

## Climatic Influence on Seed Protein Content in Soybean(*Glycine max*)

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### 기상요인이 콩 단백질 함량에 미치는 영향

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**ABSTRACT** : This study was carried out to identify how soybean seed protein concentration is influenced by climatic factors. Twelve lines selected for seed protein concentration were studied in 13 environments of North Carolina. Sensitivity of seed protein concentration, total seed protein, and seed yield to climatic variables was investigated using a linear regression model. Best response models were determined using two stepwise selection methods, Maximum R-square and Stepwise Selection. There were wide climatic effects in seed protein concentration, total protein and seed yield. The highest protein concentration environment was characterized by the most high temperature days(HTD) and the smallest variance of average daily temperature range (VADTRg), while the lowest protein concentration environment was distinguished by the fewest HTD and the largest VADTRg. For protein concentration, all lines responded positively to average maximum daily temperature(MxDT), HTD, and average daily temperature range (ADTRg) and negatively to ADRa, while they responded positively or negatively to average daily temperature(ADT), variance of average minimum daily temperature(VMnDT), and VADTRg, indicating that genotypes may greatly differ in degrees of sensitivity to each climatic variable. Eleven lines seemed to have best response models with 2 or 3 variables. Exceptionally, NC106 did not show a significant sensitivity to any climatic variable and thus did not have a best response model. This indicates that it may be considered phenotypically more stable. For total seed protein and seed yield, all the lines responded negatively to both ADTRg and VADRa, suggesting that synthesis of seed components may increase with less daily temperature range and less variation in daily rainfall.

**Key words** : Soybean, Seed protein, Climatic variables, Linear regression, Best response model.

Cropping environments are characterized by differences in soil type and fertility and climatic factors such as temperature and rainfall. These can vary considerably in East-

ern North Carolina where most soybeans are produced. This variation in environment may stimulate metabolic differences in plants which in turn affect differences in growth

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and grain productivity or quality. Both temperature and rainfall are known to be important environmental influences on plant growth and development. These effects have been investigated in research on economically important traits in crop species.

Some studies have focused on protein metabolism of plant cells influenced by temperature. Plant nitrate reductase, which is associated with incorporation steps of reduced nitrogen into amino acids and subsequently into proteins, can also be influenced by temperature. Beevers et al.<sup>2)</sup> suggested that the optimum temperature for nitrate reductase synthesis was 35°C in maize leaves, and that nitrate reductase activity was limited by supraoptimal or suboptimal temperatures. Onwueme et al.<sup>12)</sup> showed that reduction in nitrate reductase activity at supraoptimal temperatures was primarily due to an inhibition of protein synthesis. Morrilla et al.<sup>11)</sup> indicated that nitrate reductase was an unstable enzyme with a half-life of 4.5 hours at 30°C in maize, and that maintenance of nitrate reductase activity required protein synthesis and vice versa. These findings indicate that nitrate reductase activity might be important in controlling protein synthesis in plant species. Carls<sup>6)</sup> found that seven soybean varieties grown in warmer environments were characterized by having lower protein concentration. However, Cianzio et al.<sup>9)</sup> indicated that warmer temperatures in Puerto Rico did not change protein concentration and genotypic rankings in 20 F<sub>5</sub> soybean lines. These different results indicate that genotypes might differ greatly in their climatic responses.

It has been generally recognized that water deficiency would cause a decrease in protein synthesis. Barnett & Naylor<sup>1)</sup> showed that

desiccated Bermuda leaves produced less protein than turgid leaves. Besides, they suggested that certain amino acids were selectively associated with water deficiency. Ben-Zioni et al.<sup>4)</sup> demonstrated that rates of leucine incorporation into proteins were decreased by desiccation. Morrilla et al.<sup>11)</sup> showed that desiccation of leaves resulted in decreased nitrate reductase activity in maize.

Although soybean is a major source of edible protein, there have been a few studies on environmental influence on seed protein concentration. It is important to know how environment affects seed composition, because predictable protein concentration in soybean seeds produced in different environments might be an essential characteristic of new cultivars, should seed protein concentration become a factor in determining the price of a soybean crop. This study was conducted to investigate how seed protein concentration in soybean is influenced by temperature and rainfall, and to determine if genotypes differ in their sensitivity.

