

AN ABSTRACT OF THE THESIS OF

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Title: Yield and Physiological Responses of Field-Grown Soybean to

Elevated Night Temperatures

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Soybean [Glycine max (L.) Merr.] is a potential oilseed crop in the Pacific Northwest. It was hypothesized that low night temperatures prevalent in the region during the soybean growing season limits seed yield. Yield and yield components, growth and development, and physiological responses of field-grown soybean to elevated night temperatures were evaluated in 1981 and 1982 to test the hypothesis. Mean minimum night temperature treatments were: check (uncontrolled, ca 10 C), 16 C, and 24 C, and were applied from two weeks after crop emergence until physiological maturity.

Warmer nights enhanced early vegetative growth, advanced the onset of reproductive development, and hastened physiological maturity. Seed yield increased above the check by 67 and 41% for the 16 C treatment and by 32 and 30% for the 24 C treatments in 1981 and 1982, respectively. Increased seed size accounted for all the seed yield increase except for the 24 C treatment in 1982. Final numbers of pods/plant and seeds/plant were similar but number of seeds/pod

for the 16 and the 24 C treatments was significantly higher than the check in 1982.

Although warmer night temperatures increased crop growth rate (CGR) during the vegetative period, final vegetative dry matter, pod weight, and leaf area generally decreased as night temperature increased. Net assimilation rates (NAR) were similar among the treatments. Seed growth rate (SGR) of the 16 C plants increased over the check by 31 and 38% in 1981 and 1982, respectively. SGR of the 24 C plants also increased over the check by 24% in 1981. Increased seed yield of the 24 C plants in 1982 was due primarily to their longer seed growth duration (SGD). Harvest index was increased above the check by 24 and 33% in 1981 and 16 and 23% in 1982, for 16 and 24 C plants, respectively.

Mean CO_2 exchange rate (CER) during the reproductive development increased by 7 and 15% for the 16 C treatment and 11 and 32% for the 24 C treatment in 1981 and 1982, respectively. Mean stomatal resistance to CO_2 diffusion (r_s) was not affected significantly except for the 24 C treatment in 1982 where r_s was reduced by 35%. Leaf water potential (ψ) of the 24 c plants was significantly lower than the check which was attributed to their higher transpiration rate (Tr). Leaf osmotic potential (ψ_π) and leaf turgor potential (ψ_p) were similar among the treatments. Leaf starch content did not account for differences in CER among the treatments.

The data indicated that low night temperatures restrict SGR which, in turn, favors partitioning of photosynthates to vegetative organs and pod wall at the expense of seed production. Reduced assimilate demand decreased CER through mechanism(s) other than

direct feedback inhibition. Development of cultivars tolerant to cool nights is necessary in order to establish the soybean as a profitable crop in the Pacific Northwest.

YIELD AND PHYSIOLOGICAL RESPONSES OF FIELD-GROWN
SOYBEANS TO ELEVATED NIGHT TEMPERATURES

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DEDICATED TO:

All the friends who dedicated their best times of the
summer months helping the author to carry on this research.

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YIELD AND PHYSIOLOGICAL RESPONSES OF FIELD-GROWN
SOYBEAN TO ELEVATED NIGHT TEMPERATURES

INTRODUCTION

Agriculture of the Willamette Valley of Oregon is based heavily on wheat and grass seed production. The area is in great need of alternate crops. Reasons include market instability of the prominent crops of the area, local demands for protein meal in the poultry and livestock industry, and the need for crop rotations to aid in pest control and to reduce air pollution caused by field-burning of grass seed crop residue.

Oilseed plants show promise as alternate crops for the inland valleys of the Pacific Northwest. The Pacific Northwest Regional Commission (PNRC) has realized the economic potential for the development of an oilseed industry in the region (Divine et al., 1977). Recent strong soybean prices, the high cost of transporting soybean meal to the Pacific Northwest, oriental Pacific Rim market potential for soybean, and the search for a crop alternative for newly irrigated croplands are factors that stimulate interest in soybean as a possible "new crop" in Oregon (Holst, 1977).

Soybean is not a new crop to Oregon. The history of this crop goes back almost a half century (Soybeans, "New Old Crop for Oregon", Oregon's Agricultural Progress, Summer 1972. pp. 3, 16) during which several small experimental trials have evaluated existing cultivars for adaptation to this region. All these cultivars have been bred for adaptation to other areas. Although some cultivars are better adapted than others to the climate of this region, no breeding has

been done to develop specifically adapted cultivars. Consequently, the yields of all cultivars tested was not high enough to make soybean economically competitive with many other row crops grown on irrigated croplands in this area (Holst, 1977). Thus, before soybeans can be a successful crop in western Oregon, higher yielding cultivars must be developed.

Considering the outlook for the soybean market, it seems worthwhile to invest some effort to search for the factor(s) limiting growth and productivity of this crop in the inland valleys of the Pacific Northwest. Several environmental factors prevailing in the region may affect soybean productivity. Among these factors, mean minimum temperatures during the soybean growing season is substantially lower in western Oregon than the areas where nearly all of the currently available soybean cultivars have been developed (e.g. 10 C in Corvallis, Oregon, vs 16 C in Urbana, Illinois). In contrast, the mean maximum temperature of both areas is about 27 C which is optimum for soybean growth (Hesketh et al., 1973). There is a close correlation between soybean seed yield and mean minimum temperatures (Abebe, 1977). Consequently, it was hypothesized that cool night temperatures predominant in the inland valleys of the Pacific Northwest limit soybean seed yield. The objectives of the present research were to assess the direct effect(s) of low night air temperatures as an abiotic stress on:

- 1) seed yield and yield components of a soybean cultivar which has given the highest yield in western Oregon in previous experiments,
- 2) growth and development pattern of this soybean cultivar, and

3) physiological processes which might be expected to affect soybean yield.

This information may provide a basis for screening soybean germplasm for characteristics which could permit higher yields in the western Oregon environment and may be useful to soybean researchers elsewhere.

In the report which follows, the effect of night temperature on yield and yield components are described in Chapter I, the effect of dry matter partitioning in Chapter II, and the physiological responses in Chapter III. These separate discussions are followed by a general conclusion of the study.

CHAPTER I

THE EFFECTS OF NIGHT TEMPERATURE ON YIELD AND YIELD COMPONENTS
OF INDETERMINATE FIELD-GROWN SOYBEAN

INTRODUCTION

The effects of night temperature on early stages of growth and development of several plant species have been investigated under controlled environments. However, the effects of night temperature on yield and yield components of field-grown crops are much more difficult to determine and few studies have attempted to evaluate them.

Small changes in topography can result in differences in night temperature which strongly affect crop productivity (Huxley and Beadle, 1964; Huxley, 1966). Night temperature is of major importance for growth and development of soybeans and affects both the photoperiodic response (Parker and Borthwick, 1943) and the morphology of the crop (Thomas and Raper, 1978). A change in night temperature of 5 C maintained over the entire growth period markedly affected the vegetative and reproductive growth of some cultivars of both cowpea and soybean (Huxley and Summerfield, 1974). Both photoperiod and night temperature affected the time to first flower, but the rate of vegetative growth was more dependent on night temperature than on day length or day temperature. In another study, when day temperatures were kept constant at 27 or 33 C, higher night temperature (24 vs. 19 C) promoted early vegetative growth and enhanced flowering of soybean cv. TK5 but had little effect on seed yield (Huxley et al., 1976).

Dry matter accumulation in pods and seeds of the determinate soybean cultivar 'Ransom' was affected more by night temperature than by day temperature in plants exposed to combinations of day and night temperatures (14 to 30 C day and 10 to 26 C night) for 50 days after expansion of the first trifoliolate leaf (Thomas and Raper, 1978; Thomas et al., 1981). Wide adaptability of the soybean cultivar 'Clark' is attributed in part to its tolerance to low night temperatures (Van Schaik and Probst, 1958). Several other studies designed to describe soybean response to temperature (Hofstra, 1972; Hesketh et al., 1973; Thomas and Raper, 1977) have not separated the effects of day versus night temperature.

The objectives of this study were to determine: (a) if low night temperatures limit seed yield of soybeans under field conditions, and (b) which seed yield component is most sensitive to low night temperature. The experiment is the first of a series intended to determine the phenological, morphological, and physiological limitations to soybean seed production under cool nights.

MATERIALS AND METHODS

Field experiments were conducted in 1981 and 1982 on a Woodburn silt loam soil (fine silty, mixed mesic Aquultic Argixerolls) at the Oregon State University Hyslop Crop Science Field Laboratory. Indeterminate soybean cultivar 'S09-90' (group 0 maturity) was planted at 70 cm row spacing in late May. Seeds were inoculated with 'S' soybean rhizobia (Nitragin, Co., Inc., Milwaukee, WI) before planting. Alachlor [2-chloro-2', 6'-diethyl-N-(methoxymethyl) acetanilide] and Linuron [3-(3, 4-dichlorophenyl)-1-methoxy-1-methylurea] were applied preemergence for weed control. The plant population was thinned to 240,000 plants ha⁻¹. The crop received 56 kg ha⁻¹ of nitrogen at planting and 84 kg ha⁻¹ at early pod formation. Plants were irrigated with 70 mm of water every 14 days.

The experiment included mean minimum night temperature treatments of 24 C, 16 C, and the uncontrolled check (ca 10 C) in a randomized block design with four replications. Plots were 1.4 m by 3.6 m with two rows of plants completely bordered by untreated plants. Elevated night temperature treatments were achieved with plastic-covered chambers and thermostatically controlled forced-air electric heaters. Chamber temperatures were maintained within ± 1 C and ± 2 C for 16 and 24 C treatments, respectively, and recorded continuously by thermographs. The chamber covers were removed each morning to provide all plots with natural field conditions during the daylight hours. Treatments were applied from two weeks after crop emergence until physiological maturity.

Stages of growth (Fehr et al., 1971) were recorded for all plots throughout the growing season. At physiological maturity, four plants were harvested in each plot for yield component analysis (plant height, internode length, node number, branch number, pod number). Pods were dried at 60 C for 48 hours, hand-threshed, and the number of seeds/plant and seeds/pod were calculated. At harvest maturity all plants in each plot were harvested by hand and threshed with a small thresher and final seed yield and seed size were calculated. Since some plants grown too close to the heaters were severely damaged in some plots because of burning or lodging and were discarded later in the season, the final seed yield calculation was based on the measured seed weight/plant. The data for yield and yield components of each year were analyzed separately. LSD values were calculated for comparisons of the 16 and 24 C treatment means with the check.

RESULTS AND DISCUSSION

Soybean plants emerged at about the same date in 1981 and 1982, although the seeds were planted six days earlier in 1981 than in 1982. The delayed emergence in 1981 may have been due to deeper planting and to compaction of topsoil. Since all the data were collected in a field environment, the observed variation within and between years might be due to the influence of other environmental factors in addition to the treatments.

Mean minimum temperatures during the summer months of 1981 and 1982 were near normal (30-year mean) of approximately 10 C (Fig. I.1). Mean maximum temperatures during the summer months of 1981 were about 27 C, which is normal for the area and considered optimum for soybean growth (Hesketh et al., 1973). The summer of 1982 was cooler than normal and mean maximum temperatures averaged about 25 C. Variation in plant responses to night temperatures between the years might be attributed to the difference in the average daily temperature for the two years. Additionally, the row spacing used in this study was considerably wider than what is practiced in commercial production. This row spacing was used to accommodate the experimental treatment application. Plants grown under narrower row spacing might respond differently to the treatments.

Phenology and Morphology

Warmer night temperatures hastened reproductive growth and crop maturity in both years (Table I.1). Reproductive ontogeny of soybeans is affected by temperatures, especially during the dark period

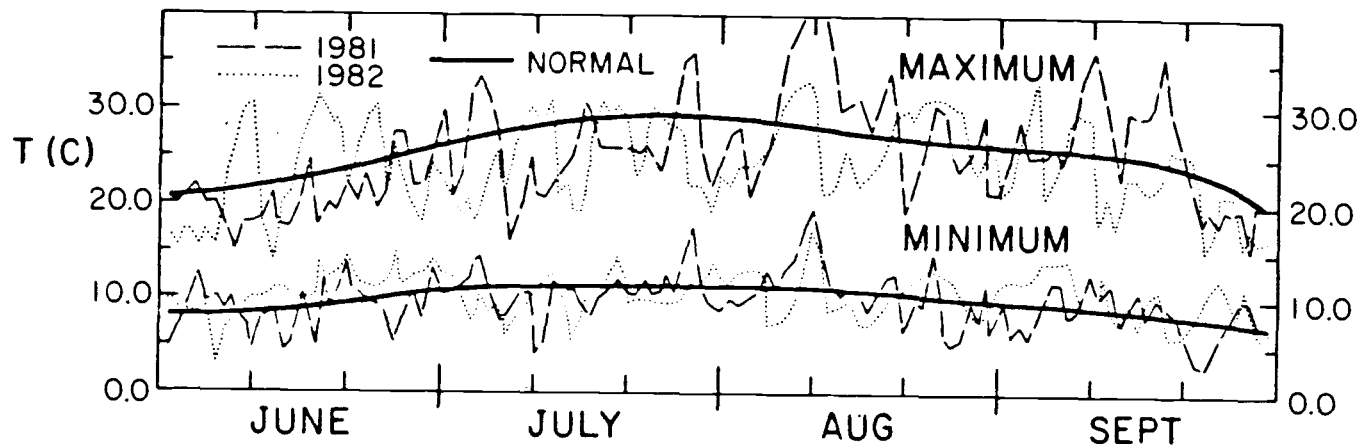


Fig. I.1. Daily maximum and minimum temperatures (T) for Corvallis, Oregon, through the months of June-September in 1981 and 1982 and the normals. Normals represent weekly averages of mean maximum and minimum temperatures for a 30-year period compiled by the National Weather Service, United States Department of Commerce, National Oceanic and Atmospheric Administration (Jim M. Crane, Wheeler Calhoun, and Earl M. Bates. Hyslop Field Laboratory Microstation Climate Survey. Special Report 516. Revised March 1979. Agric. Exp. St., Oregon State Univ., Corvallis, OR).

