SHORT-TERM EXPOSURE TO LOW TEMPERATURE AFFECTS GROWTH AND DEVELOPMENT OF SOYBEAN GROWN IN INCREASING AND DECREASING DAYLENGTHS

Wang, Z.
USDA-ARS Remote Sensing and Modeling Laboratory

Reddy, V. R.
USDA-ARS Remote Sensing and Modeling Laboratory

出版情報：BIOTRONICS. 27, pp.21-31, 1998-12. Biotron Institute, Kyushu University
バージョン：
権利関係：

BIOTRONICS **27**, 21–31, 1998

SHORT-TERM EXPOSURE TO LOW TEMPERATURE AFFECTS GROWTH AND DEVELOPMENT OF SOYBEAN GROWN IN INCREASING AND DECREASING DAYLENGTHS

Z. WANG and V. R. REDDY*

USDA-ARS, Remote Sensing and Modeling Laboratory, Beltsville, MD 20705, USA

(Received June 2, 1998; accepted July 27, 1998)

WANG Z. and REDDY V. R. *Short-term exposure to low temperature affects growth and development of soybean grown in increasing and decrensing daylangths.* BIOTRONICS **27**, 21–31, 1998. Low temperatures are a primary limitation to soybean (*Glycine max* [L.] Merr.) production in cool temperate regions. This study examined the influence of a short cold period during different growth stages on the vegetative and reproductive development of soybean under two changing (increasing and decreasing) daylength conditions. In the increasing daylength experiment, Hutcheson (MG V, determinate cultivar) soybean seedlings that emerged on 10 April in day-lit growth chambers (39°N lat.) were exposed to 8℃ for 48 h at VC, V2, V6, or V9 stage. In the decreasing daylength experiment, 'Hutcheson' seedlings that emerged on 15 July were exposed to 8℃ for 48 h at VE, VC, V6, or V11 stage. The magnitudes of the changes in daylength were the same for the two experiments, but the direction of the change was opposite. All plants were kept at a 14 h thermoperiod of 28/23℃ except during cold treatments. The cold treatments in decreasing daylength conditions delayed R1 and R2 stages by 2 to 3 d. The cold treatments imposed at VC, V2, and V9 stages in increasing daylength conditions, however, delayed the R1 stage by 11, 7, and 5 d, respectively. The cold treatments delayed V stages, while final height and biomass in the cold-treated plants reached the same or exceeded that of the control plants due to prolonged duration of vegetative growth. Our results indicate that delays in developmental stages were greater when cold temperatures occurred during earlier vegetative stages than during later stages and in increasing than in decreasing daylengths. The reductions in vegetative growth were due in part to the decreases in leaf photosynthesis.

Key words: *Glycine max* [L.] Merr.; soybean; daylength; growth; low temperature.

*Correspondence: V. R. Reddy Zhongchun Wang USDA-ARS
Remote Sensing and Modeling Laboratory Bldg. 007, Rm. 008. Beltsville, MD 20705, USA
Tel: (301) 504-5872 Fax: (301) 504-5823 E-mail: vreddy@asrr.arsusda.gov

INTRODUCTION

Low temperatures are a primary limitation to soybean production in the cool temperate regions. The effects of long-term cold temperatures on plant growth and development and of planting temperatures on seed emergence and seedling establishment of soybeans have been well documented (*5, 9, 10*). However, there are only limited data available on the influence of a cold period at various stages on soybean later vegetative and reproductive growth. The sensitivity of soybeans to short-term cold temperatures has been found to depend on the growing season temperature (*15*). Short-term cold temperatures have a greater effect on time to flowering for soybean grown at near optimum temperatures such as 28/23℃ day/night than at sub- or super-optimal temperatures.

Field-grown soybeans experience photoperiods of various lengths, various rates of change, and season fluctuation. Soybeans planted in late April and early May are exposed to increasing daylengths during early developmental stages while those planted in late June and early July are exposed to decreasing daylengths. Field-grown soybeans also experience cold temperatures both in spring when daylength is increasing and in late summer when daylength is decreasing. Limited data suggest that floral development of field-grown soybeans is influenced by the direction of change in daylength (*4*). Early studies by Garner and Allard (*7*) showed that the time to flowering for 'Biloxi' and 'Peking' grown in the field and in a temperature-controlled greenhouse was longer in increasing daylengths than in decreasing daylengths, even when the magnitudes of the changes in daylength were similar. A decrease of 1℃ in the mean temperature of 24℃ during the vegetative period caused a delay of 2–3 d in flowering time (*7*). Recent research by Acock *et al.* (*1*) indicated that the effect of changing daylength on flowering time was cultivar-dependent. Increasing or decreasing daylengths did not affect the floral initiation and development in 'Clark', but there was a significant decrease in time from floral initiation to first open flower in 'Johnston' grown in increasing photoperiod conditions.

