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Field-based Screening and Haplotyping of *J* Locus for Long Juvenile Trait in Tropical Soybean Genotypes

Enoch Sapey[1,2], Yudong Fang[1], Dalia Mohamedkheir Khojely[1], Wenwen Song[1], Bingjun Jiang[1], Shan Yuan[1], Shi Sun[1], Tianfu Han[1]

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ABSTRACT

Background: The long juvenile trait influences flowering time of soybean under tropical conditions. The trait ensures sufficient vegetative growth prior to flowering. The present study aimed at identifying tropical soybean genotypes with the long juvenile trait and harboring the loss-of-function alleles for the *J* gene and verifying the effect of loss-of-function alleles on the long juvenile trait.

Methods: A total of 159 soybean genotypes were evaluated on the field for two years in tropical city of Sanya, Hainan Islands, China for days to beginning bloom (VE-R1), days to physiological maturity (VE-R7), nodes/plant, pods/plant and plant height at maturity. The full length of the *J* gene was cloned in the 159 soybean genotypes. The sequence data was subjected to haplotype analysis to determine the genotypes with the functional and loss of function alleles.

Result: Significant differences (p<0.05) were observed among genotypes for all phenotypic traits. 53 genotypes were identified with delayed flowering based on the phenotypic data. Sequence comparison of the 159 genotypes identified 10 polymorphisms comprising 7 SNPs and three deletions in the coding sequences, the three deletions resulted in the loss of function of the *J* gene. Six genotypes with delayed flowering had the loss-of-function alleles of the *J* gene.

Key words: Delayed flowering, Haplotypes, Long juvenility, Soybean.

INTRODUCTION

Soybean is one of the key leguminous crops in the world that provides protein and oil for human use and also serves as animal feed. This rising demand for soybean is creating economic opportunities to expand soybean production in tropical regions. Soybean was domesticated ~5000 years ago in the upper reach of Yellow River in China at approximately 35°N latitude characterized by long days (Hymowitz, 1970). However, soybean as a short-day plant is sensitive to photoperiod and its flowering is induced when the day length is shorter than a critical threshold (Yang *et al*. 2019). These characteristic limits the expansion of soybean cultivation in latitudes less than 20° where day length deviates around 12 to 13 hours.

Production of soybean has conventionally centered around mid- and high-latitude temperate regions. Low-latitude areas with tropical and sub-tropical climates were previously considered unsuitable for soybean production (Destro *et al*. 2001). Hartwig and Kiihl (1979) identified a recessive trait in soybean germplasm that delayed flowering under short-day conditions and has been referred to the long juvenile trait. The long juvenile trait influences flowering time in low latitude areas, which characterize tropical climates and allows for a broader range of sowing dates, delay flowering and ensures sufficient vegetative growth prior to reproductive growth (Carpentieri-Pípolo *et al*. 2000).

The use of long juvenile trait in soybean breeding programs in South America has led to a tremendous increase in soybean production, even though almost half of its total soybean production area is located below 24°S outside the traditional soybean adaptation zone (Neumaier and James 1993). In Africa, the long juvenile trait, together with the improved agronomic performances is encouraging an increase in soybean production.

To date, only two loci, *E6* and *J*, have been reported to control the long juvenile trait (Ray *et al*. 1995; Bonato and Vello 1999). Studies by Yue *et al*. (2017) and Lu *et al*. (2017) identified the *J* gene as the Arabidopsis flowering ortholog *ELF3*. *GmELF3* has 4 exons/3 introns and is a highly conserved protein that controls flowering time in multiple species (Lu *et al*. 2017). They suggested that *J* is the dominant functional allele of *ELF3* that promotes flowering, while *j* is the recessive, loss-of-function allele that causes delayed flowering and confers the long juvenile trait that is associated with the adaptation of soybean to tropical regions.

