Environmental Stability and Correlation of Soybean Seed Starch with Protein and Oil Contents

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ABSTRACT Seed starch content (SSC) is a decisive factor influencing soy food quality. Variation in SSC affects the composition of major components, oil, and protein in soybean seeds. Therefore, understanding $G \times E$ interaction of SSC is important to produce soybeans with stable SSC. In the present study, $G \times E$ interactions of 17 soybean genotypes having different SSC (0.24-1.48%) and correlation of SSC with crude protein (CP) and crude fat (CF) were investigated. The genotypes were evaluated for SSC and other traits at two planting dates across three locations over two years (2015 and 2016). The genotype $\times$ year, genotype $\times$ location, and genotype $\times$ year $\times$ location interactions were found to be significant ($P \leq 0.001$) for SSC, CP, and CF. The average SSC content was found to be higher in 2015 than in 2016. Late planted soybeans contained higher SSC than the early planting soybeans. The SSC was negatively affected by the average daily mean and minimum temperatures and cloudiness during the pod-filling stage. Based on the mean rank, IT189276 (1.39%) was observed to be the most stable genotype among the high starch containing soybeans. Significant ($P \leq 0.0001$) negative correlations were found between SSC and CP as well as CP and CF contents. However, a significant ($P \leq 0.05$) positive correlation was observed between SSC and CF content. Results of this study showed that SSC affects the seed protein and oil contents and is significantly influenced by the growing environments.

Keywords Soybean, Seed starch content, Crude fat, Crude protein, Environmental stability

INTRODUCTION

Soybean [*Glycine max* (L.) Merr.] is an important legume crop in the world, domesticated mainly for its high oil and protein contents (Patil *et al.* 2017). Major constituents of soybean seeds are protein (~40%), carbohydrate (~34%), oil (~21%), and ash (~5%) (Burton 1997). Carbohydrate is an important component of the soybean seeds. A large proportion of the carbohydrates in soybean seeds are insoluble polysaccharides, including pectin, cellulose, hemicellulose, and starch (Liu 1997). Soluble carbohydrates are comprised of monosaccharides (glucose and fructose),

disaccharides (sucrose), and oligosaccharides (raffinose and stachyose) (Liu 1997). Soybean seeds contain 9-12% total soluble carbohydrates, which include 4-5% sucrose, 1-2% raffinose, and 3.5-4.5% stachyose (Greiner 1990). The insoluble polysaccharides include 20-30% non-starch polysaccharides (Choct 1997) and 1% starch (Wilson *et al.* 1978).

Starch, upon cooking, is converted into maltose, which adds sweetness to the vegetable soybeans (Masuda 2004). It also adds additional softness to the food after boiling (Jeong *et al.* 2010). Hence, high starch containing soybeans are preferred to make high-quality soy foods, such as boiled

Received September 22, 2017; Revised November 6, 2017; Accepted November 8, 2017; Published December 1, 2017

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soybean and fermented soybean paste. The starch in soybean seeds has been found to enhance tryptic digestion of some of the protein fractions (Boonvisut and Whitaker 1976). Resistant starch from soybean seeds has been used in producing nanoparticles, which can be used as potential encapsulating material in the colon-specific delivery of bioactive compounds such as drugs and nutrients (Sivapragasam *et al.* 2014). An inverse relationship between the seed starch content (SSC) and protein content has been observed in Korean soybean germplasm (Koo *et al.* 2014). Besides, a significant correlation between fatty acid composition and amylose, one of the two components (amylose and amylopectin) of starch, has been reported (Stevenson *et al.* 2006).

The genetic composition of the plant (genotype, G), the environment (E), and the $G \times E$ interaction influence the plant growth and development (Ei-Soda 2014). To develop the cultivars with stable trait expression across environments, $G \times E$ interactions need to be accounted in breeding programs. The plant's response in particular environment needs to be understood in terms of underlying QTL and their allelic composition. Earlier, we identified several loci controlling SSC in soybean (Dhungana *et al.* 2017) and observed that majority of the QTL for SSC were found to be significantly influenced by the growing environment. Such effects have been observed for other complex traits like forage quality (Asekova *et al.* 2016), isoflavone content (Primomo *et al.* 2005), seed weight (Kulkarni *et al.* 2016, 2017), seed protein (Panthee *et al.* 2005), fatty acid composition, oil and protein contents (Rennie and Tanner 1989; Dornbos and Mullen 1992; Primomo *et al.* 2002; Fehr *et al.* 2003; Hou *et al.* 2006; Oliva *et al.* 2006; Dhakal *et al.* 2013; Asekova *et al.* 2014), and yield (Rao *et al.* 2002; Shen *et al.* 2006) in soybean.