The physiological mechanisms that cause the delays in the development of cold-treated soybeans are not well understood. The delays may be associated with decreases in leaf photosynthesis and changes in carbohydrate transport and metabolism (*3, 11*). Cold temperature injury which delayed soybean reproductive stages was also found to decrease leaf photosynthesis and reduce photosynthate availability (*15*).

The overall objective of this study was to determine the influence of a cold period at various stages on soybean growth and development. The specific objectives of this study were: (1) to evaluate the sensitivity of soybeans to short-term cold temperatures at various developmental stages, (2) to evaluate the sensitivity of soybean to short-term cold temperature when grown in increasing and decreasing daylengths, and (3) to correlate growth changes with changes in leaf photosynthesis. This study provides essential information for predicting flowering times of field-grown soybean that is planted at different dates.

MATERIALS AND METHODS

The experiments were conducted in five day-lit environmental growth chambers (Environmental Growth Chambers, Inc., Chagrin Falls, OH, USA*) at Beltsville Agricultural Research Center, Beltsville (39°N lat.), MD, USA. Each growth chamber had a Plexiglas top, 1.2 m long, 1.0 m wide, and 1.7 m high. These chambers were located outside and plants in the growth chambers were exposed to solar radiation and changing daylength during the entire experimental period. The chambers had the capability to control temperature at predetermined set points $\pm < 0.5$℃. Continuous circulation of air maintained uniform temperatures throughout the chambers. Two separate experiments were conducted. Experiment 1 was designed to determine the effect of short-term cold temperatures on growth, development, and leaf photosynthesis of soybean in increasing daylength conditions. Experiment 2 was designed to determine the effects of short-term cold temperature on soybean in decreasing daylength conditions.

Experiment 1

The experiment was initiated in April in five day-lit environmental growth chambers under naturally increasing daylength conditions. Daylength from seedling emergence to harvest during the experimental period increased from 13.0 h on 10 April to 14.7 h on 30 May. Daylength was calculated using the equations from the soybean model GLYCIM (*2*). Seed of Hutcheson was sown in 15-L black plastic pots (three seeds per pot), filled with PRO-MIX BX growing medium (Premier Brands Inc., Red Hill, PA, USA*) consisting of Canadian sphagnum peat, perlite, and vermiculite (6 : 1 : 1 by volume). Hutcheson was selected because it is commonly grown in many soybean growing areas. To ensure satisfactory nodule formation and nitrogen fixation, the seeds were coated with the nitrogen-fixing bacteria (*Bradyrhizobium japonicum*). The growing medium was amended with a slow-release fertilizer of Osmocote (14.0N -6.1P-11.6K) (Scotts-Sierra Horticultural Products Co., Marysville, OH, USA*) at a rate of 3 g L^{-1}. Dolomitic lime was added to adjust the pH of the medium to 6.0.

Sixteen pots were placed into each of the five growth chambers set at a 14 h (0600-2000 h) thermoperiod of 28/23℃. Plants were well watered and thinned to one per pot at the cotyledon stage (VC). Five short-term cold temperature treatments were applied to the five growth chambers. These five treatments were: control, cold treatments at VC, V2, V6, and V9 (*6*). Plants at V9 were within a few days to flower. For short-term cold treatment at each stage, temperature in the chambers was adjusted to 8℃ for 48 h beginning at 1000 h. Following this cold temperature treatment the chamber was reset to the original growth temperature (28/23℃). The temperature in the control chamber

*Trade name and company name are included for the benefit of the reader and do not imply any endorsement or preferential treatment of the product by USDA-ARS.

remained at 28/23℃ day/night during the entire experiment period. The low temperature of 8℃ was selected because soybean can frequently experience this temperature during the early growing season and chilling injury does occur at this temperature (*16*).