Table I.1. Effects of night temperature on reproductive development of soybean.

Mean minimum night temperature	Year	Growth stages [†]							
		R ₁	R ₂	R ₃	R ₄	R ₅	R ₆	R ₇	R ₈
		Days after emergence							
Check (10 C)	1981	44	57	71	79	88	107	111	119
16 C		40	48	65	72	81	98	104	115
24 C		33	43	52	65	71	88	96	107
Check (10 C)	1982	59	81	91	102	109	121	124	138
16 C		55	68	83	89	94	117	121	133
24 C		50	63	75	83	89	103	109	122

[†]After Fehr, et al., 1977.

(Huxley and Summerfield, 1974; Thomas and Raper, 1978). The onset of all reproductive stages was highly correlated with night temperatures in the present study. Compared to the check, the 24 C treatment hastened seed formation at the uppermost nodes (R_5) by 17 days in 1981 and 20 days in 1982 (Table I.1). The time between first flower (R_1) and first brown pod (R_7) was relatively invariant among the treatments in both years (Table I.1). However, warmer nights advanced maturity compared to the check by 8 and 11 days for 16 C and 12 and 16 days for 24 C in 1981 and 1982, respectively. Assuming that the earlier flowering in 1981 than in 1982 (Table I.1) is because of the higher day temperature in the former year, the data support the conclusion of Van Schaik and Probst (1958) that night temperatures will not have any effect on reproductive development in soybean unless day temperature is sufficiently high.

Thomas and Raper (1978) reported that warm night temperature shortened the time to anthesis and also shortened the time period between anthesis and pod formation after soybeans were photoinduced regardless of the day temperature. The responses of reproductive ontogeny to night temperature in the present study were more pronounced than those reported by Huxley and Summerfield (1974) and Thomas and Raper (1978). This added response might be in part due to the use of an early maturing indeterminate soybean variety in the present experiment since these soybean groups are essentially insensitive to photoperiod (Criswell and Hume, 1972) while night temperature is an external factor altering the reproductive development of the plants (Parker and Borthwick, 1943).

Table I.2. Effect of night temperature on soybean seed yield and yield components

Year	Mean minimum night temperature	Plant height	Internode length	Nodes/ plant [†]	Branches/ plant [†]	Pods/ plant	Seeds/ pod	Seeds/ plant	Seed	Seed
									size	yield
		cm	No.1				mg	Mg		
							seed ⁻¹	ha ⁻¹		
1981	Check (10 C)	83	4.20	19.74	5.4	80	1.89	151	127.4	2.56
	16 C	91	4.50	20.24	5.2	86	1.94	167	148.9**	4.28**
	24 C	82	3.87*	21.26*	6.5	74	2.02	149	155.1**	3.39*
	CV %	20	9	4	11	11	9	10	5	13
1982	Check	66	3.89	16.86	6.6	58	1.98	115	164.5	2.68
	16 C	64	4.03	15.84	6.5	60	2.09*	126	183.0*	3.78**
	24 C	67	4.12	16.38	6.6	59	2.31**	136	164.3	3.49**
	CV %	5	6	6	5	12	4	13	6	18

[†]Numbers of nodes and branches were measured only on the main stem.

*,**Significant at the 0.05 and 0.01 level, respectively.

Warmer night temperatures generally enhanced vegetative growth as well as hastening reproductive development. The growth of different plant components, however, terminated earlier for plants receiving the higher night temperatures. This resulted in non-significant differences for all the morphological characteristics among the treatments measured at maturity, except for effects of 24 C nights on internode length and the number of nodes/plant in 1981 (Table I.2). Assuming that the variation of plant height and number of nodes/plant for all the treatments between the years are because of the warmer day temperature in 1981, these components seem to be more strongly affected by the average temperature than by variable day and night temperature. This agrees with the findings of Van Schaik and Probst (1958), and Thomas and Raper (1978).

Yield and Yield Components

In the following discussion, all treatment comparisons were made with the checks unless otherwise specified. Seed yield for the 16 C treatment increased 67 and 41% in 1981 and 1982, respectively. Higher seed yields for this treatment were due mainly to greater seed size in both years (Table I.2). Seed size in these plants increased 16.8 and 11.2% in 1981 and 1982, respectively, which was highly significant ($P < 0.01$). The number of seeds/plant for this treatment was not affected significantly, although it increased 10.5 and 9.5% in the corresponding years. These increases in the number of seeds/plant were due to both higher numbers of pods/plant and seeds/pod in both years.

Seed yield for the 24 C treatment increased 32 and 30% in 1981 and 1982, respectively. The treatment effects on yield component were different in the two years. In 1981, when average daily temperatures were close to optimum for crop growth, a 21.7% greater seed size was mainly responsible for the seed yield increase of the 24 C treatment (Table I.2). Lower number of pods/plant was offset by more seeds/pod. In 1982, neither seed size nor seeds/plant were significantly affected by the 24 C treatment. However, seeds/plant was increased 18.2%, which was mainly responsible for the seed yield increase of this treatment in this year. This increase in seeds/plant was due to significantly ($P < 0.01$) higher number of seeds/pod for this treatment, whereas the number of pods/plant was not significantly affected (Table I.2). It should be noted in Table I.2 that yield calculation by multiplication of components of seed yield results in a projected yield different from the measured yield. This is because yield components and yields were measured on different samples which involved different numbers of plants and, thus, the levels of precision were not the same for the two samples.

Number of pods/plant was the least variable of the seed yield components (Table I.2). Final number of pods/plant was not significantly affected by the treatments and for all treatments (Fig. I.2) was dependent more on pod retention than on pod formation. Pod formation occurred earlier in the elevated night temperatures, but the highest number of pods formed on check plants. However, pod abortion was also most severe for the check plants.

Soldati and Keller (1977) reported that pod number in the cultivar 'Chippewa', which is considered cold intolerant, was highly

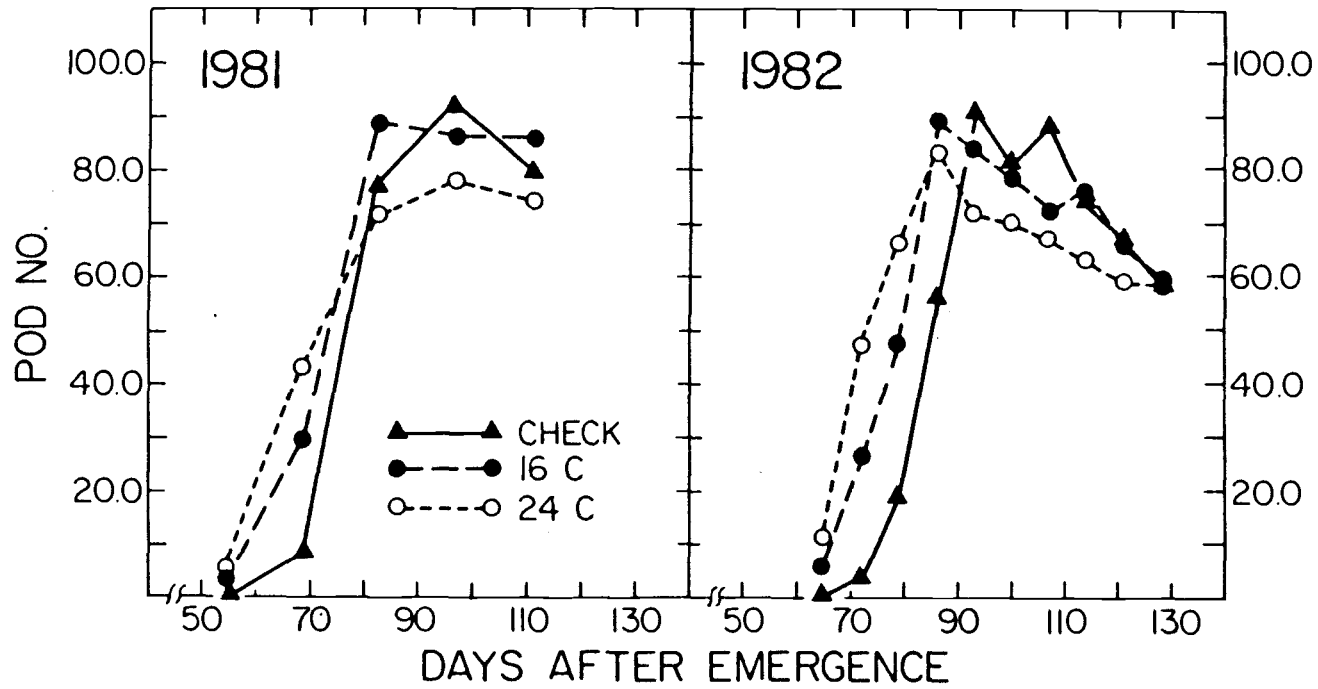


Fig. I:2. Effect of night temperature on pod number in soybean.

correlated with night temperatures. Thomas and Raper (1978) reported that a 4 C increase in night temperature from 14 to 18 doubled the number of pods in the cultivar 'Ransom' when the day temperature was kept constant at 22 C. In the same study, plants grown at higher day temperatures produced a large number of pods under several night temperatures. Van Schaik and Probst (1958) also reported that low night temperature had little effect on pod set. Appearance of first pod, however, was hastened by raising the night temperatures from 16 to 22 C. The mean number of pods/plant for the three treatments in the present study was 33% higher in 1981 than in 1982. This is much greater than the variation within the treatments in each year and is attributed, in part, to warmer day temperatures in 1981. This suggests that pod production in soybeans is more a reflection of average temperature than day or night temperature per se.

The differences in the seed yield of soybean receiving elevated night temperatures were due primarily to differences in seed size. Soybean seed size is influenced by both genetic and environmental factors (Egli et al., 1981). Soybean seed growth is influenced by temperature through a direct effect on seed metabolism as well as on other growth processes (Egli and Wardlaw, 1980). Although the growth rate of individual soybean seeds seems to be insensitive to a wide range of variations in the supply of assimilate (Egli and Leggett, 1976), seed yield might be limited by unavailability of total photosynthate required for seed growth. Further investigation is needed to determine whether low night temperatures directly affect seed growth rate and/or duration, or if it limits the ability of the plant to provide assimilates to the seed. In addition, the data suggest

that 24 C night temperatures, when kept constant for the entire growth period might be higher than optimum for maximum seed yield. However, the optimum day or night temperatures for plant growth change with the developmental stage of growth (Thomas and Raper, 1978). The effects of variable night temperatures at different stages of soybean plant development merit further investigation.

A large genetic potential for yield of major U.S. crops is unrealized because the plants are not adapted to the environments in which they are grown (Boyer, 1982). The dramatic effect of night temperature on seed yield of early maturing soybean cultivars observed in the present study raises a serious question about the latitudinal adaptation of these soybean groups. The present study emphasizes the importance of night temperature as a potential criterion for developing new soybean cultivars. Additional descriptive information about the effects of night temperature on morphological and physiological responses of soybeans will assist in breeding programs which are designed to improve soybean seed yield through more precise cultivar adaptation.

CHAPTER II

THE EFFECTS OF NIGHT TEMPERATURE ON DRY MATTER PARTITIONING
AND SEED GROWTH OF INDETERMINATE FIELD-GROWN SOYBEAN

INTRODUCTION

The productivity of grain crops depends both on the total photosynthate production and on the proportion of the assimilate allocated to the seed. The yield advantage of some recently developed soybean cultivars over older ones is due mainly to their more efficient partitioning of photosynthate to the seed, even though they might produce less total dry matter (Gay et al., 1980). Higher seed yield of some short season cultivars compared to longer season varieties is associated with differences in dry matter partitioning to seeds (Beaver and Cooper, 1982). The environmental factors which limit partitioning of photosynthate to developing sinks may regulate crop productivity (Gifford and Evans, 1981). This topic is particularly important in early maturing soybeans because their total dry matter production is limited by time and efficient allocation to the seed is crucial to produce high yields (Thorne, 1979).

Night temperature has a strong influence on the accumulation and partitioning of dry matter within soybean plants during the early reproductive growth (Thomas and Raper, 1978; Thomas et al., 1981). However, economic yield is determined by the final rather than initial distribution patterns of photosynthate which may be modified by redistribution within the plant and by respiratory losses during the plant development (Stephenson and Wilson, 1977). Soybean seed

production is limited by low night temperature largely through the effect on seed size (Chapter I). The objective of the present study was to determine if higher soybean seed yield at warmer night temperatures was due to increased production of photosynthate or to improved efficiency of photosynthate partitioning within the plant. The result would aid in understanding how night temperatures influence seed yield.