[1]MARA Key Laboratory of Soybean Biology (Beijing), Institute of Crop Sciences, Chinese Academy of Agricultural Sciences, Beijing 100081, China.
[2]CSIR-Oil Palm Research Institute, P.O Box 74. Kade, Ghana.

Corresponding Author: Tianfu Han, MARA Key Laboratory of Soybean Biology (Beijing), Institute of Crop Sciences, Chinese Academy of Agricultural Sciences, Beijing 100081, China. Email: hantianfu@caas.cn

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The objectives of this study were (i) to identify tropical soybean genotypes carrying the long juvenile trait and the loss-of-function alleles that are responsible for long juvenile trait in soybean, (ii) to verify the relationship between the *J* mutations and the long juvenile trait. The newly identified genotypes and the data provided will useful for tropical soybean breeding programs.

MATERIALS AND METHODS

A total of 159 tropical soybean genotypes from different tropical regions were used in the study (Table 1). The tropical soybean accessions were retrieved from the Gene bank of the Institute of Crop Sciences, Chinese Academy of Agricultural Sciences (CAAS) and Agricultural Research Corporation (ARC), Wad Medani, Sudan.

Field phenotyping

The 159 soybean genotypes were planted in 1.5 m single row plot; the spacing between rows was 30 cm with 5 cm spacing within plants with two replications. Seeds were sown at CAAS Experimental Station-Sanya (18.27.17° N, 109.11° E), Hainan, China, for two years on the 19th and 9th of November, 2018 and 2019, respectively. The daylength in Sanya during the field evaluation ranged from 11.4 to 11.9 hours and the temperature ranged from 19-26°C. The management of the field experiments was done according to recommended agronomic practices for soybean. Five plants were randomly tagged per row for data collection. Flowering time was recorded at the VE-R1 stage [days from emergence (VE) to the beginning bloom (R1)] and physiological maturity (R7) recorded at VE-R7 stage (days from emergence to when at least a pod had mature color), by the methods described by Fehr *et al*. (1971). Plant height from the ground to the terminal raceme apex, number of stem nodes per plant and number of pods per plant were all recorded at physiological maturity.

Table 1: Origin of the tropical soybean genotypes.

Origin	Number of genotypes
Australia	2
Brazil	36
Thailand	30
India	1
China	44
Nepal	5
Nigeria	31
USA	8
Unknown	2

Statistical analysis of the phenotypic data

The data collected were subjected to analysis of variance (ANOVA) and descriptive statistics computed using SPSS software. Boxplots were constructed using the ggplot2 package in R software.

Genotyping for *J* gene

DNA was extracted from the 159 soybean accessions using the NuClean Plant Genomic DNA Kit (CoWin Biosciences) according to the manufacturer's recommendation. The quality of the extracted DNA was evaluated by 1% agarose gel electrophoresis. The DNA concentration of each sample was determined using Nanodrop 2000 (Thermo Scientific). Six primers were designed covering the four exons of the *J* gene. Two were used for Polymerase Chain Reaction (PCR) and the remaining four for sequencing. Table 2 shows the list of the six primers used for genotyping.

PCR was done to amplify genomic regions using KOD-Plus-Neo Kit (Toyobo Life Science). The total volume of the PCR mix of 50 µL consisted of 5 µL of PCR Buffer, 5 µL of 2 mM dNTPs, 3 µL of 25 mM MgSO4, 1.5 µL of 10 mM forward and reverse primer, 5 µL of DNA template at a concentration about 100 ng, 1 µL KOD Plus Neo and 27 µL of double-distilled water. The PCR conditions were as follows: denaturation for 2 minutes at 94°C followed by 35 cycles of 10 sec at 98°C and a primer extension reaction of 68°C for 5 minutes. The PCR products were separated on 1% agarose gel, stained with ethidium and visualized with Gel Doc XR Molecular Imager System (Bio-Rad). The PCR products were directly Sanger sequenced by TSINGKE Biotech, China. DNA Sequence assembly and alignment were done using the Mega software.