Main stem height and number of main stem nodes from all 16 plants of each chamber, were measured weekly beginning at 7 days after emergence (DAE). Dates to R1 and R2 were recorded for each plant. Plants were harvested in May when all plants in the same treatment (chamber) reached R2. Thus, plants in the different treatments were harvested at different times, depending on time to R2 in each treatment. At harvest, each plant was separated into leaves, stems, petioles, and roots. The number of flowers were recorded for each plant. Each plant organ was oven-dried at 72℃ for 72 h and weighed.

Experiment 2

Experiment 2 was initiated in July under naturally decreasing daylength conditions. Daylength from seedling emergence to harvest during the experimental period decreased from 14.7 h on 15 July to 13.2 h on 30 August. The magnitudes of the changes in daylength were similar for Experiments 1 and 2, but the direction of the change in daylength was opposite. Plant materials and management in this experiment were similar to those described for Experiment 1. In this experiment, plants were grown in 7.5-L plastic pots that were filled with Jiffy-Mix Plus (Jiffy Products, Batavia, IL, USA*) consisting of Canadian sphagnum peat and vermiculite (1 : 1 v/v). Plants were grown at a 14 h (0600-2000 h) thermoperiod of 28/23℃ except during the short-term cold temperature treatments. The five cold temperature treatments (48 h 8℃) were: control, cold treatments at VE (emergence), VC, V6, and V11. A few plants had just flowered when the short-term cold treatment was applied at V11. Main stem height and number of main stem nodes were measured weekly beginning at 8 DAE. Dates to R1 and R2 were recorded for each plant. All plants were harvested in August at 44 DAE. At harvest, plants either had already reached or just reached R2.

Leaf photosynthetic rates and stomatal resistance were measured at various growth stages. A terminal leaflet of the fourth or the adjacent (third or fifth) fully-developed trifoliolate leaf counted from the main stem apex was selected for the measurements using a LI-6200 portable photosynthesis system (LI-COR, Lincoln, NE, USA*). At each stage, leaf photosynthesis and stomatal resistance were measured at 28℃, 50-55% RH and under naturally sunlight conditions (light intensity $>1300\,\mu mol\ m^{-2}\ s^{-1}$) from six different plants in each treatment immediately before, immediately after, and 24 h after the 48 h 8℃ cold temperature treatment. Photosynthetic rate was calculated on a leaf area basis and expressed in $\mu mol\ CO_2\ m^{-2}\ s^{-1}$.

Statistical analysis was performed using SAS procedures (*12*). Means ($n=16$ in Experiment 1 and $n>6$ in Experiment 2) for plant height, number of main stem nodes, dry weights, leaf photosynthetic rates, and leaf stomatal resistance in the cold-treated and control plants were separated by LSD at $p \leq 0.05$.

RESULTS

Exposure of soybean plants to 8℃ for 48 h at early vegetative stages (VE, VC, and V2) decreased soybean main stem growth for 2 to 3 weeks in both experiments when compared to the control (Table 1). Main stem heights of the cold-treated plants eventually reached the same (Experiment 2) or exceeded (Experiment 1) that of the control plants during the later growth stages. Similar responses to short-term cold temperatures were observed in the number of main stem nodes (Table 2). Short-term cold temperature imposed at V6 did not decrease main stem height and the number of nodes as significantly as at earlier growth stages (Tables 1 and 2). There was no or little effect on vegetative growth when short-term cold temperature was imposed just before R1, such as at V9 in Experiment 1 and V11 in Experiment 2.

In Experiment 2, plants exposed to a short-term cold temperature at either VE or VC had less shoot dry weight than the control plants at 44 DAE (Table 3). Cold treatments at later stages generally did not significantly affect the shoot, root, and total plant dry weights. However, in Experiment 1, soybeans exposed to a short-term cold temperature at either VC or V2 had greater shoot dry weights and smaller root/shoot ratios than control plants (Table 3) because these cold treatments significantly prolonged vegetative and delayed

Table 1. Effects of 48 h 8℃ cold temperature exposure at various stages on main stem height of soybean. Means (n=16 for Experiment 1 and>6 for Experiment 2) within a column followed by the same letter are not significantly different ($LSD_{0.05}$)*.