## MATERIALS & METHODS

### 1. Materials and procedures

Twelve lines of soybean (NC101 to NC112) that contrast sharply for seed protein concentration were developed by the USDA-ARS in cooperation with the North Carolina Agricultural Research Service.<sup>8)</sup> These lines were derived from a recurrent selection program for increased protein concentration.<sup>5)</sup> Among them, six lines, NC101, NC102, and NC103 from population IA and NC107, NC108, and NC109 from population IIA have moderate protein concentration, and six lines, NC104, NC105, and NC106 from population IA and

NC110, NC111, and NC112 from population IIA have high protein concentration. Thus, the twelve lines were used for this study because they are similar in maturity (Group 6 and 7) and differ in genetic background between populations.

The lines were planted at three locations in North Carolina in 1988 and at five locations in North Carolina in 1989 and 1990. A randomized complete block design was used with two replications in 1988 and three replications in 1989 and 1990. Each 10' plot consisted of 3 rows and all plants in the middle row of each 3-row plot were harvested in bulk. A 30 gram random sample from each plot was analyzed for seed protein concentration using an infrared grain quality analyzer at the Northern Regional Research Center, Peoria, Illinois. Total protein (kg/ha) were calculated as protein concentration multiplied by seed yield (kg/ha) and divided by 100.

Modified climatic variables were used in order to investigate the way temperature and rainfall affect seed protein concentration, total seed protein, and seed yield. Temperature and rainfall data of September and October in 1988, 1989, and 1990 were collected from the office of the North Carolina Climate Program for each environment where the tests were conducted. The climatic variables derived from the temperature and rainfall data were based on daily recordings during the seed filling period from  $R_5$  to the harvest and modified as follows : average maximum daily temperature (MxDT), average minimum daily temperature (MnDT), and average daily temperature (ADT), variance of MxDT (VMxDT), variance of MnDT (VMnDT), variance of ADT (VADT), average daily temperature range

(ADTRg) which is the difference between MxDT and MnDT, variance of ADTRg (VADTRg), high temperature days (HTD) which is the number of days above average maximum daily temperature, low temperature days (LTD) which is the number of days below average minimum daily temperature, average daily rainfall (ADRa), and variance of ADRa (VADRa).

## 2. Statistical methods of analysis

An analysis of variance for seed protein concentration, total seed protein, and seed yield was performed using the SAS programs, Proc GLM and Proc REG (SAS Institute, 1987). Combinations of year and location were considered as one environment because year-location-genotype interactions were significant. Environments were assumed to be random and lines were considered to be fixed. An assumption of homogeneous variance between environments was tested and satisfied by the original data. A linear regression model, where each environmental mean of protein concentration, total seed protein, and seed yield was regressed on each climatic variable, was used to determine the sensitivity of each line to each climatic variable.

Two stepwise selection methods, 'Maximum R-square' and 'Stepwise Selection' of the STEPWISE procedure (SAS Institute, 1987) were performed to determine the best response model, using a multiple regression method which include all modified climatic variables on which each environmental mean of protein concentration was regressed. The stepwise selection methods have criteria for terminating the processes, which are called 'stopping rules'. The stopping rules are 'SLE' (significance level to enter) and 'SLS'

**Table 1.** Analysis of variance for seed protein concentration, total seed protein, and seed yield of 12 soybean lines over 13 North Carolina environments

Source	df	Mean squares <sup>†</sup>		
		Protein concentration	Total seed protein	Seed yield
Environments(E)	12	59.86**	9955265**	46833415**
Replications(R)	23	2.32*	231284**	1043034**
Genotypes(G)	11	255.41**	343211**	1007532**
G × E	132	3.05**	89445**	373007**
Error	234	1.39	56403	24161

\*, \*\* : Significantly different at the 0.05 and 0.01 probability levels, respectively.

† : Type III sums of squares were used to test the significance of the effects because there were some missing data.