Definition of *J/j* alleles

The definition of the *J/j* alleles was done by comparing the sequence data with sequences deposited in the National Centre for Biotechnology Information (NCBI) database by Yue *et al*. (2017) and Lu *et al*. (2017).

RESULTS AND DISCUSSION

Phenotypic variations of days to flowering, maturity and other associated agronomic traits

Significant differences ($p < 0.05$) were observed among the genotypes for all the phenotypic traits measured (Table 3).

Table 2: List of primers for genotyping the *J* gene and their sequence.

Primer name	Sequence (5′-3′)	Use
J04G-F2 (F)	CATCTAATCCAATTCTCGTACGTGTG	PCR
J04G-R2 (R)	TATGACAATCACTAGTCTTCTAGGC	PCR/Sequencing
J04G-F2b (F)	GGTTCCATATCAGGGCAAAG	Sequencing
J04G-R2b (R)	GTTCCCCTGTTCAACAACTG	Sequencing
F3A (F)	TGCTTGGACCTGACAAGTTC	Sequencing
R3A (R)	CCTTTATCAGTCTATGCAAC	Sequencing

Table 3: Combined ANOVA for all the five phenotypic traits.

SV	DF	VE-R1	VE-R7	Node/plant	Plant height	Pod/plant
Replication	1	0.026^{ns}	122.64^{ns}	2.29^{ns}	780.87^{ns}	23.12^{ns}
Year	1	35.25*	70.04*	7.13*	344.05*	99.68*
Genotype	158	44.21*	363.93*	786.82*	28022.13*	3117.97*
Genotype × Year	158	5.67*	27.56^{ns}	2.10*	91.50*	45.96*

*Significant P < 0.05; NS- not significant. DF- Degrees of freedom; MS- Mean squares. VE-R1- Days to first flowering; VE-R7- Days to physiological maturity.

There was also a significant difference between years and the genotype by year interactions for these traits, except for VE-R7. This shows a high genetic variability of the tropical genotypes used in the study. Days to from emergence to beginning bloom (VE-R1) ranged from 21.67 to 41.45 days among the 159 genotypes. A box plot of VE-RI (Fig 1) showed two outliers (TGX 1987-62F and IC192) with flowering days of 35.4 and 41.8, respectively. Days from emergence to physiological maturity (VE-R7) ranged from 63.89 to 85.08 days. The plant height of the genotypes ranged from 15.3 to 68.4 cm, a box plot of plant height of genotypes showed two outliers (IC192 and CIGRAS-06). The plant heights of the two genotypes were 68.5 and 64.3 cm, respectively and the number of nodes and pods per plant ranged from 5.43 to 13.92 and 4 to 27.59 respectively.

Significant positive correlations were observed among all phenotypic traits studied (Table 4). A significant (p<0.05) and positive correlation was observed between VE-R1 and VE-R7. The correlations of plant height at maturity with the numbers of nodes per plant and pods per plant were highly positive. Plant height is an important trait that affects soybean adaptation and yield. A positive significant correlation was observed among the phenotypic traits indicating that delayed flowering resulted in an increase in the other important agronomic traits such as plant height, which sometimes correlates with high yields in tropical regions (Cober and Morrison, 2010).