A large number of studies have been carried out in recent past to estimate the amount of $G \times E$ interaction for carbohydrate components in soybean. The environmental stability study of seed carbohydrates in soybean lines containing wild-type or variant alleles of raffinose synthase 2 showed variation in carbohydrates composition across spatial and temporal environments (Bilyeu and Wiebold 2016). The authors observed a significant effect of location on the concentration of sucrose, but no such effects were

observed on raffinose and stachyose concentrations. In another study by Kumar *et al.* (2010), the genotype $\times$ location interaction was found to be significant for sucrose, raffinose, and stachyose contents in soybean. Converse to these results, Cicek (2001) observed that $G \times E$ interaction was significant for agronomic traits like maturity, plant height, canopy spread, yield, seed size, leaf length, and leaf width but was not significant for seed sucrose, stachyose, or raffinose contents. Likewise, Geater and Fehr (2000) also observed that the cultivar $\times$ location interaction was not significant for total sugar content. Cober *et al.* (1997) observed that $G \times E$ interaction effects for seed sugar levels were significant for year, but not significant for location. Additionally, they observed significant year $\times$ location and $G \times E$ interactions for the sugar levels. These studies indicate that the growing environment show variable effects on the carbohydrate components in soybean.

The $G \times E$ interaction effects on starch properties have been studied in plants other than soybean. Bach *et al.* (2013) studied genotype, year, and location effects on starch digestibility components in potato. They did not find significant $G \times E$ interaction, however, most of the variations in the components were due to environmental effects, especially location $\times$ year interactions. Significant interactions between genotypes, locations, and harvest period were observed in cassava starch yield (Mtunguja *et al.* 2016).

SSC is a quantitative trait, controlled by multiple loci and influenced by the growing environment. SSC in soybean is reported to influence soy food quality as well as protein and fat contents in seeds. Since the variation in seed constituents is affected by genetic and environmental (temporal and spatial) factors, and their interactions, understanding the $G \times E$ interaction of soybean SSC is of great importance. To date, no studies of $G \times E$ interaction for SSC in soybean have been reported. The objectives of the present study were to investigate the environmental stability of SSC, and its relationship with crude protein (CP) and crude fat (CF) contents in soybean seeds.

MATERIALS AND METHODS

Plant materials and cultivation

We screened more than 1,064 black soybean lines for high, medium, and low starch contents in their seeds. The initial screening was carried out using a rapid iodine test (Jeong *et al.* 2010). We identified 90 lines showing variation for starch content based on the iodine test. The SSC of the identified 90 lines was measured using a total starch assay kit (Megazyme International Ireland Ltd., Wicklow, Ireland) following an approved method 76-13.01 (AACC 2010) as reported in Dhungana *et al.* (2017).

Three groups of soybean genotypes, each having 5 high-

(> 1.75%), 5 medium- (0.75-1.5%), and 5 low- (< 0.5%) starch contents were randomly selected from the 90 lines. In addition, two cultivated soybeans, Pungsannamul (Suh *et al.* 1997) and Williams 82, were used as checks. Together, a total of 17 soybean genotypes were used in this study (Table 1).

The SSC of these genotypes was evaluated in two planting dates at three locations: Gunwi, Gwangju, and Cheonan in the Republic of Korea in 2015 and 2016. Geolocation information and dates of planting at each location and year are given in Table 2. The experiments were performed in a randomized complete block design with two replications at each test. Seeds were sown in hill

Table 1. Description of 17 soybean genotypes, mean starch, crude protein and crude fat contents and starch group of each grown in 11 environments to evaluate the stability of seed starch content.

Genotype	Starch group	Mean starch content (%)	Mean crude fat content (%)	Mean crude protein content (%)
IT25334	High starch line	1.34	23.4	40.8
IT141778	High starch line	1.26	19.3	39.4
IT177744	High starch line	1.02	21.5	42.0
IT183905	High starch line	1.48	18.9	42.1
IT189276	High starch line	1.39	22.1	41.5
IT25344	Medium starch line	0.66	22.3	43.7
IT115763	Medium starch line	0.75	22.1	43.2
IT143112	Medium starch line	0.80	23.4	42.6
IT177234	Medium starch line	0.85	21.9	43.2
IT189205	Medium starch line	0.99	22.8	43.0
IT228277	Low starch line	0.24	21.9	45.7
IT228577	Low starch line	0.25	24.9	42.7
IT228620	Low starch line	0.35	22.4	43.9
IT229949	Low starch line	0.41	22.2	44.4
IT230194	Low starch line	0.41	22.1	44.0
Pungsannamul	Check	0.64	16.8	42.0
Williams 82	Check	0.50	20.9	40.1

Table 2. Geolocation information and planting dates (environments) at three locations in 2015 and 2016.