(significance level to stay), where the significance levels are F-tests of partial sums of squares of variables in a model. The choice of the two criteria, SLE and SLS, have a great impact in determining the best response model. Bendel & Afini<sup>3)</sup> suggested that the optimum SLE varies between 0.15 and 0.25. Also, they recommended SLE of 0.25 and SLS of 0.125 for the stepwise selection. Therefore, several levels of SLE and SLS, which are based on Bendel's suggestion, were applied with a multiple regression in order to find best response models for seed protein concentration with independent climatic variables.

## RESULTS & DISCUSSION

There were significant genotypic and environmental and significant genotype environment interaction effects in seed protein concentration, total seed protein, and seed yield (Table 1). There were wide variations in temperature and rainfall over 13 environments of North Carolina (Table 2).

The highest protein concentration environment was characterized by the most HTD(46 days) and the smallest VADTRg, while the lowest protein concentration environment

was distinguished by the fewest HTD(20 days) and the largest VADTRg(10.2) (Table 2). Thus, more high temperature days and less variation in average daily temperature range during seed maturity appeared to increase protein concentration in soybean seeds. The environment, which is the lowest in total seed protein and seed yield, was characterized by the largest VADTRa and the smallest VMnDT (Table 2). Thus, larger variation in average daily temperature range and less variation in minimum daily temperature during seed maturity appeared to decrease total seed protein and seed yield.

### 1. Linear response of protein concentration

Most lines showed positive responses to variables associated with higher temperature (MxDT and HTD) and variables related to both higher and lower temperatures (ADT and ADTRg) (Table 3). Among the high protein lines, four (NC104, NC110, NC111, and NC112), three (NC104, NC111, and NC112), and five (NC104, NC105, NC110, NC111, and NC112) showed significant sensitivities to MxDT, ADT, and HTD, respectively. Also, three lines (NC101, NC105, and NC109) showed significant sensitivities to ADTRg (Table 3). These suggest that warmer temperature may result in increased protein con-

**Table 2.** Mean climatic variables, mean protein concentration(%), total seed protein (kg /ha), and seed yield (kg /ha) over 13 environments in North Carolina

Variables*	E1 <sup>+</sup>	E2	E3	E4	E5	E6	E7	E8	E9	E10	E11	E12	E13
HTD (days)	24	23	20	31	30	29	36	33	39	41	35	46	41
MxDt(°C)	24.5	24.3	23.6	26.9	26.3	25.6	27.1	26.2	27.0	27.5	27.1	28.2	27.4
MnDt(°C)	13.5	11.8	10.3	15.6	15.0	12.4	14.3	13.4	14.1	13.9	13.2	14.4	13.2
ADTRg(°C)	11.0	12.4	13.2	11.3	11.3	13.2	12.8	12.7	12.9	13.6	13.9	13.9	14.3
VMxDt	29.8	20.5	25.4	25.8	18.0	24.4	15.9	21.6	20.5	20.3	25.8	16.1	22.6
VMnDt	37.5	38.8	47.2	35.4	31.9	29.7	37.2	41.4	28.7	29.4	28.4	32.1	34.2
VADTRg	13.7	15.3	23.6	11.6	15.2	12.6	17.9	16.3	10.4	15.9	11.3	10.2	12.2
ADRa(mm)	3.1	2.8	4.5	3.6	6.4	3.7	3.6	4.2	2.2	2.2	4.8	3.0	3.7
VADTRa	55.2	43.2	177.5	90.5	258.5	109.7	113.1	116.7	71.5	57.1	301.9	147.5	157.5
Protein	46.5	47.9	44.5	45.3	45.9	46.5	45.9	47.4	47.8	48.1	48.5	49.7	47.5
Total protein	1898	1862	511	1629	1491	1101	694	2048	1624	2081	404	951	1028
Seed yield	4082	3888	1149	3596	3249	2383	1513	4320	3398	4327	833	1914	2165

+ : E1 to E13 : Clayton (1988), Plymouth (1988), Sandhills (1988), Clayton (1989), Plymouth (1989), Sandhills (1989), Kinston (1989), Clinton (1989), Clayton (1990), Plymouth (1990), Sandhills (1990), Kinston (1990), and Clinton (1990).