MATERIALS AND METHODS

Field experiments were established on Woodburn silt loam soil (fine silty, mixed mesic Aquultic Argixerolls) at the Oregon State Univ. Hyslop Crop Science Field Laboratory in 1981 and 1982, using the indeterminate soybean cultivar 'S09-90' (group 0 maturity). Mean minimum night temperature treatments included the check (uncontrolled, ca 10 C), 16 ± 1 C, and 24 ± 2 C in a randomized complete block field design with four replications. Treatments were applied from 2 weeks after crop emergence until physiological maturity. Weekly mean minimum, mean maximum, and normal air temperatures for the summer months of 1981 and 1982 are shown in Figure II.1. Cultural practices and the procedures used in this study were described in Chapter I.

Sampling for growth analysis was initiated 2 to 3 weeks after crop emergence and continued until physiological maturity. Four to six plants were randomly selected from the four replications of each treatment. Samples were taken at 14 and 7 day intervals in 1981 and 1982, respectively. Leaf area, leaf dry weight (petioles included), stem dry weight, pod dry weight, and seed dry weight were measured. The derived values of crop growth rate (CGR), net assimilation rate (NAR), and CGR of individual plant organs were then calculated. The apparent harvest index was calculated as the ratio of seed yield to mature plant dry weight. Regression technique (Buttery, 1970) was used for growth analysis calculations. Equations were fit to the logarithmic form of the average dry weight of the different plant components for each treatment. A quadratic exponential equation was adequate, indicated by R^2 's > 0.90 which was highly significant (0.01

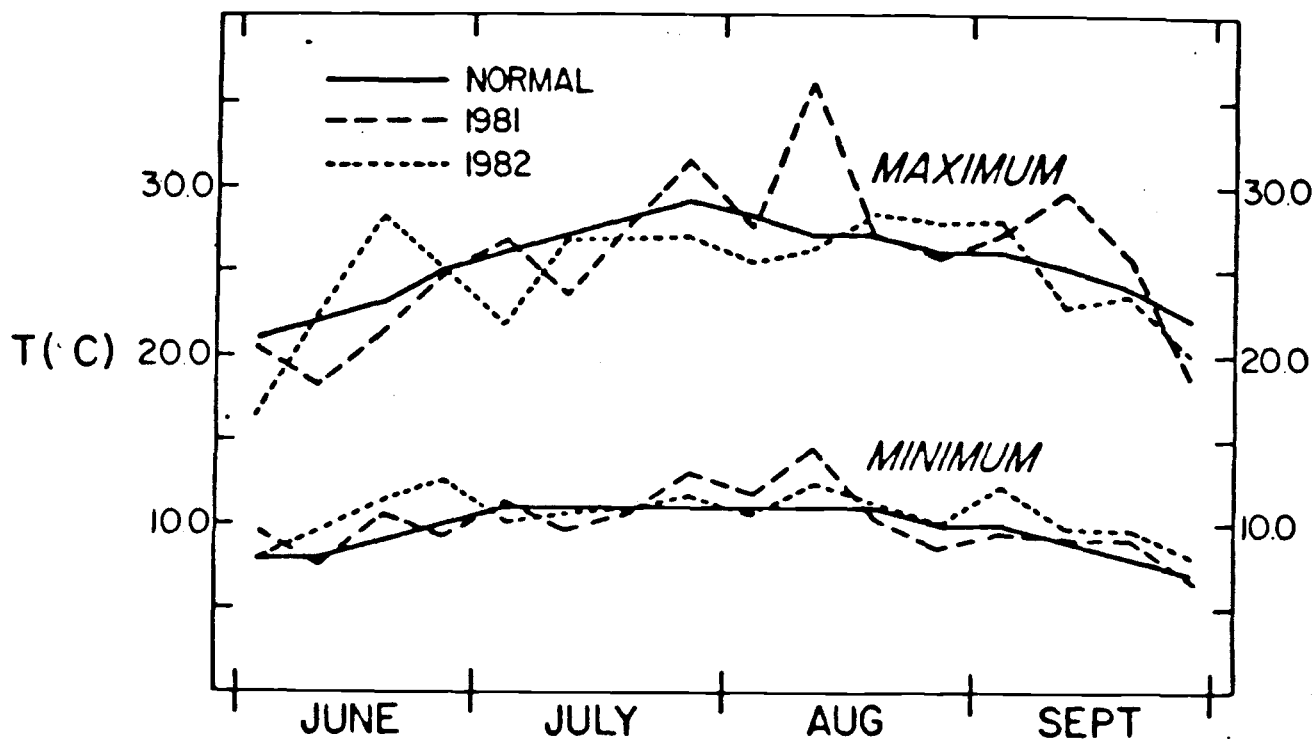


Fig. II.1. Weekly averages of maximum and minimum temperatures (T) for Corvallis, Oregon, through the months of June-September in 1981 and 1982 and the normals. Normals represent weekly averages of mean maximum and mean minimum temperatures for a 30-year period compiled by the National Weather Service, United States Department of Commerce, National Oceanic and Atmospheric Administration (Jim M. Crane, Wheeler Calhoun, and Earl M. Bates. Hyslop Field Laboratory Microstation Climate Survey. Special Report 516. Revised March 1979. Agric. Exp. St., Oregon State Univ., Corvallis, OR).

level) in all cases. Crop growth rate and NAR were then calculated using the predicted values obtained from fitted equations (Buttery, 1970). Seed growth duration (SGD) was calculated from the predicted values for seed growth rate (SGR). Accordingly, SGD is the number of days where CGR is greater than zero. Average SGR is then calculated by dividing the maximum predicted seed weight by SGD.

RESULTS

The average temperatures in the 1981 growing season were near normal whereas the summer of 1982 was cooler than normal. Although soybeans were planted 1 week later in 1982 than in 1981, plants emerged at about the same date in both years as a result of poor soil conditions for plant emergence in 1981. The period of vegetative growth was generally longer in 1982 than in 1981, apparently because of lower average temperatures in July of 1982. All treatment comparisons in the following paragraphs were made with the checks unless otherwise specified.

Higher night temperatures generally enhanced early vegetative growth as indicated by increased leaf area and total dry matter accumulation (Fig. II.2). Check plants had a higher CGR later in the season (Fig. II.3) because of delayed maturity. This resulted in no marked difference between final dry matter of check and 16 C plants. Check plants, however, produced more dry matter than 24 C plants in both years (Fig. II.2). The relative effect of night temperature on leaf area was similar to, but more pronounced than, the effect on dry matter (Fig. II.2). Although warmer nights increased early leaf growth, final leaf area of check plants exceeded that of 16 and 24 C plants. While the final leaf area was little affected by the 16 C treatment, final leaf area of the 24 C plants was reduced by 30 and 21% in 1981 and 1982, respectively. Reduced area/leaf rather than number of leaves/plant was responsible for differences in leaf area/plant among treatments. Treatments did not markedly affect NAR (Fig.

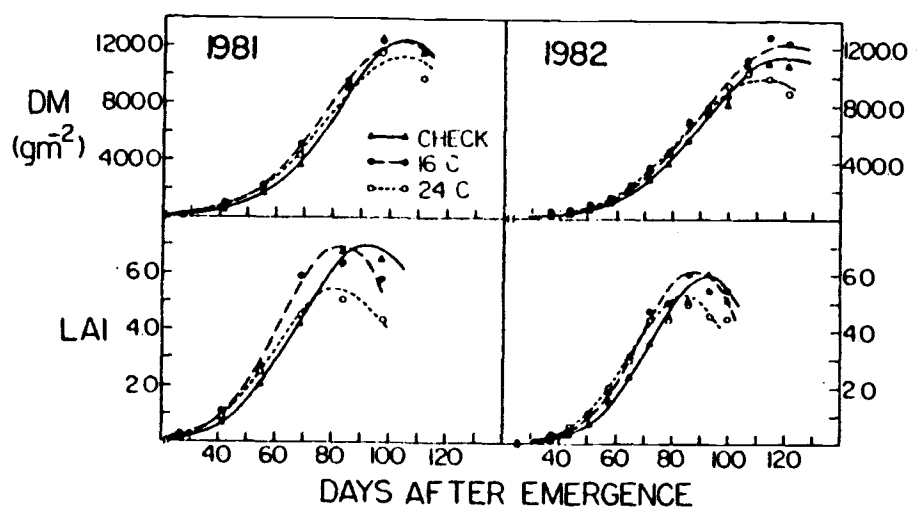


Fig. II.2. Effects of night temperature on seasonal patterns of total above-ground dry matter accumulation (DM) and LAI. Data points represent measured values and lines indicate predicted values derived from the fitted equations.

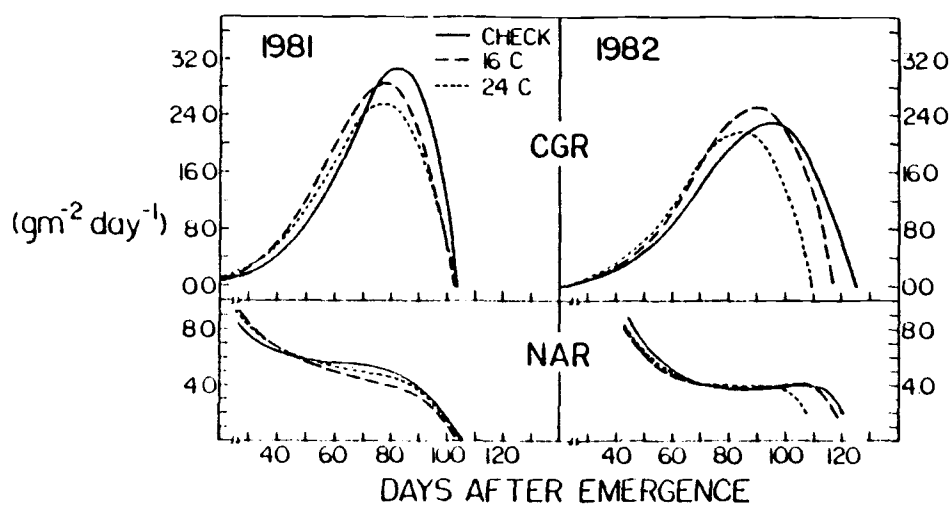


Fig. II.3. Effects of night temperature on seasonal patterns of CGR and NAR.

II.3). Earlier reduction of NAR for plants at the warmer night temperature was due to hastened maturity.

Although warmer nights increased leaf and stem growth rate during the early vegetative stage, check plants produced more total dry matter of these vegetative organs (Fig. II.4). Plants at 24 C accumulated approximately 29 and 25 % less dry matter in their leaves in 1981 and 1982, respectively. The final leaf dry weights of the 16 C plants were reduced approximately by 15 % in both years. While relative leaf growth rates among treatments varied between years, accumulation of dry matter in the leaves of plants at warmer nights terminated substantially earlier than in the checks in both years (Fig. II.5). Comparisons of leaf area and leaf dry weight among the treatments (Figs. II.2 and II.4) indicate that specific leaf weight decreased markedly as night temperature increased (data not shown).

The pattern for the effects of night temperature on stem growth were similar to, but not as pronounced as, the effects on leaf growth (Fig. II.4). In 1981, check plants accumulated approximately 12 and 30 % more dry weight in their stems than 16 and 24 C plants, respectively. These differences among the treatments were smaller in 1982. Plant height and branch numbers did not vary significantly among the treatments in either year. Thus, differences for final stem weight among the treatments were due primarily to differences in stem thickness or stem density. Assuming that the differences in the stem weight between years were due to differences in the average temperature for the two years, the larger variation of stem weight between years than within the treatment (Figs. II.4 and II.5) indicate that stem growth is more sensitive to average temperature than

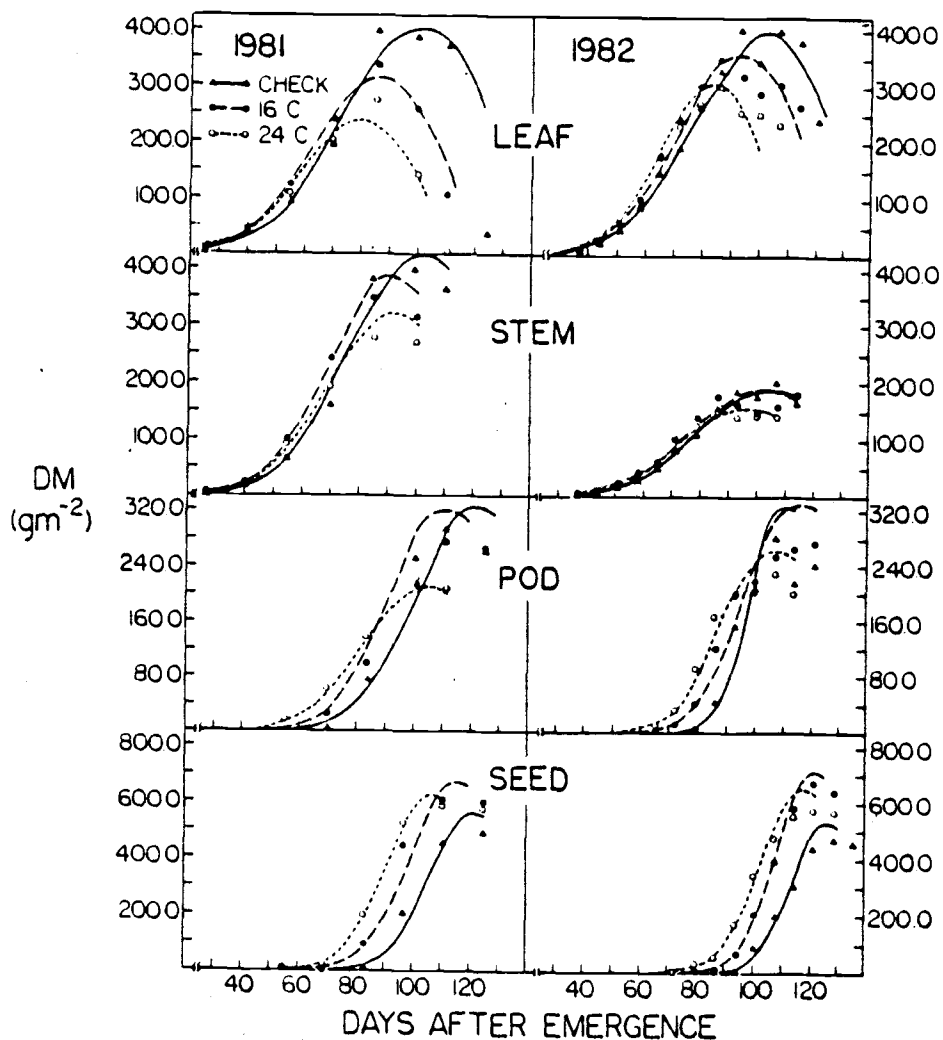


Fig. II.4. Effects of night temperature on seasonal patterns of dry matter accumulation (DM) in different plant components. Data points represent the measured values and lines indicate the values predicted from the fitted equations.

