

Soybean Seed Composition Under High Day and Night Growth Temperatures

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ABSTRACT: High diurnal temperatures often affect development of soybean [*Glycine max* (L.) Merr.], but little is known about the relative influence of high day and night temperatures on the chemical composition of the seed. This study was conducted to determine the effects of combinations of high day and night temperatures during flowering and pod set (R1–R5), seed fill and maturation (R5–R8), and continuously during the reproductive period (R1–R8) on soybean seed oil, protein, and fatty acid composition. Day/night temperatures of 30/20, 30/30, 35/20, and 35/30°C were imposed on the soybean cultivar Gnome 85 in growth chambers. The day/night temperature combinations during R1–R5 had little effect on the oil and protein concentration and the fatty acid composition of seed produced. As mean daily temperature increased from 25 (30/20) to 33 (35/30)°C during R5–R8 and 25 (30/20) to 33 (35/30)°C during R1–R8, and oil concentration decreased and protein concentration increased. Increased day temperature during R5–R8 and R1–R8, averaged across the two night temperatures, increased oleic acid and decreased linoleic and linolenic acids. When night temperature was increased at 30°C day temperature during R5–R8 and R1–R8, oleic acid decreased and linoleic acid increased. When night temperature was increased at 35°C day temperature during R1–R8, oleic acid increased, and linoleic and linolenic acids decreased. These results indicate the importance of high day and night temperatures during seed fill and maturation in the oil, protein, and fatty acid composition of soybean seed.

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Soybean seed protein and oil composition are influenced by environment during seed development. Geographic patterns associated with soybean protein and oil composition exist in domestic and world soybean markets (1). The protein concentration of soybean produced in the southern United States is generally greater than that of soybean produced in northern locations (1,2), whereas oil concentration is generally greater in soybean produced in northern and western growing areas (1).

High mean temperatures were correlated with high oil con-

centrations in early experiments (3–5). Oil concentration averaged 19.5, 20.8, and 23.2% when day temperatures (DT) during seed-filling were 21.1, 25, and 29.4°C, respectively (6). A DT of 29.4°C for one week during seed-filling increased oil concentration from 19.5 to 22% (6). A day/night regime of 33/28°C increased protein and oil concentration in soybean seed above that of seed grown in 18/13, 24/19, or 27/22°C (5). DT had the greatest effect on oil concentration 20–40 d before maturity (3).

Protein concentration in mature soybean seed has generally been inversely and linearly correlated with sugar and oil concentration (4,7–9). An increase of one percentage point in protein concentration was associated with a 0.43 percentage point decline in oil concentration (8). This relationship varied by location, with some losing less oil with an increase in protein. Protein and oil concentrations were curvilinearly related to air temperature during seed fill of soybean: protein concentration declined between 21 and 27°C, then increased as temperature increased to 35°C, whereas oil concentration increased between 21 and 29°C, and then decreased as temperature increased to 35°C. This relationship may explain the contradiction between earlier experiments that reported a positive correlation between high temperatures and oil concentration (5,6) and more recent studies that found southern areas of the United States to produce soybeans with low oil concentration (1,2). The early experiments did not include temperatures above which the oil concentration of soybean seed declines.

The fatty acid composition of soybean oil is also influenced by environment during seed development. In eight environments throughout North Carolina, Mississippi, and Puerto Rico, temperature was the most influential variable in determining the fatty acid composition of soybean oil (10). Warmer environments were associated with greater percentages of oleic acid (10–12), and smaller concentrations of linoleic and linolenic acids (5–7,12–14). Soybean seeds produced in the southern United States contained less linolenic acid and more oleic acid than seeds produced in the northern states (15). DT at 45–31 d and 30–11 d before maturity were equally important in determining linolenic acid composition, whereas DT 30–11 d before maturity was most closely related to linoleic acid (13). Palmitic and stearic acid concentrations of soybean oil were unchanged by temperature (16).

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It is generally well established that soybean seed protein, oil, and fatty acid concentrations can vary among geographical regions and are influenced by growth temperature. But, the influence of night temperature (NT) in comparison with DT on soybean seed composition has not been thoroughly studied, and diurnal variations in temperature can be large among different locations. The objective of this study was to determine the effect of different DT and NT combinations during flowering and pod set, seed fill and maturation, and over the entire reproductive period on soybean seed protein, oil, and fatty acid composition.

