	15	0.38
<i>GmWMC</i> 107	Hakka Zashi	China	20	24	4	0.17
<i>GmWMC</i> 108	Karasumame	China	27	29	2	0.07
<i>GmWMC</i> 113	Baritou 3 A	Indonesia	22	24	2	0.08
<i>GmWMC</i> 115	Williams 82	USA	21	23	2	0.09
<i>GmWMC</i> 118	Oudu	Rep.Korea	22	29	7	0.24
<i>GmWMC</i> 119	Hakubi	China	24	24	0	0.00
<i>GmWMC</i> 120	U 1416	Nepal	23	29	6	0.21
<i>GmWMC</i> 122	Gapsanjaelae (I)	Rep. Korea	22	24	2	0.08
<i>GmWMC</i> 123	N 2295	Nepal	20	31	11	0.35
<i>GmWMC</i> 125	Bhatmas	Nepal	20	29	9	0.31
<i>GmWMC</i> 129	Aoki Mame	China	23	–	–	–
<i>GmWMC</i> 132	L 2a	Philippines	21	23	2	0.09

(Continued)

Table 2. (Continued).

ID number	Genotype	Origin	DEF _{10h} (d)	DEF _{13h} (d)	DEF _{13-10h} (d)	IPF
GmWMC136	Local Var. (Seputih Raman)	Indonesia (Sumatra)	27	41	14	0.34
GmWMC142	Java 5	Indonesia	27	45	18	0.40
GmWMC143	M 44	India	20	29	9	0.31
GmWMC144	M 918	India	22	39	17	0.44
GmWMC146	Hm 39	India	22	31	9	0.29
GmWMC147	Col/Thai/1986/Thai-78	Thailand	22	29	7	0.24
GmWMC148	M 42	India	24	45	21	0.47
GmWMC150	U 1042-1	Nepal	22	34	12	0.35
GmWMC151	Java 7	Indonesia	22	33	11	0.33
GmWMC152	U 1290-1	Nepal	22	37	15	0.41
GmWMC154	Manshuu Masshokoutou	China	22	36	14	0.39
GmWMC156	U 8006-3	Nepal	23	37	14	0.38
GmWMC159	Col/Pak/1989/lbpgr/2323(2)	Pakistan	20	23	3	0.13
GmWMC160	N 2392	Nepal	23	–	–	–
GmWMC162	Col/Thai/1986/Thai-80	Thailand	22	33	11	0.33
GmWMC163	N 2491	Nepal	25	33	8	0.24
GmWMC165	Karasumame (Shinchiku)	Taiwan	25	25	0	0.00
GmWMC166	Merapi	Indonesia (Sumatra)	23	34	11	0.32
GmWMC168	L 317	India	24	39	15	0.38
GmWMC169	Hakuchikou	China	20	22	2	0.09
GmWMC170	M 652	India	31	42	11	0.26
GmWMC171	U-1741-2-2 No.3	Nepal	22	30	8	0.27
GmWMC173	Karasumame (Naihou)	Taiwan	29	49	20	0.41
GmWMC175	Bishuu Daizu	China	22	29	7	0.24
GmWMC176	Sandek Sieng	Cambodia	30	42	12	0.29
GmWMC181	Chiengmai Palmetto	Thailand	24	37	13	0.35
GmWMC182	Local Var. (Tegineneng) Purple flower	Indonesia (Sumatra)	27	49	22	0.45
GmWMC182	Local Var. (Tegineneng) White flower	Indonesia (Sumatra)	23	40	17	0.43
GmWMC183	Karasumame (Heitou) Yellow seed	Taiwan	23	26	3	0.12
GmWMC183	Karasumame (Heitou) Black seed	Taiwan	26	28	2	0.07
GmWMC186	Ringgit	Indonesia (Sumatra)	23	41	18	0.44
GmWMC187	Kadi Bhatto	Nepal	26	46	20	0.43
GmWMC188	E C 112828	India	26	47	21	0.45
GmWMC190	San Sai	Thailand	29	41	12	0.29
GmWMC191	Miss 33 Dixi	Philippines	30	48	18	0.38
GmWMC192	U 1155-4	Nepal	27	39	12	0.31

DEF_{10h} is the days from emergence to first flower open under 10 h photoperiod at 28°C temperature. DEF_{13h} is the days from emergence to first flower open under 13 h photoperiod at 28°C temperature. DEF_{13-10 h} is the difference of the days from emergence to first flower open under 13 and 10 h photoperiod. Genotypes are arranged based on ID number. – denotes failed to collect data.

delayed from 2 to 34 days under long- photoperiod among 11 genotypes. The variation (0–22 days) in this study was almost consistent with the previous reports even though under different photoperiod. However, IPF (0.00–0.47) was wider than the results (0.07–0.38) reported by Fatichin et al. (2009), which is done under long- (14:03–12:30) and short- (10:21–11:37) photoperiod. Furthermore, eight genotypes with very low photosensitivity (IPF = 0.00), and nine genotypes with high photosensitivity (IPF > 0.40) (Table 2 and Figure 1). The former genotypes are originated mainly from Sweden, Korea, China and Philippines, and later from India, Indonesia, and Nepal. These high-genotypic diversities would be potential source to expand the genetic base of soybean for wide adaptation areas, particularly tropical areas. Less information was reported previously about the photosensitivity in the controlled environments using a large number of genotypes, which is originated from diverse areas.