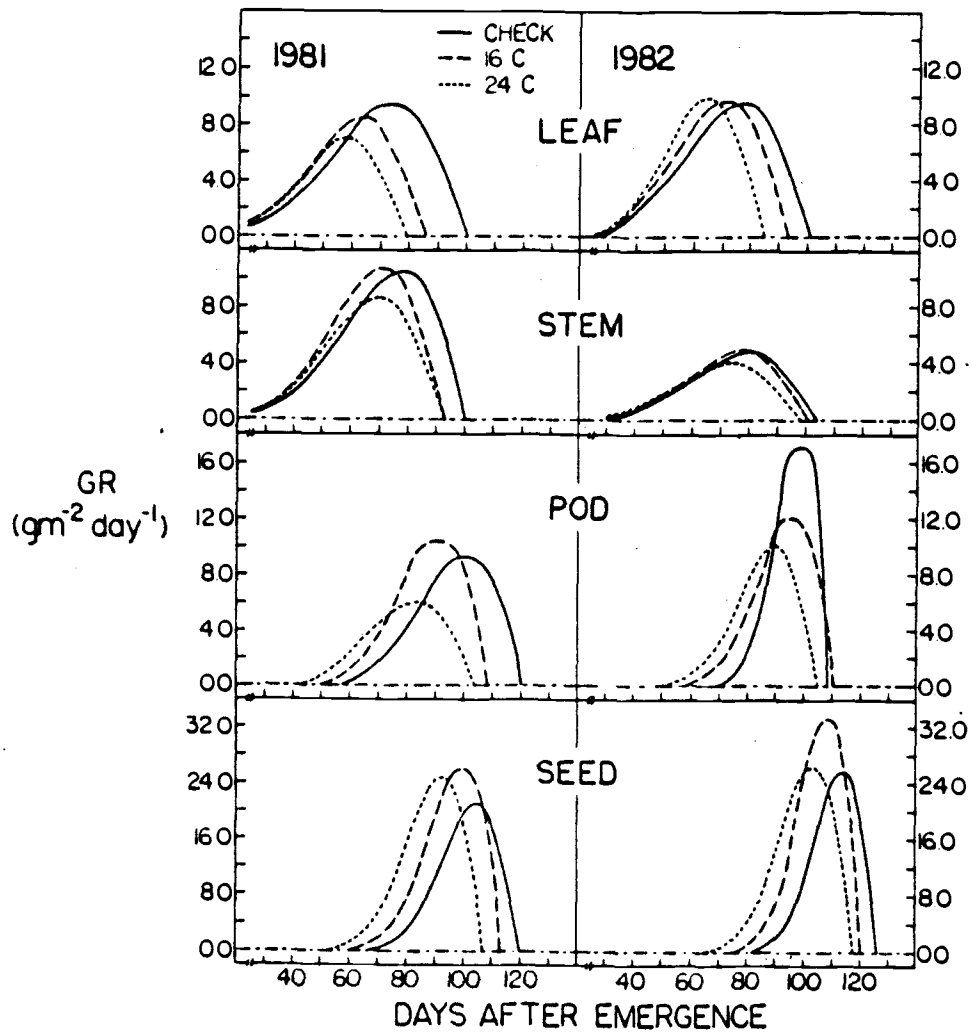


Fig. II.5. Effects of night temperature on seasonal patterns of growth rates (GR) for different plant components.

to daily fluctuation of temperature. Stem growth rates in 1982 were approximately half of those in 1981 (Fig. II.5) resulting in considerably shorter and thinner stems.

Dry matter accumulated in pods was least at the highest night temperature (Fig. II.4). Final pod dry weights of check plants were about 20% higher than of 24 C plants in both years. Final pod dry weights for checks and 16 C plants, however, were not markedly different. Numbers of pods/plant were not significantly different among treatments. Differences in total pod dry weight were thus due primarily to weight/pod rather than to the number of pods/plant. Warmer nights enhanced pod formation and hastened pod maturity (Fig. II.5), but resulted in no marked differences for pod growth period in plants at different night temperatures. Observed differences in pod dry weight among the treatments were due therefore to variations in pod growth rates.

Warm nights enhanced dry matter accumulation in seeds (Fig. II.4). Final seed dry weights increased by 31 and 25 % in 1981 and 39 and 28 % in 1982 for plants at 16 and 24 C nights, respectively. Although higher night temperatures hastened seed formation, seed growth also terminated earlier in plants at warmer nights (Fig. II.5). This resulted in only small differences for SGD among the treatments except for 24 C plants in 1982 (Table II.1). However, SGR was generally increased by warm nights in both years of the study. Seed growth rate of 16 C plants increased by 31 and 38 % in 1981 and 1982, respectively. This accounted for the total seed weight increase of 16 C plants. Seed growth rate of 24 C plants also increased by 24 % in 1981 which reflects the differences between the

Table II.1. Effects of night temperature on seed growth period, seed growth duration, and seed growth rate.

Year	Mean Minimum Night Temperatures (C)	Seed Growth Period	Seed Growth Duration	Average Seed Growth Rate
		Days After Emergence	Days	$\text{g m}^{-2} \text{ day}^{-1}$
1981	10 (check)	65-120	55	9.64
	16	60-113	53	12.50
	24	53-105	52	12.07
	10 (check)	82-127	45	11.73
	16	76-120	44	16.15
	24	55-117	51	12.37

seed yield of the 24 C plants and the check. Increased seed weight of 24 C plants in 1982 was, however, due primarily to their longer SGD (Table II.1).

Increased seed weight of plants with warmer nights, along with reduced vegetative growth of plants, resulted in significant differences among treatments for the ratio of seed weight to weight of other plant parts (Table II.2). Seed yield increase associated with warm nights was at the expense of vegetative organs and the pod wall tissue. Seed weight partitioning index [SWPI = seed dry weight / (total above ground dry weight - seed dry weight)] of 16 C plants was 38 and 76% higher than the checks in 1981 and 1982, respectively. SWPI in 24 C plants was higher than the checks by 51% in 1981 and 88% in 1982. Harvest index was also increased above the check by 27 and 33% in 1981 and 16 and 23% in 1982, for 16 and 24 C plants, respectively. Lower seed yield of 24 C plants than plants at 16 C in both years appears to be due to a substantial reduction of vegetative growth in plants at 24 C night temperature. Considerable reduction of leaf area, along with intensive SGR in plants at 24 C nights, might have limited the total photosynthate available for seed growth.

Table II.2. Effects of night temperature on the ratio of final seed dry weight to the maximum dry weight accumulated in other plant components.

Year	Mean Minimum Night Temperature (C)	Seed wt. Leaf wt. + Stem wt.	Seed wt. Pod wt.	SWPI [†]	Harvest Index
1981	10 (check)	0.57	1.90	0.45	0.36
	16	0.83**	2.25**	0.62*	0.46*
	24	0.90**	2.80**	0.68**	0.48*
1982	10 (check)	0.76	2.29	0.51	0.43
	16	1.40**	2.46	0.90**	0.50*
	24	1.52**	2.73*	0.96**	0.53*

[†]Seed weight partitioning index, as described in the text.

*,**Significantly different from the check at the 0.05 and 0.01 level, respectively.

DISCUSSION AND CONCLUSION

Grain yield may be limited by either potential seed growth capacity or by the ability to realize this capacity (Yoshada, 1972). The ability of a grain crop to realize its yield capacity might be altered by factors which (a) interfere with seed growth rate and/or seed growth duration directly (reproductive sink limitation) or (b) affect the ability of plants to provide assimilates to the seed (photosynthate source limitation). The data presented here suggest that low night temperatures directly limited sink strength through an alteration of SGR rather than by limiting the ability of the plants to provide assimilates to seeds. For plants having an indeterminate growth habit in which vegetative and reproductive growth occur simultaneously during part of the plant development, a higher SGR may shift the allocation of photosynthates from vegetative tissues to the reproductive sinks.

Although growth rate of individual seeds is not sensitive to large changes in the supply of assimilates (Egli and Leggett, 1976), SGR per unit land area could be limited by the total supply of photosynthate. Thus one might expect that earlier reproductive development in plants at higher night temperatures would increase SGR due to more available photosynthate associated with greater light intensity and duration earlier in summer (Shibles and Green, 1969). It also could be argued that low night temperatures retarded the translocation of assimilates out of the source leaves. However, the mean minimum temperature in the present study (ca. 10 C) was considerably higher than the chilling temperatures (1 to 3 C) which would

be expected to affect the translocation process (Thrower, 1965; Geiger, 1969).

High rates of growth for stems, leaves, and pods during the seed formation in plants grown at cool nights indicate high rates of assimilate production in, and translocation from, the source leaves. This supports the conclusion that higher SGR of plants associated with warm night temperatures was controlled primarily by a direct effect of night temperature on seeds as opposed to its effect on photosynthate production or assimilate translocation out of the source leaves.

There are many possible ways by which night temperature can affect SGR. Although SGR is genetically controlled (Egli, et al., 1981), metabolic processes in seeds which are responsible for seed growth are sensitive to temperatures (Egli and Wardlaw, 1980). The increase in fatty acid content of soybean seeds by warm days, and the increase in protein deposition by warm nights (Summerfield and Wein, 1980) indicates the specific differential effects of day and night temperatures on particular facets of soybean seed metabolism. Soybean seeds accumulate high concentrations of proteins and lipids. Any alteration in the metabolism of amino acids or fatty acids in seeds might result in considerable effect on the SGR. Import of assimilate by intact fruits of field-grown soybean has been shown to be temperature dependent (Thorne, 1982a). This dependency was found only within the seeds while the pod wall was insensitive to fruit temperature, suggesting a specific effect of temperature on different plant components. Thorne (1982b) also has shown that the accumulation of sucrose in isolated soybean embryos, when sucrose

concentration is at physiological levels, occurs mainly through an active transport system. At this physiological concentration, sucrose uptake in developing soybean embryos by energy dependent transport mechanism was two to five times higher than the uptake by diffusion alone. Night temperature could have influenced SGR by altering the metabolic process occurring within the seed or by affecting the energy-dependent mechanism of assimilate unloading into the seed. Furthermore, soybean seed coats have an important role in transferring assimilates from the phloem to cotyledons (Thorne, 1980). The influence on seed coat function may also be one mechanism by which night temperature affects soybean SGR.

Night temperatures might also alter the production, distribution, and/or activities of the hormones which are associated with SGR. Quebedeaux, et al. (1976) found a close correlation between abscisic acid (ABA) levels in developing soybean seeds and the SGR. Whereas vegetative sinks utilize assimilates when available (Hanson and West, 1982), developing reproductive tissues might supply stimuli which actively alter assimilate translocation and distribution (Williams and Williams, 1978). Increased translocation of assimilate from leaves to ovules of peas at higher pod temperatures was attributed both to a direct effect on seed growth and to a remote influence on the transport system via stimuli produced at the pod which enhance the export of assimilate from the leaf. Direct stimulation of more rapid seed growth through the alteration of cell division or cell expansion in the seed might be another mechanism by which night temperature influences SGR (Egli, et al., 1981). Regardless of the

mechanism involved, present data suggest that night temperatures regulate soybean SGR through a direct effect on seeds.

The effects of night temperatures on dry matter partitioning and SGR reported here are similar to the effects of photoperiod (Thomas and Raper, 1976; Raper and Thomas, 1978). This is because night temperature strongly affects the response of soybeans to photoperiods (Parker and Borthwick, 1943; Van Schaik and Probst, 1958). This effect of night temperature is expected to be even more pronounced in early maturing cultivars since these soybean groups are essentially insensitive to photoperiods (Criswell and Hume, 1972). The present study supports the conclusion of Thomas and Raper (1976) that the control of SGR is separate from the interaction of genetic and environmental factors which regulate CGR and NAR in soybeans. Apparently, night temperature influences the regulation of SGR apart from CGR in early maturing soybeans. Additionally, the fact that higher night temperatures increased SGR without affecting SGD in the present study agrees with Egli, et al. (1981) that the factors regulating SGR and SGD are not closely associated. Similarity between the effects of photoperiod and night temperature on SGR and dry matter partitioning in soybeans suggests the involvement of a process or processes occurring in seeds during the dark period. A continuous short photoperiod is required after flower induction to maintain dry matter accumulation in soybean pods, which indicates that photoperiodic control of flowering and seed-fill are separate (Thomas and Raper, 1976). We cannot draw similar conclusions for the night temperature effects since the night temperature treatments were applied continuously for the entire growth period in the present

study. The effects of various night temperatures at different stages of development on SGR and dry matter partitioning in soybeans merits further investigation.