Location	Geographic coordinates	Planting date ²⁾			
		2015		2016	
		Date1	Date2	Date1	Date2
Gunwi	36°07'N, 128°38'E	30 May (E1)	20 June (E2)	29 May (E7)	NA ³⁾
Gwangju	35°10'N, 126°54'E	2 June (E3)	25 June (E4)	29 May (E8)	23 June (E9)
Cheonan	36°49'N, 127°10'E	2 June (E5)	30 June (E6)	2 June (E10)	29 June (E11)

²⁾Letter and number in parenthesis for each planting date in various years are designated as environments.

³⁾NA: not available due to poor plant stands.

plots with 10 seeds per hill with 70 cm between rows and 50 cm between hills. Each hill was considered as a plot. A similar multi-environmental trial for fatty acid stability was conducted in an earlier study in hill plots with two replications (Chae *et al.* 2015). The plants were harvested at maturity and dried seeds were used to analyze the seed starch, CP, and CF contents.

Starch analysis

SSC was measured using a total starch assay kit (Megazyme International Ireland Ltd., Wicklow, Ireland) following an approved method 76-13.01 (AACC 2010), as reported in Dhungana *et al.* (2017). Starch content was determined using the following equation,

$$\text{Starch (\%)} = \Delta_A \times F / W \times FV \times 0.9$$

where,

Δ_A = Absorbance read against the reagent blank

F = 100 (μg of D-glucose)/absorbance for 100 μg of glucose

W = Weight in milligrams of the flour analyzed

FV = Final volume

0.9 = Adjustment from free D-glucose to anhydro D-glucose (as occurs in starch)

Crude fat and crude protein analyses

Soybean seeds were ground into powder using a commercial mixture (SFM-555SP, Shinil, Seoul, Korea) and scanned using XDS-NIRS rapid content analyzer (FOSS Analytical, Slangerupgade, Denmark) to calculate reflectance spectra. The spectra were examined using the equations which were previously developed (Chung *et al.* 2001) based on the spectra from standard samples, calibration, and validation assessments.

Meteorological data collection

Data for the average daily weather conditions (daily mean, daily maximum and daily minimum temperatures, and daily cloudiness) during the pod-filling period (September and October) at three locations (Gunwi, Gwangju, and Cheonan, Republic of Korea) in 2015 and 2016 were collected from the Meteorological stations located within 30 km from the soybean fields.

Statistical analysis

Analysis of variance (ANOVA) for SSC, CP, and CF was calculated using the PROC MIXED of SAS (SAS Institute 2013). All sources of variances were considered random as mentioned in Kulkarni *et al.* (2017). The difference among the means was compared using least significant difference (LSD) at 0.05 probability using SAS (SAS Institute 2013).

Broad-sense heritability (H^2) for SSC was calculated as $H^2 = \sigma_G^2 / (\sigma_G^2 + \sigma_{GE}^2 / E + \sigma_e^2 / rE)$ where E , G , and r are the number of environments, genotypes, and replications, respectively (Toker 2004). σ_G^2 and σ_e^2 are components of variance for genotype and error, respectively.

Stability of genotypes for SSC across environments was determined by mean, range, the coefficient of variation (CV), and stability coefficient (b_E) (Lee *et al.* 2009). b_E was calculated from the regression of the mean SSC of genotype at an environment on an environmental index. The environmental index was calculated from the mean SSC of all the genotypes at an environment minus the mean SSC of all the genotypes averaged across 11 environments (Lee *et al.* 2009). Genotypes having stability coefficients (b -value) close to zero were considered as more stable, whereas those deviate considerably from zero (either positive or negative) were considered as less stable across the environments. The PROC REG of SAS (SAS Institute 2013) package was used to calculate the slopes. The correlations among SSC, CF, and CP in seeds were analyzed using the PROC CORR of SAS (SAS Institute 2013).