8℃ exposure at stage (DAE**)	Main stem height (cm plant^{-1}) at different days after emergence						
	Experiment 1 (increasing daylength)						
	7 d	14 d	21 d	28 d	35 d	42 d	49 d
VC (4)	**2.7 b**	**5.5 b**	**11.7 bc**	**23.4 a**	**38.8 a**	**50.6 a**	**60.2 a**
V2 (9)	3.4 ab	**5.2 b**	**10.8 c**	**21.3 b**	**34.2 bc**	**43.5 b**	**43.5 b**
V6 (21)	4.3 a	8.4 a	15.0 a	**23.6 a**	**31.0 c**	**31.0 d**	**31.0 c**
V9 (30)	3.8 a	7.2 a	13.3 ab	24.6 a	**35.9 ab**	**41.7 b**	**41.7 b**
Control	4.0 a	7.5 a	14.9 a	25.6 a	35.7 ab	35.7 c	35.7 c
	Experiment 2 (decreasing daylength)						
	8 d	15 d	21 d	29 d	36 d	43 d	44 d
VE (0)	**4.0 b**	**7.3 b**	**11.8 b**	**20.0 b**	**28.1 bc**	**36.1 bc**	**38.1 b**
VC (2)	**3.8 b**	**7.6 b**	**12.3 b**	**19.1 b**	**26.6 c**	**34.1 c**	**34.3 c**
V6 (21)	5.7 a	8.8 a	13.6 a	**21.1 b**	**28.1 bc**	**35.8 bc**	**36.6 bc**
V11 (36)	5.9 a	9.0 a	14.5 a	24.6 a	**34.8 a**	**40.7 a**	**41.9 a**
Control	5.8 a	8.4 a	13.5 a	21.6 b	30.1 b	38.3 ab	39.0 ab

* Values observed after cold temperature treatments are in bold.
** DAE=days after emergence.

Table 2. Effects of 48 h 8℃ cold temperature exposure at various stages on the number of main stem nodes of soybean. Means (n=16 for Experiment 1 and>6 for Experiment 2) within a column followed by the same letter are not significantly different ($LSD_{0.05}$)*.

8℃ exposure at stage (DAE**)	Number of main stem nodes per plant at different days after emergence						
	Experiment 1 (increasing daylength)						
	7 d	14 d	21 d	28 d	35 d	42 d	49 d***
VC (4)	**0.0 b**	**2.4 b**	**5.2 b**	**8.2 bc**	**10.3 b**	**12.9 a**	**15.1 a**
V2 (9)	1.0 a	**2.4 b**	**5.1 b**	**8.0 c**	**10.3 b**	**12.9 a**	**13.5 b**
V6 (21)	1.0 a	3.3 a	6.3 a	**8.3 bc**	**10.1 b**	**10.3 c**	**10.3 d**
V9 (30)	1.0 a	3.2 a	6.1 a	8.8 ab	**10.3 b**	**12.6 a**	**12.8 b**
Control	1.0 a	3.4 a	6.3 a	9.4 a	11.1 a	11.8 b	11.8 c
	Experiment 2 (decreasing daylength)						
	8 d	15 d	21 d	29 d	36 d	43 d	44 d***
VE (0)	**1.0 a**	**3.0 b**	**5.0 b**	**8.2 b**	**10.4 b**	**13.2 a**	**14.8 a**
VC (2)	**1.0 a**	**3.0 b**	**5.1 b**	**8.1 b**	**10.7 ab**	**13.1 a**	**15.2 a**
V6 (21)	1.2 a	3.6 a	5.9 a	**8.0 b**	**10.9 ab**	**13.2 a**	**15.2 a**
V11 (36)	1.0 a	3.6 a	5.7 a	9.0 a	11.1 a	**13.3 a**	**15.1 a**
Control	1.3 a	3.7 a	5.8 a	8.7 a	10.9 ab	13.6 a	15.3 a

* Values observed after cold temperature treatments are in bold.
** DAE=days after emergence.
*** Final number of main stem nodes would be eventually reached.

Table 3. Effects of 48 h 8℃ cold temperature exposure at various stages on organ dry weights of soybean. Plant dry weights were determined at R2 stages in Experiment 1 and at 44 days after emergence (DAE) in Experiment 2. Means (n=16 for Experiment 1 and>6 for Experiment 2) within a column followed by the same letter are not significantly different ($LSD_{0.05}$).