In conclusion, SGR of early maturing soybeans appears to be responsive to night temperatures. Higher night temperatures increase reproductive sink strength through a direct effect on seeds which, in turn, regulates dry matter allocation in favor of seeds and at the expense of vegetative tissues and pod wall. This results in more efficient partitioning of total dry matter and improves SWPI and harvest index. Excessively high night temperatures, however, are deleterious to seed yield because of a dramatic disruption of vegetative growth which limits photosynthate available for seed production. Clearly, this environmental factor merits more detailed investigations than has been attempted previously. A better understanding of the relationships between night temperatures and dry matter partitioning to seed in soybean may help overcome the stubborn yield barriers which have challenged researchers for several decades.

CHAPTER III

PHYSIOLOGICAL RESPONSE OF FIELD-GROWN SOYBEAN TO INCREASED
REPRODUCTIVE LOAD INDUCED BY ELEVATED NIGHT TEMPERATURES

INTRODUCTION

It is generally accepted that decreasing the source/sink ratio in plants increases the carbon dioxide exchange rate (CER) in the source leaves (reviewed by Geiger, 1976). Some evidence (Upmeyer and Koller, 1973; Thorne and Koller, 1974; Nafziger and Koller, 1976) suggests that reduction in CER induced by a decline in assimilate demand might be due to accumulation of starch grains in the chloroplasts of mesophyll cells which results in an increase in leaf residual resistance to CO_2 fixation (residual resistance; r_m). When assimilate demand was increased in soybean by shading all but the source leaf, r_m was significantly reduced along with a sharp decline in leaf starch content whereas gas-phase resistance to CO_2 diffusion (stomatal diffusive resistance; r_s) did not vary between the treatments (Thorne and Koller, 1974). More recently, it was shown (Koller and Thorne, 1978; Setter et al., 1980a) that decreasing sink demand also increases r_s . Koller and Thorne (1978) observed that upper surface r_s of soybean leaves was doubled 24 hours after all pods were removed and increased six-fold 48 hours after the treatment was imposed. Setter et al. (1980a) reported that a 70% reduction in CER within 48 hours after depodding soybean plants was associated with increased r_s whereas calculated r_m was unaffected. Mondal et al. (1978) also observed a reduction in CER 8 hours after soybean plants

were desinked. The magnitude of this reduction in CER 24 hours after desinking was as great as that for continuously desinked plants, indicating a relatively fast response of CER to alteration of source/sink ratios. Mondal et al. (1978) did not find any correlation between CER and several traits studied although they did not measure r_s and r_m .

Warmer night temperatures increased assimilate demand in field-grown soybean plants by increasing seed growth and a concomitant reduction of leaf growth (Chapter II). The long-term effect of night temperature on CER's of field-grown soybeans was monitored in the present experiment. The components of resistance to CO₂ fixation were studied in an attempt to explain the cause of the stimulated photosynthesis by warmer night temperatures.

MATERIALS AND METHODS

Field experiments were conducted on Woodburn silt loam soil (fine silty, mixed mesic Aquultic Argixeroll) at the Oregon State University Hyslop Crop Science Field Laboratory in 1981 and 1982 to study the effects of night temperatures on physiological response of soybean plants. The indeterminate soybean cultivar 'S09-90' (group 0 maturity) was used in both years of this study. Treatments included a check (uncontrolled, ca 10 C), 16 C, and 24 C night temperatures in a randomized complete block field design with four replications. Treatments were applied from two weeks after crop emergence until physiological maturity. Soil temperature was monitored with thermistors buried at different soil depths. Temperatures were periodically recorded at 1 hour intervals using a multi-channel recorder (Esterline Angus. Model E1124E). Cultural practices and the experimental procedures used in this study were described in Chapter I.

Measurements were made on 30 July, 14 August, and 27 August in 1981 and on 19 July, 4 August, and 17 August in 1982. These dates correspond to the time of flowering, pod formation, and seed filling, respectively. In 1981, measurements were initiated at 0730 on each date and were repeated at 2.5 hour intervals for a total of six measurements per day. In 1982, measurements were initiated at 0800 on each date and were repeated at 1.5 hour intervals for a total of eight measurements per day. Simultaneous measurements of stomatal diffusive resistance (r_s), transpiration rate (Tr) and CO₂ exchange rate (CER) were made on the center leaflet of the second most recently expanded trifoliolate. In 1981, leaf water potential () and

leaf osmotic potential (ψ_{π}) were measured for the same trifoliolate. Leaf starch content was also measured on selected dates in 1981.

Leaf r_s and Tr were measured first for the adaxial and abaxial sides of the specified leaf with a LI-COR steady state porometer (LI-1600). Total Tr was calculated by adding adaxial Tr to abaxial Tr. Parallel resistance was assumed and r_s was calculated using the equation:

$$\frac{1}{\text{leaf } r_s} = \frac{1}{r_s \text{ abaxial}} + \frac{1}{r_s \text{ adaxial}}$$

Leaf CER's were then measured by depletion technique using a sealed portable chamber and sampling air from the chamber (Clegg et al., 1978). The leaflet in the chamber was held perpendicular to the sun during the 30 seconds between the two air samplings from the chamber. The leaflets and air samples were taken into the lab after sampling was completed. CO_2 concentrations from the air samples were analyzed with a Beckman 865 infrared gas analyzer. Leaf areas were measured with a LI-COR-3100 leaf area meter. The CER's were then calculated using the method described by Clegg et al. (1978).

In 1981, the leaf for which CER of the center leaflet was measured was excised at the petiole and placed in a pressure chamber (Soil Moisture Equip. Corp. Model 3005) to determine ψ . The side leaflets were then frozen on dry ice and transferred to a freezer for subsequent ψ_{π} measurement. Leaves were allowed to thaw before determining the ψ_{π} . A small amount of expressed sap was absorbed onto a filter paper disc and placed in a Wescor C-52 sample holder coupled to an HR-33T dew point hygrometer to determine ψ_p . The ψ_p was then calculated using the equation ($\psi = \psi_{\pi} + \psi_p$).

The changes in leaf starch content at night were measured by taking leaf disc samples the evening before and the morning of the days on which CER measurements were made. Two leaf discs (2 cm^2 each) were taken at sunset from the tip and the base of the one side leaflet of the third most recently expanded trifoliolate. Two more leaf discs were taken from the other side leaflet on the same trifoliolate the following dawn. Leaf discs were frozen on dry ice immediately after sampling. The frozen samples were placed in a microwave oven for 2 min., then dried in an oven at 100 C for 24 hours. Starch content was measured using the method described by Potter and Breen (1980).

Data for the two years were analyzed separately. The leaf starch content data were analyzed as a randomized complete block design. All other data were analyzed as a split-split plot design. Treatments were considered as the main plots, dates as the sub-plots, and times of day as the sub-sub plots. The treatment by date and treatment by time by date interactions were not significant. Thus, measurements were averaged over dates and the diurnal responses of the traits to the treatments were compared. LSD values were calculated for comparisons of the treatments at different measurement times. The treatment means for CER, r_s , and Tr were also compared for each date.

RESULTS AND DISCUSSION

The effects of night temperatures on the source/sink ratio of field-grown soybean plants were reported in Chapter II. In general, while raising the mean minimum night temperature to 16 C increased seed yield without significant effect on leaf area, seed yield increase for the 24 C treatment was accompanied by a reduced leaf area. All comparisons in the following discussion were made between the elevated night temperature treatments and the check.

Mean CER for the three dates of measurements was increased by 7 and 15% for 16 C plants and 11 and 32% for 24 C plants in 1981 and 1982, respectively (Table III.1). The greater treatment effects on CER in 1982 than 1981 might be explained by the shorter duration and more intensive rate of seed growth in 1982 due to delayed flowering. The effect of the treatments on CER became more apparent as plants progressed in reproductive development and was significant only for the 24 C treatment on the last two dates in 1981 and the last date in 1982 (Table III.1). This suggests that differences in CER among the treatments were due mainly to variation in assimilate demand rather than a direct effect of night temperature on CER. The effect of the 24 C treatment on the mean CER for the three dates was highly significant in both years while mean CER of the 16 C treatment increased significantly only in 1982 (Table III.1).

Treatments did not significantly affect r_s except for the 24 C plants on the last date in both years. The r_s of the 24 C treatment decreased on the last date by 30 and 42% in 1981 and 1982, respectively. When the means of the three dates were compared, r_s was

Table III.1. Effects of night temperature on some physiological traits on selected dates[†] and the means in 1981 and 1982.

Trait	Mean Minimum Night Temp.	1981				1982			
		30 July	14 Aug.	27 Aug.	Mean	19 July	14 Aug.	27 Aug.	Mean
$\mu \text{ mol m}^{-2} \text{ s}^{-1}$									
CO ₂ Exchange Rate (CER)	10 (check)	17.7	12.6	11.9	14.06	21.7	12.2	9.4	14.42
	16	18.3	13.7	13.2	15.06	23.0	14.4	12.4	16.59*
	24	18.0	14.5*	14.3**	15.60**	24.2	14.9	17.9**	10.02**
s m^{-1}									
Stomatal Diffusive Resistance (r _s)	10 (check)	76	129	191	132	23.4	103	287	138
	16	85	119	186	130	26.1	100	270	132
	24	86	131	153*	123	23.2	78	166**	89**
$\text{m mol m}^{-2} \text{ s}^{-1}$									
Transpiration (Tr)	10 (check)	8.3	7.0	4.7	6.7	24.7	8.0	4.4	12.4
	16	8.0	8.6**	4.9	7.2*	23.2	10.1	4.3	12.5
	24	7.9	8.1	6.2*	7.4**	25.5	9.7	6.3	13.8*

[†]Each number is the mean of six times of measurements and four replications in 1981 and eight times of measurements and four replications in 1982.

*,**Significant at the 0.05 and 0.01 level, respectively, when comparing numbers on the same column.

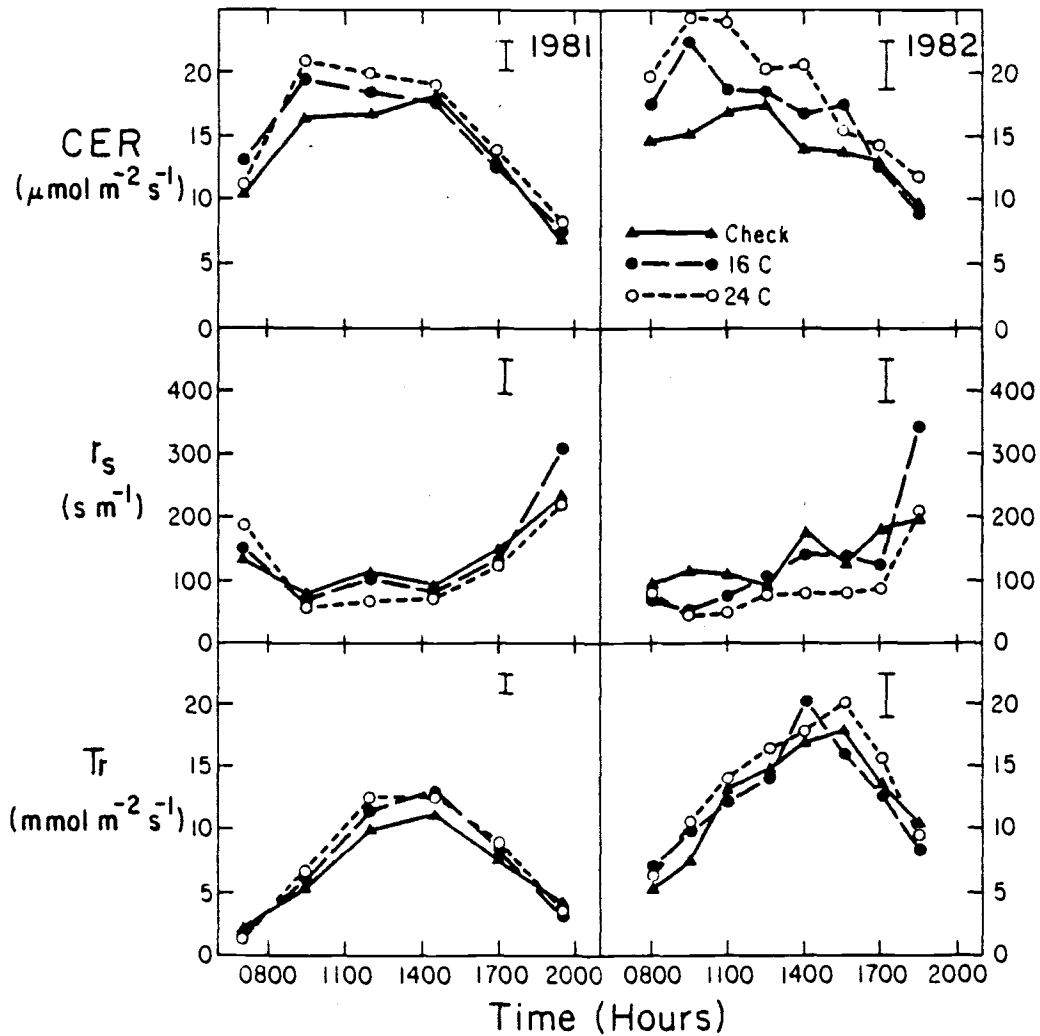


Fig. III.1. Effects of night temperature on diurnal patterns of CO_2 exchange rate (CER), stomatal diffusive resistance (r_s), and transpiration rate (T_r) in 1981 and 1982. Vertical lines represent LSD at the 5% level for comparing treatment means within times.