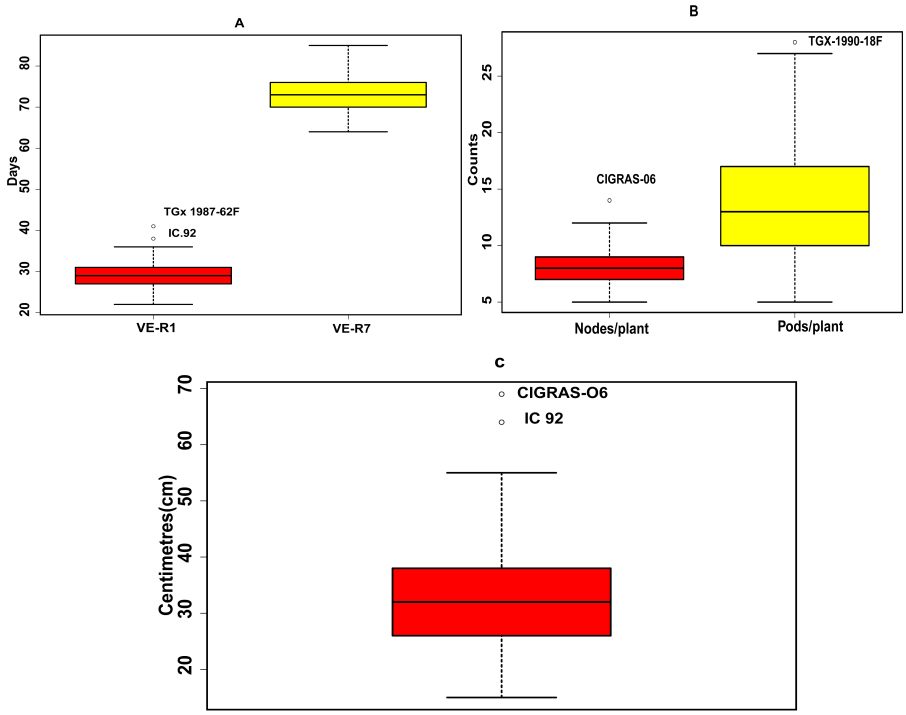


Fig 1: Box plot of the five phenotypic traits observed on the 159 genotypes.

Table 4: Correlation coefficients among the five phenotypic traits.

Trait	VE-R1	VE-R7	Node/plant	Plant height	Pod/plant
VE-R1	1	.547**	.583**	.483**	.601**
VE-R7		1	.523**	.588**	.574**
Node/plant			1	.734**	.785**
Plant height				1	.636**
Pod/plant					1

**Correlation is significant at the 0.01 level.

Table 5: List of selected delayed flowering genotypes.