8℃ exposure at stage (DAE)	Dry weight (g plant^{-1})			Root/shoot
	Shoot	Root	Total	
	Experiment 1 (increasing daylength)			
VC (4)	23.1 a	2.9 a	27.1 a	0.12 b
V2 (9)	15.3 b	1.8 b	16.8 bc	0.12 b
V6 (21)	10.3 c	1.7 b	12.1 c	0.17 a
V9 (30)	16.6 b	2.5 ab	18.3 b	0.15 ab
Control	12.3 c	2.0 ab	14.6 bc	0.16 a
	Experiment 2 (decreasing daylength)			
VE (0)	20.1 cd	3.7 b	24.8 b	0.18 ab
VC (2)	19.7 d	4.0 ab	24.0 b	0.20 a
V6 (21)	22.0 bc	3.9 ab	24.9 b	0.19 ab
V11 (36)	25.6 a	4.7 a	31.0 a	0.18 ab
Control	23.2 b	4.2 ab	28.1 ab	0.17 b

Table 4. Effects of 48 h 8℃ cold temperature exposure at various stages on reproductive development of soybean. The number of flowers was counted at R2 stages in Experiment 1 and at 44 days after emergence (DAE) in Experiment 2. Means (n=16 for Experiment 1 and >6 for Experiment 2) within a column followed by the same letter are not significantly different ($LSD_{0.05}$).

8℃ exposure at stage (DAE)	Time to R1 (DAE)	Time to R2 (DAE)	R2–R1 (day)	No. flowers per plant
	Experiment 1 (increasing daylength)			
VC (4)	40.8 a	46.9 a	6.1 a	204 a
V2 (9)	36.2 b	40.6 b	4.4 b	150 b
V6 (21)	29.0 d	31.7 c	2.7 c	75 d
V9 (30)	33.8 c	40.1 b	6.3 a	148 b
Control	29.3 d	32.1 c	2.8 c	108 c
	Experiment 2 (decreasing daylength)			
VE (0)	38.0 b	40.9 b	2.9 b	237 a
VC (2)	38.9 ab	41.8 ab	2.9 b	252 a
V6 (21)	39.1 a	42.1 a	3.0 b	251 a
V11 (36)	38.2 ab	42.3 a	4.1 a	268 a
Control	36.4 c	38.9 c	2.4 b	256 a

reproductive growth.

A 48 h exposure to 8℃ cold temperature at VE, VC, V6, and V11 delayed R1 and R2 by 2 to 3 d for plants grown in naturally decreasing daylengths (Table 4, Experiment 2). The number of flowers per plant was the same for all five treatments at 44 DAE. Reproductive development of soybeans grown in naturally increasing daylengths (Experiment 1), however, had greater sensitivity to short-term cold temperature than those grown in naturally decreasing daylengths (Experiment 2). Under increasing daylength conditions, the cold treatments at VC, V2, and V9 delayed R1 by 11, 7, and 5 d, respectively, and R2 by 15, 9, and 8 d, respectively. The cold treatments at VC, V2, and V9 also delayed the time period between R1 and R2 by up to 4 d. The total number of flowers at R2 was increased by cold temperature treatments (Table 4). Increases in the number of flowers were primarily due to the larger shoot systems at R2 stage in the cold-treated plants. Cold treatment at V6 did not affect the time to R1 and to R2. The number of flowers for the V6 treatment was less than the other treatments.

Leaf photosynthetic rates of soybeans measured at V11 (Experiment 2) were greater than those measured at V2 and V6 stages (Table 5). There were no differences in leaf photosynthesis between the same stage treatments prior to the cold temperature treatments. However, leaf photosynthesis in the cold-temperature treated plants was only 26, 19, and 16% of controls measured immediately (0 h) after the treatment at V2, V6, and V11, respectively. Twenty

Table 5. Effects of 48 h 8℃ cold temperature exposure at V2, V6 and V11 stages on leaf photosynthesis and stomatal resistance of soybean (Experiment 2). The terminal leaflets of the fourth or the adjacent trifoliolate leaves counted from the main stem apex were selected for the photosynthesis and stomatal resistance measurements. Measurements were taken immediately before (0 h before), immediately after (0 h after), and 24 h after the 48-h 8℃ cold treatments. Means (n=6) within a column followed by the same letter are not significantly different ($LSD_{0.05}$).