EXPERIMENTAL PROCEDURES

Soybean seeds of the determinate cultivar Gnome 85 (Maturity Group II) were planted in a greenhouse at Iowa State University (Ames, IA) on September 30 and December 30, 1990, and April 26 and August 9, 1991, representing four replications in time. A determinate cultivar was used to minimize the variation of reproductive development commonly observed in indeterminate soybeans. Four seeds were planted in each of 80 plastic pots (11.3-L vol) that contained equal parts of soil (silt loam), peat, and perlite. The population was thinned to one plant per pot when two trifoliolate leaves unfolded, growth stage V3 (17). The plants were fertilized weekly with 3.5 L of Peters Professional (W.R. Grace and Co., Fogelsville, PA) 20.0-8.7-16.6 soluble fertilizer at 225 $\mu\text{g mL}^{-1}$ by using a Dos-matic injector (Dos-matic USA, Inc., Carrollton, TX). High-intensity sodium lights were used to supplement natural sunlight and maintain a 15-h photoperiod.

Plants were transferred to Conviron (Pembina, ND) model PGW-36 growth chambers at flowering (R1). Eighteen pots were placed in each of four growth chambers. Each chamber was set to one of four day/night temperature regimes: 35/30, 35/20, 30/30, or 30/20°C. The day/night temperature change occurred gradually over a 2-h period, and photoperiod was set at 14 h. When plants from all treatments reached beginning seed (R5), four plants from each of the 35/30, 35/20, and 30/30°C temperature regimes were switched with four plants from the 30/20°C temperature regime. Plants moved from 35/30, 35/20, and 30/30°C into 30/20°C were grown to maturity and evaluated to determine the effects of temperature during flowering and pod formation (R1–R5). Plants moved from 30/20°C into 35/30, 35/20, and 30/30°C were used to determine temperature effects during seed filling and maturation (R5–R8). Pots remaining in each chamber from flowering to maturity allowed the study of temperature effects during the entire reproductive growth stage (R1–R8). Plants were grown to maturity, and composition determinations were made on the mature seeds. The temperature in each chamber was adjusted to 20/20°C day/night when half of the plants in that chamber had reached harvest maturity (R8). Seeds were hand-harvested 10–20 d after R8.

Plants in the growth chambers were watered twice daily and fertilized twice a week until beginning physiological maturity (R7) with the same type and amount of liquid fertilizer

used during greenhouse growth. The initial 14-h photoperiod and the DT duration were decreased by 1 h and NT duration increased by 1 h when plants reached beginning seed fill (R5) in each treatment and again at 2 wk after R5.

Seeds from each plant within a treatment were bulked, and 15-g samples were randomly taken from each bulked seedlot for protein and oil analysis. The seed material was ground, and protein and oil concentrations were analyzed by near-infrared reflectance spectroscopy at the Iowa State University Grain Quality Lab. The protein and oil data were converted to mg g^{-1} of total seed weight on a 13% moisture basis.

Fatty acid composition of the seed oil was determined on three five-seed samples from each treatment by gas chromatography. Seed samples for fatty acid analysis were crushed with a hydraulic press at 8.5 kPa seed⁻¹. The total oil was extracted by soaking the crushed seed material in 1.5 mL of distilled hexane for 24 h. Fatty acid methyl esters were prepared by the addition of 0.5 mL of 1 N sodium methoxide in methanol to 0.1 mL of the oil–hexane extract. The vials for the transesterification reaction were shaken every 5 min of the 30-min reaction time. The reaction was stopped by the addition of 0.15 mL distilled water, then 1 mL distilled hexane was added. Approximately 1.5 mg of fatty acid esters in hexane was injected into a Hewlett-Packard (Avondale, PA) 5890 gas chromatograph, equipped with two 15-m Durabond-23 (J&S Scientific, Deerfield, IL) capillary columns. The columns had an inside diameter of 0.25 μm and a film thickness of 0.25 μm . Helium was used as the carrier gas at approximately 100 mL min^{-1} . Fatty acids were detected by flame ionization. The oven temperature was maintained at approximately 200°C. A Hewlett-Packard computer was used to control injection and convert peak areas into percentages of palmitic stearic, oleic, linoleic, and linolenic acids. The percentage of each fatty acid was converted to mg of palmitic, stearic, oleic, linoleic, or linolenic acid per gram of total fatty acids.

Statistical analysis. The experimental design consisted of three 4 × 4 Latin squares, one for each growth stage, with four replications in time and four growth chambers. Data were statistically analyzed within growth stages with the general linear models procedure of SAS (18). The main effects of day and night temperatures and their interactions were tested within growth stages by orthogonal contrasts.