RESULTS

Variation in seed starch, crude protein, and crude fat contents

The SSC, CP, and CF of 17 soybean genotypes were evaluated in two planting dates at three locations over two years. Crude protein and CF contents of seeds of the 15 soybean lines ranged from 39.4-45.7% and 18.9-24.9%, respectively; whereas those of the check were 40.1-42.0% and 16.8-20.9% (Table 1), respectively. There was a significant difference for SSC in years, genotypes,

Table 3. Analysis of variance for seed starch, crude protein, and crude fat contents of 17 soybean genotypes grown at two planting dates at three locations over two years.

Source of variation	Starch			Crude protein			Crude fat		
	df ²⁾	F value	Pr	df	F value	Pr	df	F value	Pr
Year	1	136.12	< .0001	1	696.53	< .0001	1	6018.34	< .0001
Location	2	107.52	0.0092	2	136.16	0.0073	2	0.62	0.6166
Genotype	16	64.02	< .0001	16	68.44	< .0001	16	97.59	< .0001
Date	1	18.33	< .0001	1	0.19	0.6606	1	0.15	0.6986
Replication	1	0.1	0.7806	1	0.77	0.4717	1	0.01	0.9225
Year × genotype	16	6.92	< .0001	16	16	< .0001	16	42.94	< .0001
Year × location	2	14.18	< .0001	2	2.15	0.1192	2	58.95	< .0001
Location × genotype	32	3.98	< .0001	32	2.89	< .0001	32	2.53	< .0001
Genotype × date	16	3.03	0.0001	16	1.44	0.1274	16	1.26	0.2256
Year × location × genotype	32	2.17	0.0006	29	3.15	< .0001	29	2.18	0.001
Total	332			307			307		

²⁾Degree of freedom.

locations, planting dates, and their interactions (Table 3). Late planted (0.88%) soybeans had higher SSC than those grown at early planting (0.71%) dates. The average SSC of the 17 genotypes in 2015 (0.93%) was higher than that in 2016 (0.60%) (Supplementary Table S1).

Broad-sense heritability (H^2) for SSC was consistent (95.5–96.6%) over the two years (Supplementary Table S1). The consistent high H^2 values (> 95%) over two years indicated that a high proportion of phenotypic variance in SSC was a result of genetic effects.

Stability of seed starch content

The range, CV, and b_E for mean SSC were calculated to evaluate the stability of soybean genotypes in each seed starch category (high, medium, and low) including checks (Table 4). Among the five genotypes in the high seed starch group, IT177744 had the lowest (1.87%) and IT183905 had the highest (2.27%) ranges for SSC. IT189276 had the lowest (36.6%) and IT177744 had the highest (53.0%) CV. In the medium seed starch group, IT177234 had the lowest range SSC (1.01%) and CV (34.4%) followed by IT143112 and IT25344. The range of SSC for IT229949 was the highest (0.58%), whereas that for IT228577 was the lowest (0.18%). The IT228620 had the lowest CV (14.8%) among the five genotypes of the low seed starch group. Between the two checks, Pungsannamul ranked higher for range (0.57%) and CV (23.64%) than Williams 82.

The stability coefficient (b_E) among the high, medium, and low-seed starch categories, and check genotypes ranged from 1.55–2.44, 0.83–1.51, 0.003–0.35, and 0.31–0.49, respectively. Based on the b_E values, IT141778 and IT183905; IT177234 and IT115763; and IT228620 and IT229949 were found to be the most stable and the most unstable genotypes for high, medium, and low seed-starch groups, respectively. From the checks, Williams 82 was found to be more stable (lower b_E value) than Pungsannamul.

Mean rank was estimated based on the average values of three stability parameters: range, CV, and b_E (Table 4). Based on the mean rank, IT189276 was the most stable genotype in the high seed starch group. Similarly, IT177234, IT228620, and Pungsannamul were the most stable genotypes for medium and low seed starch groups and check, respectively. The overall pattern of the stability results from this study showed that the high starch soybean genotypes were less stable than medium or low seed starch genotypes across environments.

Correlation analysis of seed starch, crude protein, and crude fat contents

Pearson's correlation coefficients for SSC, CP, and CF showed a significant negative correlation between SSC and CP as well as CP and CF, and a significant positive correlation between SSC and CF (Table 5).

Table 4. Stability parameters range, the coefficient of variation (CV), stability coefficient (b_E), and stability coefficient of determination (r^2) for mean seed starch content of 17 soybean genotypes calculated from 11 environments to evaluate the stability of seed starch among high, medium, and low starch genotypes.