\* : Variables : HTD, number of days above average maximum daily temperature ; MxDt, average maximum daily temperature ; MnDt, average minimum daily temperature ; ADTRg, average daily temperature range ; VMxDt, variance of maximum daily temperature ; VMnDt, variance of minimum daily temperature ; VADTRg, variance of average daily temperature range ; ADRa, average daily rainfall ; VADTRa, variance of average daily rainfall.

**Table 3.** Linear response of 12 lines when each of environmental protein concentration is regressed on each of climatic variables

Lines	Climatic variables <sup>#</sup>						
	MxDt	ADT	HTD	ADTRg	VMnDt	VADTRg	ADRa
NC101	.35(.33) <sup>+</sup>	.08(.38)	.10(.05)	.98*(.35)	-.09(.08)	-.17(.12)	-.65(.38)
NC102	.29(.32)	.19(.36)	.08(.05)	.48(.41)	-.13(.07)	-.19(.11)	-.81*(.33)
NC103	.03(.28)	-.08(.31)	.04(.05)	.36(.36)	.06(.07)	.00(.11)	-.66*(.29)
NC104	1.35**(.30)	1.29**(.39)	.25**(.05)	.94(.60)	-.27*(.10)	-.44**(.14)	-.30(.62)
NC105	.59(.32)	.40(.38)	.13*(.05)	.91*(.40)	-.11(.09)	-.20(.13)	-.27(.45)
NC106	.11(.32)	-.03(.36)	.04(.06)	.49(.40)	.06(.08)	.06(.12)	-.13(.40)
NC107	.05(.30)	-.10(.33)	.05(.05)	.45(.38)	-.02(.08)	-.06(.11)	-.73*(.30)
NC108	.45(.23)	.36(.27)	.08(.04)	.52(.32)	-.16**(.05)	-.21*(.08)	-.36(.31)
NC109	.40(.33)	.14(.39)	.11(.05)	.97*(.37)	-.12(.08)	-.22(.12)	-.72(.38)
NC110	.77*(.34)	.63(.41)	.15*(.06)	.84(.49)	-.16(.09)	-.40**(.10)	-.52(.49)
NC111	1.03**(.33)	.91*(.41)	.19**(.06)	.91(.53)	-.26**(.08)	-.38*(.13)	-.23(.55)
NC112	1.21**(.34)	1.23**(.40)	.23**(.06)	.63(.63)	-.29**(.09)	-.45**(.13)	-.66(.58)

<sup>#</sup> : MxDt, average maximum daily temperature; ADT, average daily temperature; HTD, high temperature days which is the number of days above average maximum daily temperature ; ADTRg, average daily temperature range; VMnDt, variance of maximum daily temperature; VADTRg, variance of average daily temperature range; ADRa, average daily rainfall.

\* , \*\* : Significantly different at the 0.05 and 0.01 probability levels, respectively.

<sup>+</sup> : Standard errors of regression coefficients in a linear model.

centration during seed maturity. However, three lines (NC103, NC106, and NC107) showed just negative responses to ADT (Table 3).

Most lines showed negative responses to variables associated with variation in temperature (VMnDT and VADTRg) (Table 3). Among the lines, four (NC104, NC108, NC111, and NC112) and five (NC104, NC108, NC110, NC111, and NC112) showed significant sensitivities to VMnDT and VADTRg, respectively (Table 3). This suggests that smaller variation in minimum daily temperature and average daily temperature range may produce increased protein concentration during seed maturity. However, two lines (NC103 and NC106) showed just positive responses to both VMnDT and VADTRg (Table 3).

All 12 lines showed negative responses to ADRa. Among the lines, three (NC102, NC103, and NC107) were significantly sensitive in a linear fashion (Table 3). This suggests that, with less daily rainfall during seed maturity, the protein concentration

tends to increase.