RESULTS AND DISCUSSION

Protein and oil. Temperature treatments had no influence on soybean seed protein or oil concentrations in plants exposed during flowering and pod set (R1–R5) and returned to 30/20°C during seed fill and maturation (Table 1). Seed protein or oil concentrations of plants grown at 30/20°C during flowering and pod set and exposed to temperature treatments during seed fill and maturation (R5–R8) showed no change in response to an increase in DT from 30 to 35°C, when averaged across NT. Increased DT increased seed protein concentration but did not change seed oil concentration in plants ex-

TABLE 1
Seed Protein and Oil Concentrations of Soybean Exposed to Differing Day and Night Temperatures During Reproductive Growth

Component	Treatment stage	Treatment effects					Main effects					LSD ^d	Int ^e
		Temperature (°C)				LSD ^c	DT ^a		NT ^b				
		30/20	35/20	30/30	35/30		30	35	20	30			
(mg g ⁻¹)													
Protein	R1–R5 ^g	364	368	371	367	9	368	367	366	369	6	ns	
	R1–R8 ^h	364	370	382	382	8	373	376	367	382	6	ns	
	R1–R8 ⁱ	364	384	392	397	5	378	390	374	394	3	j	
Oil	R1–R5	183	181	183	180	7	183	180	182	181	5	ns	
	R5–R8	183	187	177	173	5	180	180	185	175	3	k	
	R1–R8	183	181	172	171	2	177	176	182	172	1	ns	

^aMean value of day temperature (DT) averaged across night temperature (NT) (°C).

^bMean value of NT averaged across DT (°C).

^cLeast significant difference used to compare treatment means within growth stages ($P = 0.05$).

^dLeast significant difference used to compare main effects of DT and NT within growth stages ($P = 0.05$).

^eInteraction of temperature treatments.

^fmg of Component per g of total seed material.

^gPlants grown in temperature treatments during flowering and pod set and 30/20°C during seed fill and maturation.

^hPlants grown in 30/20°C during flowering and pod set and temperature treatments during seed fill and maturation.

ⁱPlants grown in temperature treatments for the entire reproductive period (flowering to maturity).

^{j,k}Significant at ^j0.01 and ^k0.05 probability levels (ns = $P < 0.05$).

posed to temperature treatments for the entire reproductive period (R1–R8). An increase in NT from 20 to 30°C, when averaged across DT, resulted in increased protein concentration and decreased oil concentration in plants exposed during R5–R8 and R1–R8. Greater seed protein concentration in the 35/20, 30/30, and 35/30°C treated plants in comparison with 30/20°C resulted in a DT and NT interaction during R1–R8. Seed oil concentration in plants exposed during R5–R8 increased as temperature was increased from 30/20 to 35/20°C, but decreased from 30/30 to 35/30°C, also resulting in a treatment interaction.

Both DT and NT during seed growth were important in determining the protein and oil concentrations of soybean seed. This suggests that protein and oil concentrations were under 24-h temperature control. Thus, the influence of temperature on seed protein and oil concentrations may best be explained by changes in mean daily temperatures. When DT and NT combinations were converted to mean daily temperature, protein concentration increased 18 mg g⁻¹ as mean temperatures increased from 25 (30/20°C) to 30°C (30/30°C) and then stabilized from 30 to 33°C (35/30°C) when applied during R5–R8 (Table 1). When treatments were applied during R1–R8, the protein concentration increased 33 mg g⁻¹ as mean temperature was increased from 25 to 33°C. Declines in oil concentration of 10 and 12 mg g⁻¹ were found as mean temperature increased from 25 to 33°C during R5–R8 and R1–R8, respectively. Alterations in protein and oil concentrations were generally greater when plants were exposed to high temperatures during R1–R8 than R5–R8, indicating that the duration of the temperature treatments was important for seed composition. Mean temperature increases between 26 and 33°C during flowering and pod set had no effect on soybean seed protein and oil concentrations when plants were returned to 25°C during seed fill.

Responses of seed protein and oil concentrations to temperature in our study were similar to the curvilinear responses reported by Dornbos and Mullen (11). They suggested that a critical temperature for maximum oil and minimum protein content exists near 28°C. This temperature was determined from daytime temperature observations. Combinations of DT and NT used in our study establish that NT also influences soybean seed composition and suggests that the critical mean daily temperature may be closer to 25°C. We found an increase in protein concentration and a decrease in oil concentration as mean daily temperatures increased from 25 to 33°C. In previous studies, mean DT/NT ranging from 16 to 25°C had little effect on soybean seed protein concentration, but increases in mean temperature from 25 to 31°C increased protein (5,11). Likewise, oil concentration increased as mean temperature increased from 16 to 25°C, and decreased or remained level as mean temperature was increased from 25 to 31°C (5,6,11).