Relationship between IPF and DEF under short photoperiod (10 h)

There was a positive significant relationship between IPF and DEF under short photoperiod ($r = 0.39$, $p < 0.001$) (Figure 2); however, a wide distribution range was also observed in both IPF and DEF. Since DEF was minimum under this short photoperiod in most of the genotypes (Table 1), the long DEF under short photoperiod would be caused by some other factors such as JGP or post-inductive phase. DEF could be separated into three phases: (A) pre-inductive phase, which is the JGP and insensitive to photoperiod; (B) inductive phase, which is sensitive to photoperiod; and (C) post-inductive phase, which is the duration for flower organs development and insensitive to photoperiod (Roberts & Summerfield, 1987; Ellis et al., 1992). When the inductive phase is shortened in maximum, DEF is consisted of pre-inductive and post-inductive phases; however, post-

inductive phase is considered less varied among the genotypes. Therefore, the DEF under short photoperiod in this study could be resulted mostly by JGP.

The JGP responsiveness for soybean is a crucial factor in its latitudinal adaptation. It is hard to determine exact JGP because of the difficulty to separate the effects on DEF by individual phase. According to previous reports, Wilkerson et al. (1989) transferred six soybean cultivars from long (22 h) to short (9 h) photoperiod and vice versa at a constant temperature of 26°C, resulted in a range of JGP 3.0–8.5 d from germination among genotypes. Similarly, Collinson et al. (1993) transferred four genotypes from 11.5 h to 13.5 h photoperiod and vice versa at a mean temperature of 25°C and identified that JGP varied from 11 d to 33 d from sowing among four genotypes. Wang et al. (1998) transferred the plants from a 22-h photoperiod to 8-, 10-, 12-, or 14-h photoperiods at a constant temperature of 26°C and concluded that there was no JGP from emergence in Hutcheson soybean. The differences in these reports could be caused by different photoperiod or genotypes. In our results, DEF under short photoperiod were 20 days in the earliest genotypes, whereas were 31 days in the longest genotype. Therefore, the difference of DEF under short photoperiod among 82 *GmWMC* genotypes, may represent the relative JGP. Considering with about 20 d from flower bud initiation to flower open (Saitoh et al., 1999) and the existence of genotypes without JGP (Wang et al., 1998), the relative JGP in *GmWMC* could be considered as 0–11 d in maximum from emergence. Even the estimation of JGP using DEF under short photoperiod could not exclude the influence by post-inductive phase, however, it could be an indicator as a comparison between the genotypes, and it is easier to conduct for examining a large number of genotypes. Moreover, even there was a positive relationship between IPF and DEF under short photoperiod (DEF_{10h}), the DEF_{10h} was not always associated with IPF. It implies that there were some special genotypes having low IPF with medium DEF_{10h} (Karasumame; Karasumame (Shinchiku); Karasumame (Heitou) Black Seed) or high IPF with short DEF_{10h} (M 44, N 2295, Bhatmas, Nezumi Meta) (Table 2 and Figure 2). These genotypes may have unique genetic backgrounds and be useful for the breeding of new varieties. Furthermore, as mentioned above, some long DEF_{10h} genotypes may be good resources to broaden the adaptation in low-latitude areas by ensuring sufficient vegetative growth even in short photoperiod condition.

In conclusion, our study provided a wide variation of IPF in *GmWMC* genotypes and important insights into the introduction of several special genotypes which have long DEF_{10h} regardless of IPF. This study will help breeders in selecting diverse source with different

combination of IPF and DEF_{10h} to enrich the genetic base in soybean. Miranda et al. (1990) conducted breeding using Parana, Davis, Hardee, Hill, and Santa Rosa genotypes including genes for long JGP in São Paulo State, Brazil (23°31' S), and released a genotype (IAC-15) that produced high plant height and seed yield. Hence, future work will be focused on soybean breeding programs using special genotypes that may help to extend soybean production in tropical areas.

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Author contributions

MRI performed the experiments, all data collection, paper writing. DF advised for research plan and experiment management. SW advised for research plan and experiment management. SHZ contributed to the research design and paper edition.

Disclosure statement

No potential conflict of interest was reported by the authors.

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