Starch Group	Genotype	Mean (%)	Range (%)	CV (%)	Stability coefficients			Mean rank ^{y)}
					b_E ^{z)}	P	r^2	
High	IT25334	1.34	1.94	48.15	2.32	< .0001	0.89	15
	IT141778	1.26	2.06	41.84	1.55	0.036	0.49	13
	IT177744	1.02	1.87	53.01	1.94	< .0001	0.85	16
	IT183905	1.48	2.27	48.80	2.44	0.001	0.71	17
	IT189276	1.39	2.11	36.58	1.74	< .0001	0.89	12
Mean		1.30	2.05	45.68	2.00		0.77	
Medium	IT25344	0.66	1.04	42.83	1.00	0.0002	0.80	10
	IT115763	0.75	1.26	57.28	1.51	< .0001	0.94	14
	IT143112	0.80	1.04	38.59	0.99	0.0002	0.84	9
	IT177234	0.85	1.01	34.36	0.83	0.0049	0.60	8
	IT189205	0.99	1.49	47.08	1.49	0.0028	0.69	11
Mean		0.81	1.17	44.03	1.16		0.77	
Low	IT228277	0.24	0.34	37.52	0.25	0.0173	0.48	3
	IT228577	0.25	0.18	22.18	0.02	0.82	0.01	2
	IT228620	0.35	0.19	14.81	0.00	0.9641	0.00	1
	IT229949	0.41	0.58	30.30	0.35	0.0036	0.63	5
	IT230194	0.41	0.39	35.00	0.32	0.0372	0.44	6
Mean		0.33	0.34	27.96	0.19		0.31	
Check	Pungsannamul	0.64	0.57	23.64	0.49	0.0001	0.88	4
	Williams 82	0.50	0.82	34.27	0.31	0.1181	0.22	7
LSD _{0.05} ^{x)}		0.18	0.24	11.46	0.41		0.29	

^{z)} b_E was calculated from the regression of mean seed starch content of genotypes at each environments regressed on the environmental index.

^{y)}Mean rank was calculated as the average value of three stability parameters range, CV, and b_E .

^{x)}LSD for comparison of means of each starch group.

Table 5. Correlation among seed starch (SS), crude fat (CF), and crude protein (CP) contents of 17 soybean genotypes grown at two planting dates at three locations over two years (2015 and 2016).

Trait	SS	CF	CP
SS	1		
CF	0.1295*	1	
CP	-0.63****	-0.391****	1

* and **** significant at the 0.05 and 0.0001 probability level, respectively.

DISCUSSION

Evaluating genotypes at different planting dates is important to understand the variation in SSC during

pod-filling at different temperatures (Bilyeu and Wiebold 2016). In order to better understand the stability of SSC across environments, data from the two planting dates of about a month apart, three locations, and two years were utilized in this study. The significant $G \times E$ interactions for SSC observed in this study may be due to the differences in genotypes and the growing environments as observed for other carbohydrates components in soybean (Kumar *et al.* 2010; Bilyeu and Wiebold 2016).

The SSC over two years was significantly different ($P < 0.0001$) which could likely be due to the discrepancies in average daily weather conditions during the pod-filling stage in September and October (Supplementary Table S2). Significant negative correlations between SSC and weather parameters such as average daily mean temperature ($P < 0.0001$, $r^2 = -0.92376$), average daily minimum

Table 6. Correlation of seed starch content with weather parameters during the seed-filling period (September and October).

	Average daily mean temperature	Average daily maximum temperature	Average daily minimum temperature	Average daily cloudiness
Correlation coefficient	-0.92376	-0.26284	-0.91073	-0.71239
<i>P</i> value	< .0001	0.4349	< .0001	0.0139