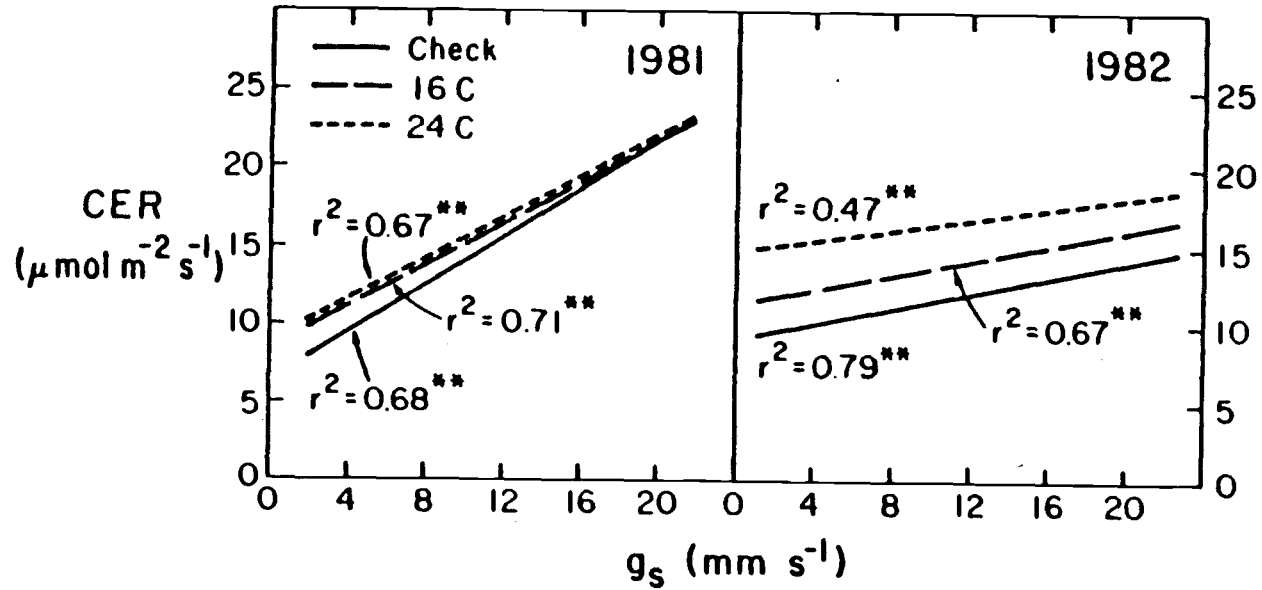


Fig. III.2. Effects of night temperature on the relationship between CO_2 exchange rate (CER) and the stomatal conductivity (g_s) in 1981 and 1982.

significantly affected only by the 24 C treatment in 1982. The mean Tr increased significantly for plants receiving warmer nights except for the 16 C treatment in 1982 (Table III.1). This increase was 7% for 16 C treatment in 1981 and 10 and 11% for 24 C treatment in 1981 and 1982, respectively. Similar to CER and r_s , differences for Tr among treatments became larger as plants matured.

The treatment effect on CER was largest during the morning hours in both years. The CER of 16 C plants was significantly higher than the check at 0700 and 0930 hours in 1981 and at 0900 hours in 1982 (Fig. III.1). Plants at 24 C nights also had significantly higher CER than the check at 0930 and 1200 hours in 1981 and 0730, 0900, and 1130 hours in 1982. There were no significant differences for Tr and r_s among the treatments at any time of day except for Tr of the 24 C plants at 1200 hours in 1981 and r_s of 16 C plants at 1950 and 1900 hours in 1981 and 1982, respectively (Fig. III.1). Although CER and stomatal conductance ($g_s = 1/r_s$) were highly correlated for all treatments, plants with warmer nights had higher CER at any g_s value observed (Fig. III.2). Given that any alteration of CER would be ultimately through an effect on r_s or r_m , plants at warmer nights, having higher CER's at the same r_s values as the checks, would have lower r_m . Higher r_m in plants at cool nights, however, would result in increased intercellular CO_2 concentration which causes stomatal closure (Dubbe et al., 1978). This might not be evident in short-term studies where sink demand is manipulated experimentally (Setter et al., 1980a) because a longer period is usually required for the adjustment of CER (Geiger, 1976). Since cool temperatures sensitize the stomata to the intercellular CO_2 concentration (Drake and

Table III.2. Effect of night temperature on leaf starch content[†] on selected dates and times in 1981.

Mean Minimum Night Temp.	30 July 2000	31 July 0800	14 Aug. 2000	15 Aug. 0800	27 Aug. 2000	28 Aug. 0800
C	g m ⁻²					
10 (check)	1.50	0.78	1.38	0.40	1.18	0.56
16	1.15	0.45	0.81	0.01**	1.03	0.30**
24	1.25	0.37	1.37	0.09**	1.12	0.30***

[†]Each number is the mean of four replications.

**Significant at the 0.01 level, when comparing numbers on the same column.

Raschke, 1974; Martin et al., 1981), treatments in the present study could have amplified the response of stomata to the intercellular CO_2 concentration, particularly during the morning hours. However, the more direct effect of increased assimilate demand on stomatal opening cannot be totally discounted. Developing soybean seeds accumulate high concentrations of ABA which is imported from the leaves (Quebedeaux et al., 1976) and high leaf ABA content might be one mechanism by which r_s of desinked plants is increased (Setter et al., 1980b). ABA also sensitizes stomata to intercellular CO_2 concentration (Dubbe et al., 1978).

Decreased CER associated with increased r_m has generally been attributed to accumulation of starch in the mesophyll cells of plants having reduced assimilate demand or increased assimilate supply and is referred to as supportive of the concept of feedback inhibition (Hilliard and West, 1970; Chatterton et al., 1972; Upmeyer and Koller, 1973; Thorne and Koller, 1974; Nafziger and Koller, 1976). Although the starch content of the leaves in the present study was measured only in 1981, the data (Table III.2) indicate that the lower CER in plants grown at cool nights was not associated with high starch content in the leaves. Although the starch content in the leaves of plants with warmer nights was significantly lower than in the check plants in the morning hours of the last two measurement dates, the starch content in the leaves of the check plants was much lower than the concentrations which would be expected to affect CER. In addition, Potter and Breen (1980) did not find a correlation between CER of soybean plants and accumulation of high levels of starch in the leaves. Mondal et al. (1978) also found no significant

correlation between reduced CER of desinked soybean plants and leaf concentration of carbohydrates and they suggested involvement of hormonal activity which increases CER in plants with reduced source/sink ratios. Geiger (1976) also proposed a hormonal control of CER when manipulating sink-source ratios.

A decrease in CER following a short-term exposure of plants to chilling temperatures during the dark period has been demonstrated for many crops (Izhar and Wallace, 1967; Hilliard and West, 1970; Chatterton et al., 1972; Pasternak and Wilson, 1972; People and Koch, 1978). More recently, Sinclair (1980) observed that CER of some cultivars of field-grown soybeans was significantly reduced following a cool night of 5 to 10 C. It is unlikely that these short-term exposures of plants to cool nights had any considerable effect on the source/sink ratio. This implies that the treatments in the present study could have directly affected the CER of plants. The reduction in CER following cool nights sometimes has been attributed to feedback inhibition of CER due to reduced degradation and translocation of starch grains from mesophyll chloroplasts (Hilliard and West, 1970; Chatterton et al., 1972; People and Koch, 1978) and sometimes to an increase in r_s induced by a temporary water stress (Izhar and Wallace, 1967; Pasternak and Wilson, 1972; Crookston et al., 1974). Low temperatures also might affect r_s directly (Drake and Salisbury, 1972). As mentioned already, starch content was low in the leaves of all plants in the present study. Thus, the inhibition of CER by cool nights due to retention of starch grains in the leaves is not indicated in this study.

The data for 1981 (Table III.3) indicate that cool nights did not have any adverse effect on water status of plants. Indeed, ψ generally decreased as night temperature increased. The mean ψ of 24 C plants was lower than the check by 10%, a difference which was highly significant (Table III.3). Plants at 24 C nights also had significantly lower ψ than the check plants at 0930 and 1200 hours, when they had lower r_s but significantly higher CER (Table III.3 and Fig. III.1). This further supports the conclusion that r_s was affected more by intercellular CO_2 concentration than by the water status of the plant. Lower ψ in plants at warmer nights might be explained by their higher Tr for most hours of the day (Fig. III.1).

There were no significant differences for ψ_{π} and ψ_p among the treatments (Table III.3). Reduced ψ in plants following a cool night is sometimes attributed to the effect on the temperature of the root zone (Pasternak and Wilson, 1972; Crookston et al., 1974). Treatments in the present study, however, did not affect the soil temperature at depth below 5 cm. Thus it is improbable that temperature effects on soil temperature were responsible for the differences in ψ observed among the treatments in this study.

In conclusion, elevated night temperatures increased CER of soybean plants by increasing assimilate demand. Higher CER in plants receiving warmer nights was due mainly to lower r_m , while it appeared that r_s was reduced, in part, in response to lower intercellular CO_2 concentration in these plants.

Table III.3. Effects of night temperature on water status of leaves at different times of day[†] and the means in 1981.

Trait	Mean Minimum Night Temperature	Time of Day (Hours)						Mean
		0700	0930	1200	1430	1700	1930	
C		M Pa						
Leaf water potential (ψ)	10 (check)	-0.18	-0.63	-1.06	-1.17	-0.96	-0.67	-0.78
	16	-0.28	-0.71	-1.17	-1.18	-0.99	-0.72	-0.81
	24	-0.23	-0.76**	-1.20**	-1.17	-1.08*	-0.74	-0.86**
Leaf osmotic potential (ψ_{π})	10 (check)	-0.97	-1.12	-1.28	-1.33	-1.30	-1.26	-1.21
	16	-1.00	-1.13	-1.23	-1.34	-1.27	-1.25	-1.20
	24	-1.04	-1.14	-1.29	-1.37	-1.33	-1.22	-1.23
Leaf turgor potential (ψ_p)	10 (check)	0.79	0.49	0.22	0.16	0.34	0.59	0.43
	16	0.77	0.42	0.16	0.21	0.27	0.53	0.39
	24	0.81	0.38	0.09	0.20	0.25	0.48	0.37

[†]Each number is the mean of three dates and four replications.

*,**Significant at the 0.05 and 0.01 levels, respectively, when comparing numbers on the same column.

CONCLUSION

The genetic potential for seed yield of existing soybean cultivars is not realized under cool night temperatures of the Willamette Valley. Cool nights delay reproductive development and restrict seed growth rate of the best adapted indeterminate soybean cultivars. Low seed growth rate, in turn, favors partitioning of photosynthate to vegetative organs and pod wall at the expense of seed production. This implies that the reproductive sink is limited under the environmental condition of the area while total assimilate production appear to be quite favored by the climate of the region. However, cool nights indirectly reduced CO_2 exchange rate per unit leaf area through a decrease in assimilate demand by the seeds. This effect does not appear to be a direct feedback inhibition caused by accumulation of photosynthate in leaves or an adverse effect of low night temperatures on water status of plants, but is hypothesized to be a hormonal effect through which mesophyll resistance to CO_2 diffusion is increased in plants having low assimilate demand.

Further effort to improve soybean seed yield in the Willamette Valley of Oregon or in the areas with similar climate should be based on developing varieties tolerant to cool nights, particularly at reproductive stages. Additional descriptive information on the effects of cool night temperatures on physiological response of soybean will assist in such breeding programs. The mechanism through which low night temperatures restrict seed growth rate or soybean is of particular interest. A summary of the research is given in the following schematic form:

EXPERIMENT I
(Yield and Yield Components)

Soybean plant
↓
Low night temperature

↓
Reduced seed size

↓
Reduced seed yield

EXPERIMENT II
(Dry Matter Partitioning)

Direct effect on seed growth

↓
Metabolic process in the seed?
Unloading of assimilates in the seed?
Hormonal control?

↓
Reduced seed growth rate

↓
Sink strength effect?
Hormonal control?

↓
More dry matter partitioned to vegetative organs

↓
Reduced harvest index

EXPERIMENT III
(Physiological Responses)

Reduced reproductive load

↓
Reduced assimilate demand per unit leaf area

↓
Effect on photosynthesis apparatus?
Photosynthesis enzymes?
Hormonal control?
Not feedback inhibition through starch accumulation

↓
Increased residual resistance to CO₂ fixation

↓
Increased CO₂ concentration in stomatal cavity?
Hormonal control?
Not leaf water stress.

↓
Increased stomatal resistance to CO₂ diffusion

↓
Reduced net photosynthesis rate per unit leaf area

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A P P E N D I C E S

A P P E N D I X I

Appendix I-1. Analysis of variance for seed yield and yield components in 1981.