Genotype	Origin	VE-R1(days)	VE-R7(days)	Nodes/ plant	Pods/plant	Height	Haplotype
TGx 1987-62F	Nigeria	41.5±2.5	79.1±13.4	12.3±2.2	18.7±7.1	37.9±13.1	j2
I.C.192	USA	38.1±2.5	85.1±1.5	12.2±3.1	24.5±11.2	68.5±8.3	J1
TGx 1990-95F	Nigeria	35.8±7.2	82.0±3.7	10.2±2.7	27.2±11.5	37.7±12.0	Hap1
TGx 1965-7F	Nigeria	35.1±2.9	75.8±7.7	8.4±1.8	24.8±11.1	42.6±9.6	Hap1
TGx 1989-42F	Nigeria	34.6±1.2	70.6±3.2	8.2±2.9	13.0±11.6	34.0±10.3	Hap1
TGx 1835-10E	Nigeria	34.4±0.9	72.7±2.6	8.3±1.2	13.7±5.0	31.6±9.5	j2
EMGQRA-314	Brazil	33.0±2.4	81.8±1.2	8.7±1.3	23.1±12.3	44.4±15.4	Hap1
Sudan 2	Sudan	33.0±1.5	77.9±1.8	9.2±0.9	19.3±10.7	37.9±10.6	Hap1
TGx 536-02D	Nigeria	33.9±2.3	78.8±2.7	9.1±3.1	20.6±14.1	35.5±17.7	Hap3
UFV-8	USA	33.9±1.4	80.5±2.6	8.9±1.9	20.5±9.5	52.1±15.6	Hap1
TGx 1949-7F	Nigeria	33.8±1.7	79.3±2.6	10.7±1.7	20.4±13.6	44.2±9.1	Hap1
ITAL SOJA-1	Brazil	33.8±1.6	80±2.7	9.2±2.3	17.8±9.3	51.3±18.2	Hap1
Huaxia3	South-China	33.6±1.7	75.3±1.9	10.0±2.2	19.9±9.2	41.8±15.8	J4
Soya4	Sudan	33.3±2.1	78±1.3	11.3±2.7	22.1±7.0	41.4±12	Hap1
G 2120 M7(69-1)	-	33.1±1.1	69.3±2.9	10.7±2.3	21.4±8.8	51.4±9.7	Hap3
MT/BR-52	Brazil	32.0±1.8	73.6±14.1	9.1±1.7	20.2±6.7	32.4±17.6	Hap1
TGx 1990-18F	Nigeria	32.0±1.7	79.2±0.7	10.9±1.8	27.6±19.7	37.8±16.6	Hap1
Huaxia10	South-China	32.0±1.5	74.8±1.6	9.1±0.9	13.3±4.2	31.8±8.6	J4
MG/BR-48	Brazil	32.9±1.4	78±1.1	10.9±2.0	14.7±7.6	45.8±18.3	j2
Nigeria4	Nigeria	32.8±1.9	77±3.8	10.4±1.9	19.6±10.5	37.0±17	Hap4
TGx 1990-80F	Nigeria	32.7±3.6	73.4±5	8.8±0.9	26.8±8.6	32.2±8	Hap1
ITAL SOJA-2	Brazil	32.5±2	79.3±2.3	8.8±2.6	20.4±12.5	54.6±15.2	Hap1
TGx 1977-2F	Nigeria	32.3±2.6	76.2±2.8	8.8±1.5	19.4±7.2	29.0±11.9	Hap3
MT/BRS-63	Brazil	32.3±1.9	81.7±2.8	9.3±1.8	15.6±5.1	48.8±11.8	Hap3
TGx 1971-1F	Nigeria	32.3±1.4	70.8±12.9	8.5±2.0	13.9±7.1	42.1±19.3	Hap4
Nigeria5	Nigeria	31.9±3.1	75.3±4.4	8.1±1.1	11.8±5.1	34.6±6.5	Hap3
BR/IAC-21	Brazil	31.9±2.4	79.8±1.4	10.4±2.7	20.7±11.4	53.6±12	Hap1
CIGRAS-06	USA	31.8±1.8	83.1±1.9	13.9±3.1	26.2±13.7	64.3±8.6	Hap3
TGx 1448-2E	Nigeria	31.6±2.9	72±12.2	8.4±3.8	16±11.9	38.2±21.7	Hap3
Nannong99-10	South-China	31.6±2.5	71.5±3.7	6.0±1.4	7.9±5.0	19.7±3.9	Hap3
Sudan 1	Sudan	31.6±2.3	77.9±3.5	8.6±1.9	16.8±9.4	34.1±9.4	Hap3
TGx 1991-10F	Nigeria	31.6±1.7	77.0±3.5	9.0±2.2	19.7±10.9	38.8±15.1	Hap1
Emgopa-314	Brazil	31.6±1.6	80.5±1.8	9.2±1.3	26.3±9.6	36.8±10.2	Hap1
TGx 1990-101F	Nigeria	31.6±1.1	74.5±9.7	8.8±1.5	19.1±9.6	30.5±9.2	Hap3
AGS32	Thailand	31.5±4.8	70.8±4.6	11.1±7.4	18.3±17.4	33.8±20.2	Hap3
MT/BR-51	Brazil	31.5±2.8	72.3±13.9	9.3±1.8	16.9±9.6	35.6±24.4	Hap1
AGS167	Thailand	31.4±2.0	75.5±1.7	8.0±2.0	14.1±7.4	39.8±8.3	Hap1
AGS160	Thailand	31.3±2.7	74.3±4.6	7.9±1.8	9.1±6.4	31.9±9.1	Hap1
UFV-16	Brazil	31.3±2.2	77.9±4.1	8.8±2.7	12.9±5.6	50.2±13.5	Hap1
G 2120 M7(69-4)	-	31.3±2.0	68.7±4.0	10.5±1.8	22.9±7.5	55.3±11.2	Hap3
AGS126	Thailand	30.0±2.0	70.3±3.6	10.3±1.5	19.9±7.5	43.3±13.7	Hap3
MT/BR-55	Brazil	30.0±1.0	76.8±4.7	9.5±1.6	16.3±7.6	40.3±12.1	Hap3
Guixia7	China	30.9±2.2	65.5±1.4	6.9±1.2	8.8±2.0	19.6±8.1	Hap3
TGx 1989-19F	Nigeria	30.9±1.3	76.8±1.5	9.4±1.9	16.4±9.2	36.8±15.3	Hap1
CIGRAS-51	USA	30.7±1.8	79.4±2.4	8.3±1.1	20.4±10.9	35.7±12.8	Hap3
AGS269	Thailand	30.6±1.7	70.8±4.6	7.3±2.2	12.9±7.6	29.1±4.4	Hap3
TGx 1990-57F	Nigeria	30.6±1.6	75.3±2.6	9.7±2.5	21.1±12.4	40.8±17.7	Hap1
TGx 1989-11F	Nigeria	30.5±4.2	73.4±1.0	9.1±2.7	14.3±6.2	28.8±13	Hap1
Nannong415	South-China	30.4±3.8	69.8±2.0	5.8±1.4	6.7±5.5	20.5±6.2	Hap3
TGx 1989-20F	Nigeria	30.4±2.2	76.9±1.7	9.8±1.9	22.4±8.8	38.4±12	Hap1
TGx 1989-45F	Nigeria	30.3±2.7	76.4±2.8	8.5±2.4	14.6±7.0	30.6±15.2	Hap1
UFV-17	Brazil	30.3±1.9	80.0±2.9	8.3±2.2	13.8±5.5	45.7±8.3	Hap1
A9	Thailand	30.2±1.6	74.6±2.9	7.8±1.6	15.0±8.0	38.0±16.0	Hap1