Using a linear response to each of HTD, ADTRg, VADTRg, VMnDT, and ADRa as a criterion, the twelve lines were classified into 2 groups, sensitive or not (Table 4). Based on HTD, the lines, NC104, NC105, NC110, NC111, and NC112 are sensitive and the others not. Based on ADTRg, the lines, NC101, NC105, and NC109 are sensitive and the others not. Based on VADTRg, the lines, NC104, NC108, NC110, NC111, and NC112 are sensitive and the others not. Based on VMnDT, the lines, NC104, NC108, NC111, and NC112 are sensitive and the others not. Based on ADRa, the lines, NC102, NC103, and NC107 are sensitive and the others not (Table 4). However, NC106 did not show any significant sensitivity to all the climatic variables (Table 3 and 4), indicating that NC106 may be considered relatively more stable in protein concentration over environments.

Cianzio et al.<sup>9)</sup> found that warmer temperatures in Puerto Rico did not change protein concentration. However, Carls<sup>6)</sup> found

**Table 4.** Classification of twelve lines based on linear sensitivities to climatic variables

Climatic variables*	Classification	
	Sensitive <sup>+</sup>	No response
HTD	NC104, NC105, NC110, NC111, NC112	NC101, NC102, NC103, NC106, NC107, NC108, NC109
ADTRg	NC101, NC105, NC109	NC102, NC103, NC104, NC106, NC107, NC108, NC110, NC111, NC112
VADTRg	NC104, NC108, NC110, NC111, NC112	NC101, NC102, NC103, NC105, NC106, NC107, NC109
VMnDT	NC104, NC108, NC111, NC112	NC101, NC102, NC103, NC105, NC106, NC107, NC109, NC110
ADRa	NC102, NC103, NC107	NC101, NC104, NC105, NC106, NC108, NC109, NC110, NC111, NC112

\* : HTD, high temperature days which is the number of days above average maximum daily temperature; ADTRg, average daily temperature range; VADTRg, variance of average daily temperature range; VMnDT, variance of minimum daily temperature; ADRa, average daily rainfall.

+ : Significant in linear responses.

**Table 5.** Linear response of 12 lines when environmental total protein(kg /ha) and seed yield (kg /ha) is regressed on each of climatic variables

Lines	Total protein		Seed yield	
	VADRa*	ADTRg	VADRa	ADTRg
NC101	-5.57* (1.90) <sup>+</sup>	-269(169)	-11.8* (4.1)	-646(353)
NC102	-5.27* (1.77)	-298(150)	-10.8* (3.8)	-687*(306)
NC103	-4.11* (1.80)	-229(146)	-8.7 (4.0)	-540(316)
NC104	-5.68**(1.80)	-287(161)	-11.2**(3.4)	-602(303)
NC105	-5.54* (1.77)	-289(157)	-11.1* (3.6)	-636(309)
NC106	-4.49* (2.01)	-311(151)	-9.1* (4.1)	-663(303)
NC107	-3.33 (1.53)	-185(122)	-7.1 (3.5)	-462(269)
NC108	-4.55* (2.01)	-329*(149)	-9.9* (4.5)	-765*(323)
NC109	-4.25* (1.43)	-151(133)	-9.6* (3.3)	-415(299)
NC110	-5.23* (1.60)	-257(146)	-11.1**(3.5)	-588(309)
NC111	-5.54* (2.01)	-357*(160)	-11.6* (4.1)	-778*(323)
NC112	-5.13* (2.21)	-288(180)	-10.0* (4.3)	-608(340)

# : VADRa, variance of average daily rainfall ; ADTRg, average daily temperature range.

\*, \*\* : Significantly different at the 0.05 and 0.01 probability levels, respectively.

<sup>+</sup> : Standard errors of regression coefficients in a linear model.

that seven soybean varieties grown in warmer environments were characterized by having lower protein concentration. In this study, most lines showed positive responses to warmer temperature and negative responses to variation in temperature and to average daily rainfall. Therefore, these different results may demonstrate another example indicating that genotypes may differ greatly in degrees of sensitivity to temperature and rainfall.