Geographical patterns in soybean protein and oil compositions may be explained by the influence of temperature on these seed components. Soybeans grown in southern locations had higher protein (1,2) and lower oil concentration than soybeans grown in northern locations (1). Mean temperatures during soybean seed growth in the southern United States would, on average, be above those in the northern United States, resulting in increased seed protein and decreased oil concentrations.

It is well established that protein and oil concentration are significantly and inversely correlated (4,7–11). In the current study, a 3.9 mg g⁻¹ decrease in oil was measured for each 10 mg g⁻¹ increase in protein (Fig. 1).

Fatty acids. There were small differences in soybean seed fatty acid composition when plants were exposed to temperature treatments during flowering and pod set (R1–R5) and

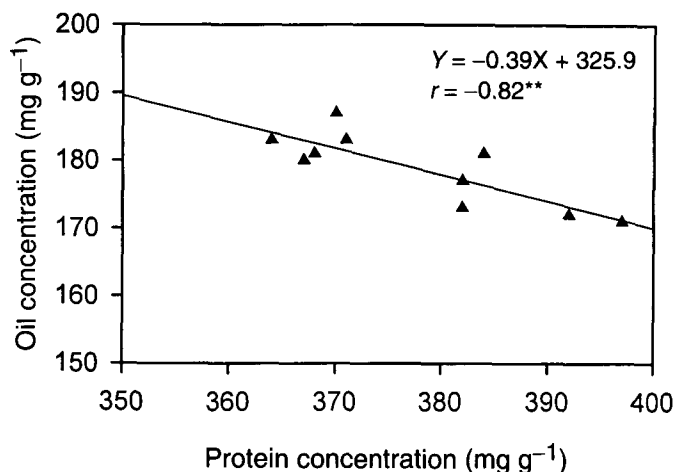


FIG. 1. The relationship between protein and oil content of soybean seed exposed to different combinations of day/night temperatures during flowering and pod set, seed fill and maturation, and the entire reproductive period. **Significant at the $P \leq 0.01$ level.

grown at 30/20°C during seed fill and maturation (Table 2). An increase in DT from 30 to 35°C during R1–R5, when averaged across NT, resulted in 2 and 8 mg g⁻¹ decreases in palmitic and linoleic acids, respectively, and a 10 mg g⁻¹ increase in oleic acid. An increase in NT from 20 to 30°C during R1–R5, when averaged across NT, resulted in a 6 mg g⁻¹ decrease in palmitic acid, but did not appreciably alter the concentration of other fatty acids.

In soybean plants grown at 30/20°C during flowering and

pod set and exposed to temperature treatments during seed fill and maturation (R5–R8), temperature changes altered the fatty acid composition of the seed considerably. The increase in DT resulted in increased palmitic, stearic, and oleic acids of 5, 2, and 50 mg g⁻¹, respectively, and decreased linoleic and linolenic acids of 45 and 12 mg g⁻¹, respectively. Increased NT resulted in decreased oleic acid of 27 mg g⁻¹ and increased linoleic acid of 24 mg g⁻¹.

Changes in oleic, linoleic, and linolenic acids due to increased DT were greatest in seeds from plants exposed for the entire reproductive period. The increased DT imposed during R1–R8 resulted in increased oleic acid of 87 mg g⁻¹ and decreased linoleic and linolenic acids of 72 and 17 mg g⁻¹, respectively. Increased NT during R1–R8, when averaged across DT, resulted in 2, 3, and 3 mg g⁻¹ less palmitic, stearic, and linolenic acids, respectively.

Although there were significant changes in palmitic and stearic acid in this study, differences among treatments were slight and inconsistent. Others also found that palmitic and stearic acid concentrations of soybean oil were relatively unchanged by temperature during seed fill (16). Oleic, linoleic, and linolenic acid concentrations were altered considerably by temperature increases during seed fill and the entire reproductive period. DT had a greater influence than NT in determining the concentration of these fatty acids.