*The mean phenotypic values were averaged across the two years, plus or minus the standard deviation.

Selection of the genotypes that delayed flowering based on the phenotypic data

Sanya-Hainan Islands, the experimental site used for phenotyping of the long juvenile trait, is the southernmost region of China with a typical tropical climate. The day length and temperatures provided an ideal environment for screening for the long juvenile trait in China. Two long juvenile varieties Huaxia-3 and Huaxia-10 reported by Yue *et al*. (2017) and Lu *et al*. (2017) were included in the study to serve as checks. The two check varieties flowered about 32-33 days after emergence. Since the determination of juvenility of a genotype is determined by the photoperiod of the given environment, genotypes that have same or similar flowering days as the check varieties or flowered later than the check varieties were considered to be long juvenile. Based on the phenotypic data we have identified 53 genotypes that flowered 30 days and above (Table 5).

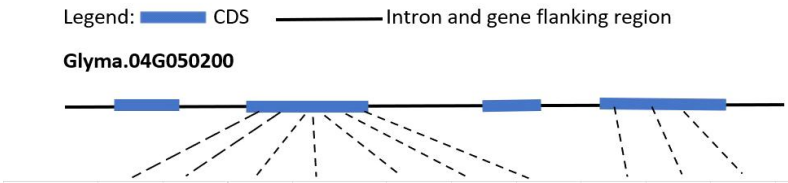
SNP haplotyping to distinguish different alleles of the *J* gene

Based on the phenotypic differences observed, we have genotyped the 159 soybean genotypes and carried out haplotype analysis to determine the genotypes carrying the functional or non-functional alleles of the gene. Sequence comparison identified 10 polymorphisms comprising of seven SNPs and three deletions in the coding sequence, three of which resulted in the loss-of-function of the *J* gene. Fig 2 shows the position of the base substitution in the coding sequence and the number of haplotypes identified. Seven haplotypes were defined of which three haplotypes (*j1*, *j2* and *j4*) resulted in the loss-of-function of the *J* gene. The other functional haplotypes include Hap1, Hap2, Hap3 and Hap 4. Only one soybean germplasm from Brazil MG/BR-48 had the loss-of-function allele *j2*. Huaxia 3 and Huaxia 10, the two Chinese tropical check varieties, had the *j4* allele. Two genotypes TGx 1835-10E and TGx 1987-62F from IITA-Nigeria had the *j2* allele. I.C.192 from the US had the *j1* allele (Table 5, Fig 3). The identification of these alleles confirms studies by Lu *et al*. (2017) that the multiple loss-of-function *J* alleles existing in soybean germplasm worldwide may be responsible for delayed flowering and maturity.