Yield component	Source of variation	df	Mean square	f
Plant height	Replications	3	47.1	2.70
	Treatments	2	101.8	
	Error	6	37.6	
Internode length	Replications	3	0.132	5.00
	Treatments	2	0.375	
	Error	6	0.075	
Nodes/plant	Replications	3	0.665	5.31*
	Treatments	2	2.385	
	Error	6	0.449	
Branches/plant	Replications	3	0.831	0.52
	Treatments	2	0.150	
	Error	6	0.287	
Pods/plant	Replications	3	9115	1.73
	Treatments	2	2304	
	Error	6	1330	
Seeds/pod	Replications	3	0.012	0.50
	Treatments	2	0.014	
	Error	6	0.028	
Seeds/plant	Replications	3	30467	1.59
	Treatments	2	5946	
	Error	6	3720	
Seed size	Replications	3	38.29	18.47**
	Treatments	2	847.22	
	Error	6	45.85	
Seed yield	Replications	3	3.71	13.61**
	Treatments	2	52.54	
	Error	6	3.86	

*,** Significant at the 0.05 and 0.01 level, respectively.

Appendix I-2. Analysis of variance for seed yield and yield components in 1982.

Yield component	Source of variation	df	Mean square	F
Plant height	Replications	3	7.8	0.87
	Treatments	2	14.4	
	Error	6	16.5	
Internode length	Replications	3	0.039	0.55
	Treatments	2	0.053	
	Error	6	0.096	
Nodes/plant	Replications	3	1.41	1.36
	Treatments	2	1.02	
	Error	6	0.75	
Branches/plant	Replications	3	0.126	1.35
	Treatments	2	0.190	
	Error	6	0.140	
Pods/plant	Replications	3	26.4	0.42
	Treatments	2	35.5	
	Error	6	83.1	
Seeds/pod	Replications	3	0.0016	46.12**
	Treatments	2	0.1153	
	Error	6	0.0025	
Seeds/plant	Replications	3	118	0.29
	Treatments	2	124	
	Error	6	424	
Seed size	Replications	3	42.9	9.67*
	Treatments	2	462.6	
	Error	6	47.8	
Seed yield	Replications	3	6.54	17.23**
	Treatments	2	22.41	
	Error	6	1.30	

*,** Significant at the 0.05 and 1.01 level, respectively.

Appendix I-3. Number of pods per plant for each treatment on selected dates in 1981 and 1982.

Number of pods per plant								
1981				1982				
Days after emergence	Treatment			Days after emergence	Treatment			
	Check	16 c	24 c		Check	16 c	24 c	
No.				No.				
55	1	2	3	65	1	6	11	
69	8	30	43	72	4	26	46	
83	77	59	71	79	19	47	66	
97	92	87	78	86	56	89	83	
111	80	86	74	93	91	84	72	
				100	81	79	70	
				107	88	72	67	
				114	74	75	63	
				121	67	64	59	
				128	58	60	59	

A P P E N D I X I I

Appendix II-1. Quadratic polynomial exponential equations describing the relationship between cumulative dry matter production (DM; gm⁻²) and days after emergence (x), and the observed and predicted values for each treatment on selected dates in 1981.

Treatment	Equation	R ² value												
Check	$\ln DM = -0.34 + 0.130 x - 0.00056 x^2$	0.997												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>7</td> <td>4.64</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>16.21</td> </tr> <tr> <td>Error</td> <td>5</td> <td>0.015</td> </tr> </tbody> </table>	Source	df	Mean square	Total	7	4.64	Regression	2	16.21	Error	5	0.015	
Source	df	Mean square												
Total	7	4.64												
Regression	2	16.21												
Error	5	0.015												
16 c	$\ln DM = -0.68 + 0.150 x - 0.00073 x^2$	0.999												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>7</td> <td>4.81</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>16.84</td> </tr> <tr> <td>Error</td> <td>5</td> <td>0.016</td> </tr> </tbody> </table>	Source	df	Mean square	Total	7	4.81	Regression	2	16.84	Error	5	0.016	
Source	df	Mean square												
Total	7	4.81												
Regression	2	16.84												
Error	5	0.016												
24 c	$\ln DM = -0.47 + 0.143 x - 0.00069 x^2$	0.998												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>7</td> <td>4.47</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>15.62</td> </tr> <tr> <td>Error</td> <td>5</td> <td>0.012</td> </tr> </tbody> </table>	Source	df	Mean square	Total	7	4.47	Regression	2	15.62	Error	5	0.012	
Source	df	Mean square												
Total	7	4.47												
Regression	2	15.62												
Error	5	0.012												

Days after emergence	Observed DM check [†]	Predicted DM check	Observed DM 16 c [†]	Predicted DM 16 c	Observed DM 24 c	Predicted DM 24 c [†]
	g m ⁻²					
13	4	4	3	3	4	4
27	15	16	18	17	17	18
41	54	57	70	71	74	71
55	157	167	221	222	202	210
69	363	390	507	519	437	476
85	905	785	957	961	921	870
97	1274	1099	1265	1195	1171	1085
111	1145	1324	1146	1180	976	1092

[†]Average of four replications.

Appendix II-2. Quadratic polynomial exponential equations describing the relationship between cumulative dry matter production (DM; gm⁻²) and days after emergence (x), and the observed and predicted values for each treatment on selected dates in 1982.

Treatment	Equation	R ² value												
Check	$\ln DM = -0.95 + 0.127 x - 0.00051 x^2$	0.995												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>13</td> <td>2.39</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>15.47</td> </tr> <tr> <td>Error</td> <td>11</td> <td>0.011</td> </tr> </tbody> </table>	Source	df	Mean square	Total	13	2.39	Regression	2	15.47	Error	11	0.011	
Source	df	Mean square												
Total	13	2.39												
Regression	2	15.47												
Error	11	0.011												
16 c	$\ln DM + -1.21 + 0.139 x - 0.00058 x^2$	0.996												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>13</td> <td>2.44</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>15.86</td> </tr> <tr> <td>Error</td> <td>11</td> <td>0.009</td> </tr> </tbody> </table>	Source	df	Mean square	Total	13	2.44	Regression	2	15.86	Error	11	0.009	
Source	df	Mean square												
Total	13	2.44												
Regression	2	15.86												
Error	11	0.009												
24 c	$\ln DM + -1.34 + 0.147 x - 0.00066 x^2$	0.998												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>13</td> <td>2.19</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>14.21</td> </tr> <tr> <td>Error</td> <td>11</td> <td>0.004</td> </tr> </tbody> </table>	Source	df	Mean square	Total	13	2.19	Regression	2	14.21	Error	11	0.004	
Source	df	Mean square												
Total	13	2.19												
Regression	2	14.21												
Error	11	0.004												

Days after emergence	Observed [†] DM check	Predicted DM check	Observed [†] DM 16 c	Predicted DM 16 c	Observed [†] DM 24 c	Predicted DM 24 c
	g m ⁻²					
30	13	11	13	11	13	12
37	23	21	21	23	26	24
44	32	39	37	43	43	48
51	63	69	82	79	87	87
58	106	115	132	134	135	148
65	196	181	242	215	237	235
72	279	273	344	327	360	350
79	388	390	486	468	479	489
86	556	531	671	633	688	640
93	767	688	749	809	766	785
100	809	848	858	977	944	902
107	1095	994	1099	1114	1047	971
114	1088	1110	1286	1200	976	979
121	1078	1178	1232	1221	854	926

[†]Average of four replications.

Appendix II-3. Quadratic polynomial exponential equations describing the relationship between cumulative leaf area index (LAI) and days after emergence (x), and the observed and predicted values for each treatment on selected dates in 1981.

Treatment	Equation	R ² value												
Check	$\ln \text{LAI} = -5.59 + 0.163 x - 0.00088 x^2$	0.999												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>6</td> <td>2.19</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>5.48</td> </tr> <tr> <td>Error</td> <td>4</td> <td>0.002</td> </tr> </tbody> </table>	Source	df	Mean square	Total	6	2.19	Regression	2	5.48	Error	4	0.002	
Source	df	Mean square												
Total	6	2.19												
Regression	2	5.48												
Error	4	0.002												
16 c	$\ln \text{LAI} = -5.80 + 0.187 x - 0.00113 x^2$	0.994												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>5</td> <td>1.86</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>4.63</td> </tr> <tr> <td>Error</td> <td>3</td> <td>0.022</td> </tr> </tbody> </table>	Source	df	Mean square	Total	5	1.86	Regression	2	4.63	Error	3	0.022	
Source	df	Mean square												
Total	5	1.86												
Regression	2	4.63												
Error	3	0.022												
24 c	$\ln \text{LAI} = -5.48 + 0.175 x - 0.00106 x^2$	0.997												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>5</td> <td>1.57</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>3.91</td> </tr> <tr> <td>Error</td> <td>3</td> <td>0.008</td> </tr> </tbody> </table>	Source	df	Mean square	Total	5	1.57	Regression	2	3.91	Error	3	0.008	
Source	df	Mean square												
Total	5	1.57												
Regression	2	3.91												
Error	3	0.008												

Days after emergence	Observed LAI check [†]	Predicted LAI check	Observed LAI 16 c [†]	Predicted LAI 16 c	Observed LAI 24 c [†]	Predicted LAI 24 c
27	0.16	0.16	0.19	0.20	0.20	0.21
41	0.67	0.68	1.15	0.97	0.97	0.91
55	2.06	2.05	2.68	2.92	2.55	2.52
69	4.20	4.34	5.86	5.64	4.55	4.59
83	6.91	6.49	6.32	6.97	5.08	5.47
97	6.66	6.84	5.83	5.52	4.55	4.33
111	2.80	5.09	-	-	-	-

[†]Average of four replications.

Appendix II-4. Quadratic polynomial exponential equations describing the relationship between cumulative leaf area index (LAI) and days after emergence (x), and the observed and predicted values for each treatment on selected dates in 1982.

Treatment	Equation	R ² value
Check	$\ln \text{LAI} = -8.40 + 0.220 x - 0.00119 x^2$	0.959
	<u>Source</u>	<u>df</u> <u>Mean square</u>
	Total	13 1.75
	Regression	2 11.17
	Error	11 0.046
16 c	$\ln \text{LAI} = -8.43 + 0.233 x - 0.00133 x^2$	0.966
	<u>Source</u>	<u>df</u> <u>Mean square</u>
	Total	13 1.67
	Regression	2 10.76
	Error	11 0.025
24 c	$\ln \text{LAI} = -9.70 + 0.248 x - 0.00148 x^2$	0.900
	<u>Source</u>	<u>df</u> <u>Mean square</u>
	Total	13 2.10
	Regression	2 12.23
	Error	11 0.26

Days after emergence	Observed LAI check [†]	Predicted LAI check	Observed LAI 16c [†]	Predicted LAI 16c	Observed LAI 24c [†]	Predicted LAI 24c
44	0.37	0.36	0.48	0.40	0.58	0.52
51	0.76	0.76	1.01	1.05	1.09	1.10
58	1.53	1.43	1.89	2.22	1.95	2.02
65	2.34	2.40	3.10	3.84	2.93	3.20
72	3.61	3.59	4.45	5.44	4.52	4.38
79	4.13	4.77	5.61	6.30	4.40	5.19
86	5.11	5.63	6.21	5.97	4.92	5.31
93	6.12	5.93	6.03	4.62	4.60	4.70
100	5.16	5.55	5.15	2.93	4.51	3.60
107	5.74	4.63	3.86	1.52	4.03	2.38
114	4.99	3.43	2.54	0.64	0.84	1.36
121	1.57	2.26	1.47	0.22	0.09	0.67

[†]Average of four replications.

Appendix II-5. Quadratic polynomial exponential equations describing the relationship between cumulative leaf dry matter production (LDM; gm^{-2}) and days after emergence (x), and the observed and predicted values for each treatment on selected dates in 1981.

Treatment	Equation	R^2 value												
Check	$\ln \text{LDM} = -1.19 + 0.144 x - 0.000723 x^2$	0.995												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>5</td> <td>2.21</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>5.50</td> </tr> <tr> <td>Error</td> <td>3</td> <td>0.017</td> </tr> </tbody> </table>	Source	df	Mean square	Total	5	2.21	Regression	2	5.50	Error	3	0.017	
Source	df	Mean square												
Total	5	2.21												
Regression	2	5.50												
Error	3	0.017												
16 c	$\ln \text{LDM} = -1.49 + 0.169 x - 0.000998 x^2$	0.998												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>5</td> <td>1.75</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>4.36</td> </tr> <tr> <td>Error</td> <td>3</td> <td>0.004</td> </tr> </tbody> </table>	Source	df	Mean square	Total	5	1.75	Regression	2	4.36	Error	3	0.004	
Source	df	Mean square												
Total	5	1.75												
Regression	2	4.36												
Error	3	0.004												
24 c	$\ln \text{LDM} = -1.73 + 0.182 x - 0.001154 x^2$	0.988												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>5</td> <td>1.43</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>3.55</td> </tr> <tr> <td>Error</td> <td>3</td> <td>0.028</td> </tr> </tbody> </table>	Source	df	Mean square	Total	5	1.43	Regression	2	3.55	Error	3	0.028	
Source	df	Mean square												
Total	5	1.43												
Regression	2	3.55												
Error	3	0.028												

Days after emergence	Observed LDM check [†]	Predicted LDM check	Observed LDM 16 c [†]	Predicted LDM 16 c	Observed LDM 24 c [†]	Predicted LDM 24 c
	g m^{-2}					
27	9	9	11	11	11	10
41	36	34	45	44	46	44
55	91	96	118	125	106	121
69	184	206	236	239	196	208
83	396	333	338	308	287	228
97	381	406	257	269	143	159

[†]Average of four replications.

Appendix II-6. Quadratic polynomial exponential equations describing the relationship between cumulative leaf dry matter production (LDM; gm⁻²) and days after emergence (x), and the observed and predicted values for each treatment on selected dates in 1982.