Stage (DAE*)	Treatment	Time (h) before and after the cold treatments		
		0 h before	0 h after	24 h after
		Leaf photosynthesis (μmol CO_2 m^{-2} s^{-1})		
V2 (9)	Control	10.5 c	15.7 b	14.2 b
	Cold exposure	11.3 c	4.0 c	14.1 b
V6 (21)	Control	12.7 bc	16.0 b	14.6 ab
	Cold exposure	13.4 abc	3.1 c	12.1 b
V11 (36)	Control	16.4 a	20.1 a	18.7 a
	Cold exposure	15.3 ab	3.3 c	18.6 a
		Stomatal resistance (sec cm^{-1})		
V2 (9)	Control	0.73 b	0.58 b	0.48 a
	Cold exposure	0.70 b	0.86 b	0.49 a
V6 (21)	Control	1.02 ab	0.84 b	0.55 a
	Cold exposure	0.83 b	4.03 a	0.32 bc
V11 (36)	Control	1.01 ab	0.41 b	0.11 d
	Cold exposure	1.38 a	4.51 a	0.22 cd

*DAE=Days after emergence

-four hours after the treatments, the photosynthetic rates were not statistically different from the control plants.

Leaf stomatal resistance was the same between the treatments before the cold treatment, increased immediately (0 h) after the 48-h cold temperature treatment, and recovered at 24 h after the treatment except for V6 (Table 5).

DISCUSSION

Exposure of soybean plants to 8℃ for 48 h at early vegetative stages (VE, VC, and V2) decreased soybean main stem growth for 2 to 3 weeks (Table 1). However, the main stem heights of the cold-treated plants were not significantly different from that of the control plants 2-3 weeks later. Similar recovery and compensatory growth was also reported in water-stressed soybean plants (*8, 14*). Shoots of non-irrigated soybean plants were found to grow more rapidly than those of irrigated plants during periods of rainfall (*8*). The effects of the short-term cold treatments imposed at the vegetative stages on seed development and final yield, though not determined, could be minimal due to compensatory

growth during the later growth stages.

Our results indicate that the responses of vegetative growth and development of soybean to short-term cold temperatures differ between plants grown in increasing and decreasing daylength conditions. Under naturally increasing daylength conditions, final height (Table 1), number of nodes (Table 2), and biomass (Table 3) at harvest in plants exposed to a cold period at early stages (VC and V2) were greater than control plants. The increased vegetative growth was primarily due to prolonged vegetative and delayed reproductive growth in the cold-treated plants. Under naturally decreasing daylength conditions, short-term cold temperatures had less effect on vegetative growth of soybeans. Less effect on vegetative growth was probably due to decreasing carbon assimilation in decreasing daylength conditions.

Short-term exposure to low temperatures also generally delayed reproductive development of soybean. The delays were greater for plants grown in increasing than decreasing daylengths, even when the magnitudes of the changes in daylength were similar (Table 4). For example, under increasing daylength conditions (Experiment 1), the delays were 11 d for R1 and 15 d for R2 when the cold period occurred at VC. Under decreasing daylength conditions (Experiment 2), however, cold temperatures at VE, VC, V6, and V11 delayed R1 and R2 stages by only 2 to 3 d (Table 4). The 2 to 3 d delays were probably directly due to inhibited growth and development of soybean during the 2 d cold temperature treatments. Our results are in agreement with early field and greenhouse results by Garner and Allard (*7*). The reason for this different response to the direction of the changes in daylength is not clear. Nevertheless, since soybean is a short-day plant, any delay caused by short-term cold temperatures could be augmented by naturally increasing daylengths. Under naturally decreasing daylength conditions, however, delays in flowering by short-term cold temperature could be minimized because reproductive growth of soybean is more sensitive to the shortening of daylength, thus completing reproductive development without further delays.

Delays in vegetative and reproductive growth in increasing daylength conditions (Experiment 1) by short-term cold temperature also depend on the developmental stage at which the cold period occurs. Sensitivity of soybeans to a 48 h 8℃ temperature was greater at VC than at other later stages. Under naturally increasing daylength conditions, the cold treatments delayed R1 by 11 d when the cold period occurs at VC, but only by 7 and 5 d when cold temperature occurred at V2 and V9, respectively (Table 4). A young plant at VC stage may be more susceptible to adverse temperatures. At VC, the cotyledon is the only nutrient source for new growth. Cold temperature at this stage could significantly inhibit cotyledon photosynthesis and reduce the transport of the stored nutrients from cotyledon to the new growth, thus influencing subsequent growth and development. As plants reached later vegetative stages, short-term cold temperature had less impact on vegetative growth of soybean compared to the cold treatment at earlier stages. Cold temperature which occurred just before R1 (V9) delayed R1 and R2 stages,

probably by directly inhibiting the rates of floral development.