The interaction of DT and NT played a significant role in determining the oleic, linoleic, and linolenic acid compositions when plants were exposed during R1–R8. The increase

TABLE 2
Seed Fatty Acid Composition of Soybean Exposed to Differing DT and NT During Reproductive Growth

Fatty acid	Treatment stage	Treatment effects					Main effects					LSD ^d	Int ^e
		Temperature (°C)				LSD ^c	DT ^a		NT ^b				
		30/20	35/20	30/30	35/30		30	35	20	30			
		(mg g ⁻¹)											
Palmitic	R1–R5 ^g	117	113	110	108	3	113	111	115	109	2	ns	
	R5–R8 ^h	117	118	115	124	3	116	121	118	119	2	j	
	R1–R8 ⁱ	117	117	114	115	2	116	116	117	115	2	ns	
Stearic	R1–R5	39	40	39	41	2	39	40	39	40	1	ns	
	R5–R8	39	45	42	42	2	41	43	42	42	1	j	
	R1–R8	39	43	40	36	2	40	40	41	38	1	j	
Oleic	R1–R5	239	254	252	257	14	246	256	247	255	10	ns	
	R5–R8	239	275	198	263	31	219	269	257	230	22	ns	
	R1–R8	239	281	210	343	27	225	312	260	276	19	j	
Linoleic	R1–R5	544	534	541	534	11	542	534	539	537	8	ns	
	R5–R8	544	512	581	522	25	562	517	528	552	18	ns	
	R1–R8	544	511	575	465	22	560	488	527	520	15	j	
Linolenic	R1–R5	60	60	59	59	4	60	60	60	59	3	ns	
	R5–R8	60	50	64	50	4	62	50	55	57	3	ns	
	R1–R8	60	47	61	41	3	61	44	54	51	2	k	

^aMean value of DT averaged across NT (°C). Abbreviations as in Table 1.

^bMean value of NT averaged across DT (°C).

^cLeast significant difference used to compare treatment means within growth stages ($P = 0.05$).

^dLeast significant difference used to compare main effects of DT and NT within growth stages ($P = 0.05$).

^eInteraction of temperature treatments.

^fmg of Fatty acid per g of oil.

^gPlants grown in temperature treatments during flowering and pod set and 30/20°C during seed fill and maturation.

^hPlants grown in 30/20°C during flowering and pod set and temperature treatments during seed fill and maturation.

ⁱPlants grown in temperature treatments for the entire reproductive period (flowering to maturity).

^{j,k}Significant at ^j0.001 and ^k0.05 probability levels (ns = $P < 0.05$).

in DT from 30 to 35°C increased oleic acid and decreased linoleic and linolenic acid more at 30 than at 20°C NT. The increase in NT at 30°C DT had an opposite effect on oleic, linoleic, and linolenic acid than at 35°C. At 30°C DT, the increase in NT decreased oleic acid and increased linoleic acid. At 35°C DT, the increase in NT increased oleic acid and decreased linoleic and linolenic acids.

It is generally accepted that warmer environments are associated with greater percentages of oleic acid (10,11,13) and lesser percentages of linoleic and linolenic acids (5–7,13,14). This was true for increases in DT in our study. But, an increase in NT from 20 to 30°C resulted in increased oleic acid and decreased linoleic and linolenic acids only when applied at 35°C DT during R1–R8. At 30°C DT during R5–R8 and R1–R8, an increase in NT from 20 to 30°C decreased oleic acid and increased linoleic acid.

The 35/30°C, R1–R8 treatment was unique in that it increased oleic acid above and decreased linoleic and linolenic acids substantially below the 30/30, 35/20, and 35/30°C treatments. These changes in fatty acids were not seen in the R1–R5 or R5–R8 35/30°C treatments, suggesting that the high temperature was required during the entire reproductive growth period to increase oleic acid and decrease linoleic and linolenic acid at 35/30°C.

Oleic acid is converted to linoleic acid, which is converted to linolenic acid through desaturation reactions (19). The high DT combined with the high NT, when applied during the entire reproductive period, appeared to slow the conversion of oleic acid to linoleic and linolenic acids.

The enzymes for fatty acid desaturation can be rapidly modulated in response to growth temperatures (20). Oleoyl desaturase, responsible for the conversion of oleic to linoleic acid, and linoleoyl desaturase, responsible for the conversion of linoleic to linolenic acid, had negligible activity in seed grown in culture at 35°C as compared with 20°C (20). This may explain the increase in oleic acid and the decrease in linoleic and linolenic acids in the 35/30, R1–R8 treatment. This high DT/NT combination may have resulted in less oleoyl desaturase activity. But, smaller increases in oleic acid and decreases in linoleic and linolenic acids were measured in the 35/30, R5–R8 treatment in our study. And when the treatments were applied R5–R8, the most oleic acid and the least linoleic acid was found at 35/20°C. These results suggest that the timing and duration of temperature during reproductive growth were important in determining the effect of high temperature on the fatty acid profile.

This study suggests that at moderate DT, increases in NT during soybean seed growth increase the conversion of oleic to linoleic acid. But, at high DT, especially when they occur for the entire reproductive period, increases in NT are detrimental to the oleic-to-linoleic acid conversion.

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