temperature ($P < 0.0001$, $r^2 = -0.91073$), and average daily cloudiness ($P = 0.0139$, $r^2 = -0.71239$) were observed (Table 6). Lower SSC observed in 2016 than in 2015 might be due to longer average daily cloudiness as well as higher average daily temperatures. Gong *et al.* (2014) observed reduced leaf starch content in soybean grown in shade than those grown under the higher light, which might be due to down-regulation of starch biosynthesis-related genes encoding ADP-glucose pyrophosphorylase, granule-bound starch synthase, and starch-branching enzyme. Egli and Bruening (2001) also observed a reduction in SSC in soybeans grown under shade. The average daily mean and average daily minimum temperatures during active seed filling stage were negatively correlated with the SSC in our study, indicating that the higher temperature reduces SSC. These results are in line with previous reports (Piper and Boote 1999; Thomas *et al.* 2003) in which the starch and soluble sugar contents in soybean seeds were found to decrease with rise in temperature. Similar correlations have been observed in other crops such as rice (Ahmed *et al.* 2015) and wheat (Rijven 1986; Zhao *et al.* 2006; Yan *et al.* 2008; Liu *et al.* 2011). The reasons for this phenomenon were supposedly the lower activities of starch synthase, ADP-glucose pyrophosphorylase, starch phosphorylase, and soluble starch synthase enzymes involved in sucrose to starch conversion at higher temperatures (Rijven 1986).

In the present study, high SSC was observed in late (Date 2) planted soybeans than the early planted soybeans. Such differences might be observed due to relatively lower average daily temperatures and shorter average daily cloudiness in October than in September at all the three locations in both the years (Supplementary Table S2). The late planted soybeans experienced relatively lower average daily temperatures and longer sunshine duration during the pod-filling stage than the early (Date 1) planting dates. Piper and Boote (1999) suggested that at lower tem-

peratures, carbohydrate is not utilized for oil and protein synthesis because of reduced enzymatic activities. Wolf *et al.* (1982) reported decreased sucrose content with an increase in temperature after the onset of seed development. Similarly, Sato and Ikeda (1979) studied the effect of increasing temperature on soybean seed composition and found that the total carbohydrate concentrations were found to decrease with an increase in temperature. Relatively longer periods of day-light duration during seed-filling of late-planted soybeans might be another reason for high SSC in the present study. Egli and Bruening (2001) reported decreased SSC in soybean under shade condition. Bilyeu and Wiebold (2016) also observed the higher mean carbohydrate content in late-planted soybeans than in early planted soybeans.

The stability parameters range, CV, and b_E for mean SSC were calculated to evaluate the stability of different genotypes for various starch classes. Lower values of the range, CV, and b_E for SSC of soybeans indicate more stable genotypes across environments (Oliva *et al.* 2006; Lee *et al.* 2012). Higher b_E value of the genotypes in high and medium starch groups than the low starch group and check genotypes indicated that they were less stable than the latter groups.

Various physiological and biochemical studies in soybean (Heim *et al.* 1993; Chopra *et al.* 2005; Saldivar *et al.* 2011; Vriet *et al.* 2014) and sorghum (Bhatia and Singh 2002) imply that biosynthesis of starch and sucrose might be governed by similar genetic factors. Hence, correlation studies of CP and CF were carried out in the present study. The correlation analysis revealed that SSC and oil content in soybean seeds were positively correlated with each other, but negatively correlated with protein content. These results are similar to those reported by Hymowitz *et al.* (1972). In another study, a significant negative correlation of sucrose with protein has been reported in soybean (Li *et al.*

al. 2012). A significant positive correlation of soybean carbohydrates was found with oil whereas a significant negative correlation was shown with protein (Sakla *et al.* 1988). The total sugar and oil contents in soybean seeds were positively correlated with each other but negatively correlated with protein concentration (Openshaw and Hadley 1978). A high negative correlation was observed between the protein and sucrose contents in soybean (Wee *et al.* 2017). Similarly, in lupin seeds, a negative correlation was reported between CP and starch content (Straková *et al.* 2006). The negative correlation between protein and fat found in our study is in line with previous reports in soybean (Sakla *et al.* 1988; Tajuddin *et al.* 2003; Haghi *et al.* 2012; Qin *et al.* 2014).

In summary, the present study showed that the SSC in soybean was highly affected by the genotype, environment, and their interaction. High seed starch soybean genotypes were found to be less stable than the medium or low starch genotypes across environments (temporal and spatial). The SSC was found to negatively correlate with the average daily mean and average daily minimum temperatures and, with the average daily cloudiness during the pod-filling stage. Further, it was also observed that the late-planted soybeans accumulate higher seed starch than the early planted ones. The results also suggest that the environmental conditions like presence of low temperature and long sunshine period during seed filling stage might be favorable for enhancing the SSC in soybean genotypes. The findings from this study provide an insight into the variation and stability of SSC in soybean genotypes evaluated across environments.

ACKNOWLEDGEMENTS

This work was carried out with the support of "Cooperative Research Program for Agriculture Science and Technology Development (Project No. PJ0129300 12017)" Rural Development Administration, Republic of Korea.

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