Association of the haplotypes with the phenotypic traits

Fig 3 shows the variability of the phenotypic traits among the haplotypes defined. Haplotypes Hap1 and Hap3 are the most common among the genotypes with high variability in all the six phenotypic traits. Hap 4 is the least common in only two genotypes. Some genotypes with functional *J* haplotypes had similar flowering days and, in some cases, even higher (Table 3) than those harboring the loss-of-function alleles indicating that the *J* gene might not be the only gene responsible for the long juvenile trait. The same observations were recorded on the other associated phenotypic traits such as the plant height, number of nodes per plant and number of pods per plant. This confirms the polygenic nature of the long juvenile trait by previous studies (Ray *et al*. 1995, Carpentieri-Pipolo *et al*. 2000, Cober and Morrison 2010, Lu *et al*. 2017, Yue *et al*. 2017 and Fang *et al*. 2020).

The present study mainly focused on identifying new long juvenile genotypes and verifying whether the *J* mutations are associated with delayed flowering in soybean. The long juvenile genetic mechanism in most tropical genotypes especially Sub-Sahara Africa is not known (Miranda *et al*. 2020). Huaxia 3, the check variety, was introduced to some African countries and resulted in an increased productivity (Yue *et al*. 2017). Introgression of the loss-of-function alleles Hap *j2* and Hap *j4* to temperate cultivars has also resulted in the development of new long juvenile varieties in Brazil and southern China (Lu *et al*. 2017), indicating that the loss-of-function *J* alleles will be a good strategy to enhance the adaptation and yield increases in the tropics. Therefore, there exists a possibility that incorporation of the identified long juvenile genotypes with or without the loss of function alleles for the *J* gene in tropical soybean breeding programs will lead to yield increases. However, proper yield trials have to be conducted first, as past studies reported background effects could influence delayed flowering in soybean (Ray *et al*. 1995). The lack of



Haplotypes	A217G	A381G	A518G	del 10bp588	G630A	G920T	G993T	A1282-	C1352-	C1773T	No. of Genotypes
Hap1	A	A	A	TACAAGTA	G	G	G	A	C	C	65
Hap2	G	G	G	TACAAGTA	A	G	T	A	C	T	4
Hap3	G	A	A	TACAAGTA	G	T	T	A	C	C	82
Hap4	G	A	G	TACAAGTA	G	T	T	A	C	C	2
Hapj1	G	A	A	TACAAGTA	G	T	T	A	-	C	1
Hapj2	A	A	A	-	G	G	G	A	C	C	3
Hapj4	A	A	A	TACAAGTA	G	G	G	-	C	C	2

Fig 2: Haplotypes and polymorphisms in the coding sequence of the *J* gene (Glyma.04G050200) in the 159 soybean genotypes. The haplotype is shown as a linear combination of alleles**.**