Short-term cold temperature significantly decreased leaf photosynthesis (Table 5). A cold period of 8℃ for 48 h reduced leaf photosynthetic rates by >75% regardless of the developmental stage. Thus, the reductions in vegetative growth during and shortly after the cold treatments could result from the significant decreases in leaf photosynthesis. It appears that a cold period decreased leaf photosynthesis primarily by influencing leaf stomatal opening and thus altering plant water relations. The significant increases in leaf stomatal resistance by short-term cold temperatures (Table 5) indicate partial stomatal closure after the cold period. In addition, leaf wilting, a symptom similar to water stress, was observed at the end of the cold treatments. This observation indicates that cold stress may alter water relations in a way similar to water stress. As discussed above, soybeans have the ability to recover from the cold stress. Full leaf turgidity was observed within a few hours after the cold temperature treatments. Leaf photosynthetic rates were fully recovered within 24 h after the 48 h 8℃ cold treatment. A similar quick recovery of leaf photosynthesis was also found in field-grown soybean (*13*). The quick recovery of leaf photosynthesis from a cold period may account for the quick and compensatory recovery of vegetative growth.

Acknowledgments

We thank Mr. Robert Jones and Mr. Yi Zhou for their excellent technical assistance.

REFERENCES

1. Acock M. C., Bunce J. A. and Acock B. (1994). Effect of changing daylength on flower initiation and development in two soybean cultivars. *Biotronics* **23**, 93–104.
2. Acock B. and Trent A. (1991). The soybean crop simulator GLYCIM: documentation for the modular version 91. Response of vegetation to carbon dioxide. No. 017, Joint Program of the U.S. Department of Agriculture and U.S. Department of Energy.
3. Caulfield F. and Bunce J. A. (1988). Comparative responses of photosynthesis to growth temperature in soybean (*Glycine max* (L.) Merrill) cultivars. *Can. J. Plant Sci.* **68**, 419–425.
4. Constable G. A. and Rose I. A. (1988). Variability of soybean phenology response to temperature, daylength and rate of change in daylength. *Field Crops Res.* **18**, 57–69.
5. Egli D. B. and Wardlaw I. F. (1980). Temperature response of seed growth characteristics of soybeans. *Agron. J.* **72**, 560–564.
6. Fehr W. R. and Caviness C. E. (1977). Stages of soybean development. Special Report 80. Iowa State University, Ames PP. 1–11.
7. Garner W. W. and Allard H. A. (1930). Photoperiodic response of soybeans in relation to temperature and other environmental factors. *J. Agri. Res.* **41**, 719–735.
8. Hoogenboom G., Peterson C. M. and Huck M. G. (1987). Shoot growth rate of soybean as affected by drought stress. *Agron. J.* **79**, 598–607.
9. Matthews D. J. and Hayes P. (1982). Effect of temperature on germination and emergence of six cultivars of soybean (*Glycine max*). *Seed Sci. Technol.* **10**, 547–555.
10. Orr W., de La-Roche A. I. and Singh J. (1983). Imbibitional chilling injury in cultivars

of soybeans differing in temperature sensitivity to pod formation and maturation periods. *Can. J. Bot.* **61**, 2996–2998.

11. Purcell L. C., Ashley D. A. and Boerma H. R. (1987). Effects of chilling on photosynthetic capacity, and leaf carbohydrate and nitrogen status of soybean. *Crop Sci.* **27**, 90–95.

12. SAS Institute. (1989). SAS User's Guide. SAS Inst., Inc., Cary, North Carolina.

13. Sinclair T. R. (1980). Leaf CER from post-flowering to senescence of field-grown soybean leaves. *Crop Sci.* **20**, 196–200.

14. Sionit N. and Kramer P. J. (1976). Water potential and stomatal resistance of sunflower and soybean subjected to water stress during various growth stages. *Plant Physiol.* **58**, 537–540.

15. Wang Z., Reddy V. R. and Quebedeaux B. (1997). Growth and photosynthetic responses of soybean to short-term cold temperature. *Env. Exp. Bot.* **37**, 13–24.

16. Wolfe D. W. (1991). Low temperature effects on early vegetative growth, leaf gas exchange and water potential of chilling-sensitive and chilling-tolerant crop species. *Ann. Bot.* **67**, 205–212.