## 2. Linear response of total seed protein and seed yield

Total seed protein and seed yield of all the lines showed negative responses to both ADTRg and VADRa(Table 5). The extent to which they respond to each of the two variables appeared to differ among them. For total protein, most lines showed significantly linear sensitivities to VADRa, but only NC107 showed just a negative response (Table 5). Also, most lines showed just negative responses to ADTRg, but two lines

(NC108 and NC111) showed significantly negative sensitivities(Table 5). These suggest that protein synthesis may increase with smaller variation in average daily rainfall, i. e., continuous supply of water and with less average daily temperature range. For seed yield, two lines(NC103 and NC107) showed just negative responses to VADRa, but the other lines showed significant sensitivities. Also, three lines(NC102, NC108, and NC111) showed significant sensitivities to ADTRg, but the other lines showed just negative responses.

## 3. Best response models for seed protein concentration

Best response models of a multiple regression included the most significant variables in a linear model(Table 3 and 6). Determination coefficients ranged from 44 to 78, which explains how much protein concentration of a given line vary with changing climatic variables. Nine lines(NC101, NC102, NC103, NC104, NC105, NC109, NC110, NC111

**Table 6.** The best response models of twelve lines for protein concentration

Lines	Climatic variables <sup>#</sup>									R <sup>2+</sup>
	MnDT	ADTRg	HTD	LTD	VMxDT	VMnDT	VADT	VADTRg	ADRa	
NC101		.94*						-.15		.54
NC102	-.11								-.73*	.51
NC103					-.14		-.65*	.50		
NC104			.20**					-.21		.77
NC105	-.45		.17*							.44
NC106										
NC107				.16	-.15			-.76*		.54
NC108		.31				-.14*			-.20	.62
NC109		.91*						-.20		.58
NC110		.74						-.39**		.75
NC111							-.29*	-.29*		.64
NC112					-.30**			-.44**		.78

\* : MnDT, average minimum daily temperature ; ADTRg, average daily temperature range ; HTD, high temperature days which is the number of days above average maximum daily temperature ; LTD, low temperature days which is the number of days below average minimum daily temperature ; VMxDT, variance of maximum daily temperature ; VMnDT, variance of minimum daily temperature ; VADT, variance of average daily temperature ; VADTRg, variance of daily temperature range ; ADRa, average daily rainfall.

\*, \*\* : where partial sums of squares in the best response models are significantly different at the 0.05 and 0.01 probability levels, respectively.

+ : Determination coefficients.

and NC112) appeared to have 2 variables. Two lines (NC107 and NC108) appeared to have three variables (Table 6). However, NC106 did not have any significant variable and thus appeared to have no best response model for protein concentration (Table 6). These suggest that the line may be considered phenotypically more stable over environments.

Carter et al.<sup>7)</sup> showed that, taken as a whole, high protein materials from population IA accumulated more vegetative N than high protein materials from population II A. Also, Kwanyuen<sup>10)</sup> indicated that the high protein concentration of NC106 selected from population IA was due to gene action which increased the biochemical capacity for protein synthesis, and that the high protein concentration of NC111 was not attributed to such an increase. These may be consistent with the result of this study, which de-

monstrates that genotypes may differ in response of protein concentration to climatic variables.

Nitrogen from soil and air gases and energy from photosynthesis are known to be two essential requirements for protein synthesis in soybean seeds. In addition, plant vegetative tissues such as leaves, pods, and stems are another source of nitrogen for protein synthesis. Generally, temperature is believed to have an indirect influence on seed protein synthesis through a direct effect on photosynthesis. If a genotype can rely more heavily on N remobilized from vegetative tissue for protein synthesis, the genotype would need much less energy for synthetic N fixation and assimilation of the nitrogen into ammonia and subsequently into amino acids than a genotype which relies more heavily on N fixation for its N supply. That is to say, the former genotype (eg, NC106) would be



less affected by temperature than the latter genotype(eg, NC111). Therefore, the above findings<sup>7,10</sup> appear to be consistent with the result of this study, showing that NC111 was more sensitive to temperature than NC106 (Table 3).

We have collected cultivars which are low or absent in one of storage protein subunits. The cultivars may provide more information about an environmental response of seed protein concentration. Therefore, our research work on how differently seed protein and seed storage protein(7S and 11S protein subunits) in soybean seeds would respond to temperature is in progress in a phytotron controlled growth chamber.

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