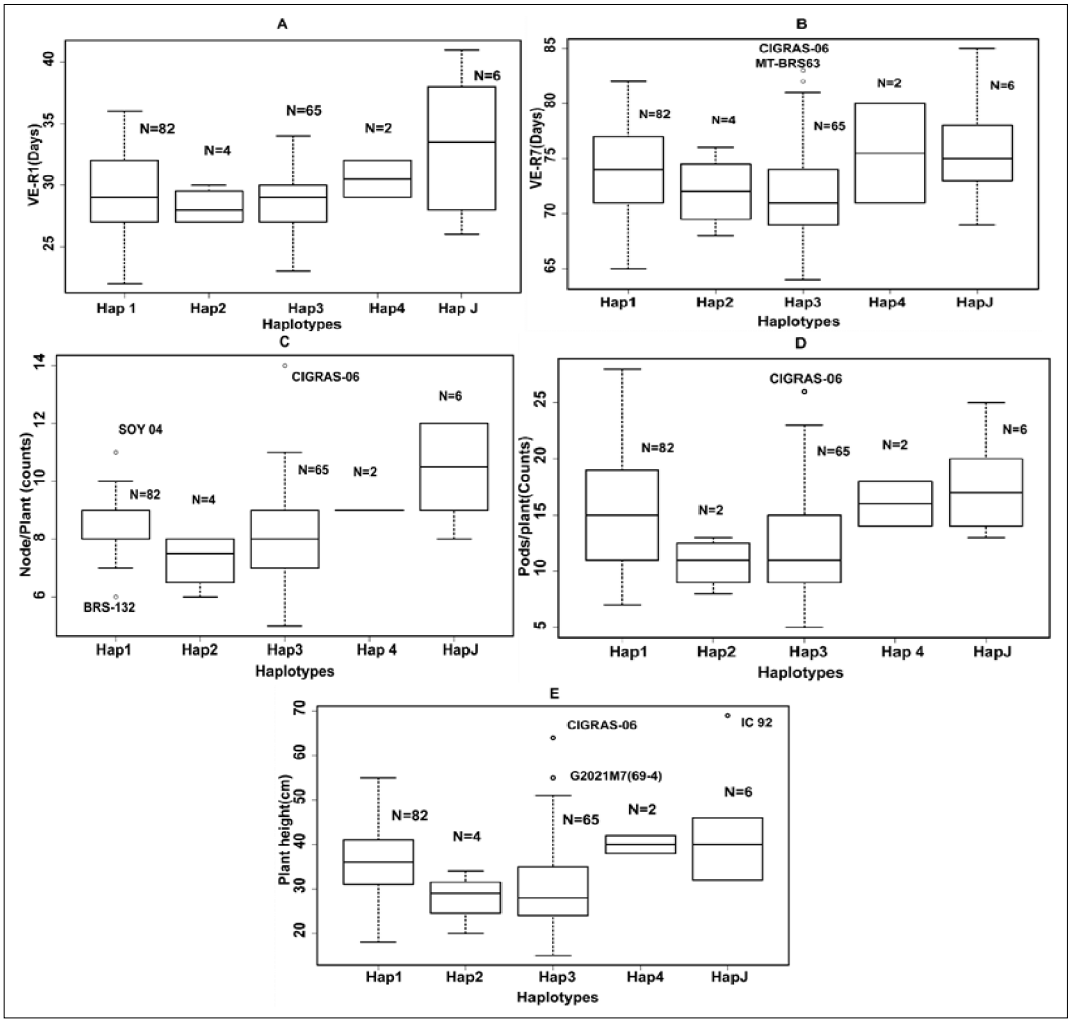


Fig 3: Variation in the five phenotypic traits of the various haplotypes of the *J* gene.
*HapJ comprise of haplotypes *j1, j2* and *j4*, *N= Number of genotypes per haplotypes.

proper yield data is a key limitation to the study. Future studies will focus on comprehensive yield trials on the identified long juvenile genotypes.

CONCLUSION

In this study, we screened 159 tropical soybean genotypes from tropical regions worldwide. We have identified 53 soybean genotypes with the delayed flowering. Haplotype analysis revealed six of them carried the loss-of-function alleles of the *J* gene. We also observed not all the genotypes with delayed flowering had the loss of function alleles for the *J* gene. This is indicative that some other genes may be acting with the *J* gene. The information we provided and the new long juvenile germplasm resources identified will be useful for tropical soybean breeding programs. Future studies should be directed towards mining other genes that may also be responsible for the long juvenile trait.

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