Treatment	Equation	R ² value
Check	$\ln \text{LDM} = -2.32 + 0.163 x - 0.000805 x^2$	0.987
	<u>Source</u>	<u>df</u> <u>Mean square</u>
	Total	12 1.24
	Regression	2 7.37
	Error	10 0.018
16 c	$\ln \text{LDM} = -3.02 + 0.191 x - 0.001033 x^2$	0.988
	<u>Source</u>	<u>df</u> <u>Mean square</u>
	Total	12 1.03
	Regression	2 6.15
	Error	10 0.014
24 c	$\ln \text{LDM} = -4.32 + 0.241 x - 0.001445 x^2$	0.900
	<u>Source</u>	<u>df</u> <u>Mean square</u>
	Total	12 1.08
	Regression	2 5.88
	Error	10 0.129

Days after emergence	Observed LDM check †	Predicted LDM check	Observed LDM 16 c †	Predicted LDM 16 c	Observed LDM 24c †	Predicted LDM 24 c
	g m ⁻²					
37	17	14	15	14	19	14
44	23	27	28	30	31	33
51	46	50	59	58	63	67
58	75	85	92	101	93	121
65	146	133	177	159	178	188
72	192	194	235	226	226	255
79	264	259	307	291	261	299
86	338	322	351	337	301	304
93	409	368	320	354	259	269
100	336	389	281	335	259	206
107	400	381	299	287	240	137
115	389	337	267	212	108	72
122	243	278	130	146	17	36

†Average of four replications.

Appendix II-7. Quadratic polynomial exponential equations describing the relationship between cumulative stem dry matter production (TDM; gm⁻²) and days after emergence (x), and the observed and predicted values for each treatment on selected dates in 1981.

Treatment	Equation	R ² value												
Check	$\ln \text{TDM} = -2.62 + 0.171 x - 0.0008450 x^2$	0.996												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>6</td> <td>3.07</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>9.19</td> </tr> <tr> <td>Error</td> <td>4</td> <td>0.017</td> </tr> </tbody> </table>	Source	df	Mean square	Total	6	3.07	Regression	2	9.19	Error	4	0.017	
Source	df	Mean square												
Total	6	3.07												
Regression	2	9.19												
Error	4	0.017												
16 c	$\ln \text{TDM} = -2.77 + 0.188 x - 0.001021 x^2$	0.995												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>6</td> <td>2.68</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>8.02</td> </tr> <tr> <td>Error</td> <td>4</td> <td>0.018</td> </tr> </tbody> </table>	Source	df	Mean square	Total	6	2.68	Regression	2	8.02	Error	4	0.018	
Source	df	Mean square												
Total	6	2.68												
Regression	2	8.02												
Error	4	0.018												
24 c	$\ln \text{TDM} = -2.29 + 0.174 x - 0.000941 x^2$	0.995												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>6</td> <td>2.29</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>6.84</td> </tr> <tr> <td>Error</td> <td>4</td> <td>0.17</td> </tr> </tbody> </table>	Source	df	Mean square	Total	6	2.29	Regression	2	6.84	Error	4	0.17	
Source	df	Mean square												
Total	6	2.29												
Regression	2	6.84												
Error	4	0.17												

Days after emergence	Observed TDM check [†]	Predicted TDM check	Observed TDM 16c [†]	Predicted TDM 16c	Observed TDM 24c [†]	Predicted TDM 24c
	g m ⁻²					
27	4	4	5	5	5	6
41	18	20	25	26	28	26
55	68	69	101	93	95	85
69	156	174	241	222	190	190
83	287	314	349	357	279	295
97	396	406	314	384	269	316
111	360	376	312	277	264	234

[†]Average of four replications.

Appendix II-8. Quadratic polynomial exponential equations describing the relationship between cumulative stem dry matter production (TDM; gm⁻²) and days after emergence (x), and the observed and predicted values for each treatment on selected dates in 1982.

Treatment	Equation	R ² value												
Check	$\ln \text{TDM} = -3.52 + 0.167 x - 0.000801 x^2$	0.993												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>12</td> <td>1.51</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>9.05</td> </tr> <tr> <td>Error</td> <td>10</td> <td>0.012</td> </tr> </tbody> </table>	Source	df	Mean square	Total	12	1.51	Regression	2	9.05	Error	10	0.012	
Source	df	Mean square												
Total	12	1.51												
Regression	2	9.05												
Error	10	0.012												
16 c	$\ln \text{TDM} = -3.52 + 0.173 x - 0.000854 x^2$	0.982												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>12</td> <td>1.39</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>8.24</td> </tr> <tr> <td>Error</td> <td>10</td> <td>0.028</td> </tr> </tbody> </table>	Source	df	Mean square	Total	12	1.39	Regression	2	8.24	Error	10	0.028	
Source	df	Mean square												
Total	12	1.39												
Regression	2	8.24												
Error	10	0.028												
24 c	$\ln \text{TDM} = -3.05 + 0.165 x - 0.000848 x^2$	0.989												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>12</td> <td>1.05</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>6.25</td> </tr> <tr> <td>Error</td> <td>10</td> <td>0.013</td> </tr> </tbody> </table>	Source	df	Mean square	Total	12	1.05	Regression	2	6.25	Error	10	0.013	
Source	df	Mean square												
Total	12	1.05												
Regression	2	6.25												
Error	10	0.013												

Days after emergence	Observed TDM check [†]	Predicted TDM check	Observed TDM 16c [†]	Predicted TDM 16c	Observed TDM 24c [†]	Observed TDM 24c
	g m ⁻²					
37	6	5	6	6	7	7
44	9	10	9	12	13	14
51	17	19	23	22	23	25
58	31	33	40	39	42	41
65	50	54	65	62	63	64
72	86	82	103	92	110	90
79	117	113	145	125	125	118
86	158	145	184	157	155	141
93	188	172	156	181	130	156
100	175	189	147	192	139	159
107	212	191	157	187	135	148
115	164	176	176	164	136	124
122	146	151	158	134	103	97

[†]Average of four replications.

Appendix II-9. Quadratic polynomial exponential equations describing the relationship between cumulative pod dry matter production (PDM; gm⁻²) and days after emergence (x), and the observed and predicted values for each treatment on selected dates in 1981.

Treatment	Equation	R ² value												
Check	$\ln \text{PDM} = -11.04 + 0.276 - 0.00114 x^2$	0.973												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>6</td> <td>7.96</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>23.26</td> </tr> <tr> <td>Error</td> <td>4</td> <td>0.31</td> </tr> </tbody> </table>	Source	df	Mean square	Total	6	7.96	Regression	2	23.26	Error	4	0.31	
Source	df	Mean square												
Total	6	7.96												
Regression	2	23.26												
Error	4	0.31												
16 c	$\ln \text{PDM} = -12.06 + 0.326 - 0.00149 x^2$	0.990												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>6</td> <td>6.87</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>20.43</td> </tr> <tr> <td>Error</td> <td>4</td> <td>0.094</td> </tr> </tbody> </table>	Source	df	Mean square	Total	6	6.87	Regression	2	20.43	Error	4	0.094	
Source	df	Mean square												
Total	6	6.87												
Regression	2	20.43												
Error	4	0.094												
24 c	$\ln \text{PDM} = -6.48 + 0.226 - 0.00108 x^2$	0.989												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>5</td> <td>2.96</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>7.34</td> </tr> <tr> <td>Error</td> <td>3</td> <td>0.050</td> </tr> </tbody> </table>	Source	df	Mean square	Total	5	2.96	Regression	2	7.34	Error	3	0.050	
Source	df	Mean square												
Total	5	2.96												
Regression	2	7.34												
Error	3	0.050												

Days after emergence	Observed PDM check [†]	Predicted PDM check	Observed PDM 16c [†]	Predicted PDM 16c	Observed PDM 24c [†]	Predicted PDM 24c
	g m ⁻²					
41	0.24	0.20	0.24	0.30	2.4	2.7
55	2.4	2.08	6	4	18	15
69	5.6	14	26	29	62	54
83	77	60	136	116	96	129
97	277	163	205	258	225	199
111	287	286	270	320	209	201
125	261	320	264	221	-	-

[†]Average of four replications.

Appendix II-10. Quadratic polynomial exponential equations describing the relationship between cumulative pod dry matter production (PDM; gm⁻²) and days after emergence (x), and the observed and predicted values for each treatment on selected dates in 1982.

Treatment	Equation	R ² value												
Check	$\ln \text{PDM} = -41.45 + 0.864 x - 0.00395 x^2$	0.968												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>6</td> <td>1.82</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>5.31</td> </tr> <tr> <td>Error</td> <td>4</td> <td>0.087</td> </tr> </tbody> </table>	Source	df	Mean square	Total	6	1.82	Regression	2	5.31	Error	4	0.087	
Source	df	Mean square												
Total	6	1.82												
Regression	2	5.31												
Error	4	0.087												
16 c	$\ln \text{PDM} = -17.80 + 0.420 x - 0.00187 x^2$	0.959												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>8</td> <td>1.15</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>4.42</td> </tr> <tr> <td>Error</td> <td>6</td> <td>0.061</td> </tr> </tbody> </table>	Source	df	Mean square	Total	8	1.15	Regression	2	4.42	Error	6	0.061	
Source	df	Mean square												
Total	8	1.15												
Regression	2	4.42												
Error	6	0.061												
24 c	$\ln \text{PDM} = -15.85 + 0.408 x - 0.000194 x^2$	0.904												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>7</td> <td>0.60</td> </tr> <tr> <td>Regression</td> <td>5</td> <td>1.90</td> </tr> <tr> <td>Error</td> <td>2</td> <td>0.080</td> </tr> </tbody> </table>	Source	df	Mean square	Total	7	0.60	Regression	5	1.90	Error	2	0.080	
Source	df	Mean square												
Total	7	0.60												
Regression	5	1.90												
Error	2	0.080												

Days after emergence	Observed PDM check [†]	Predicted PDM check	Observed PDM 16c [†]	Predicted PDM 16c	Observed PDM 24c [†]	Predicted PDM 24c
	g.m ⁻²					
72	-	-	12	16	23	32
79	7	9	44	41	94	71
86	45	38	124	90	179	131
93	159	114	205	163	202	200
100	207	233	217	247	207	253
107	284	321	255	311	220	265
114	226	301	265	326	206	229
121	244	191	273	285	200	163
128	-	-	255	207	-	-

[†]Average of four replications.

Appendix II-11. Quadratic polynomial exponential equations describing the relationship between cumulative seed dry matter production (SDM; gm⁻²) and days after emergence (x), and the observed and predicted values for each treatment on selected dates in 1981.

Treatment	Equation	R ² value												
Check	$\ln \text{SDM} = -23.93 + 0.500 x - 0.002070 x^2$	0.988												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>5</td> <td>4.87</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>12.03</td> </tr> <tr> <td>Error</td> <td>3</td> <td>0.095</td> </tr> </tbody> </table>	Source	df	Mean square	Total	5	4.87	Regression	2	12.03	Error	3	0.095	
Source	df	Mean square												
Total	5	4.87												
Regression	2	12.03												
Error	3	0.095												
16 c	$\ln \text{SDM} = -21.08 + 0.479 x - 0.002084 x^2$	0.983												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>5</td> <td>8.86</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>21.79</td> </tr> <tr> <td>Error</td> <td>3</td> <td>0.24</td> </tr> </tbody> </table>	Source	df	Mean square	Total	5	8.86	Regression	2	21.79	Error	3	0.24	
Source	df	Mean square												
Total	5	8.86												
Regression	2	21.79												
Error	3	0.24												
24 c	$\ln \text{SDM} = -17.94 + 0.453 x - 0.002113 x^2$	0.998												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>5</td> <td>5.23</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>15.07</td> </tr> <tr> <td>Error</td> <td>3</td> <td>0.011</td> </tr> </tbody> </table>	Source	df	Mean square	Total	5	5.23	Regression	2	15.07	Error	3	0.011	
Source	df	Mean square												
Total	5	5.23												
Regression	2	15.07												
Error	3	0.011												

Days after emergence	Observed SDM check †	Predicted SDM check	Observed SDM 16c †	Predicted SDM 16c	Observed SDM 24c †	Predicted SDM 24c
	g m ⁻²					
55	-	-	0.5	0.4	2	2
69	2.4	2	4	8	24	28
83	18	28	95	78	192	178
97	218	164	456	336	524	499
111	454	434	600	639	582	611
118	-	-	-	-	500	495
125	463	511	500	538	-	-
130	456	445	-	-	-	-

†Average of four replications.

Appendix II-12. Quadratic polynomial exponential equations describing the relationship between cumulative seed dry matter production (SDM; g m⁻²) and days after emergence (x), and the observed and predicted values for each treatment on selected dates in 1982.

Treatment	Equation	R ² value												
Check	$\ln \text{SDM} = -45.27 + 0.819 x - 0.00325 x^2$	0.990												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>8</td> <td>6.5</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>26</td> </tr> <tr> <td>Error</td> <td>6</td> <td>0.079</td> </tr> </tbody> </table>	Source	df	Mean square	Total	8	6.5	Regression	2	26	Error	6	0.079	
Source	df	Mean square												
Total	8	6.5												
Regression	2	26												
Error	6	0.079												
16 c	$\ln \text{DSM} = -39.40 + 0.761 x - 0.00315 x^2$	0.995												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>7</td> <td>4</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>14</td> </tr> <tr> <td>Error</td> <td>5</td> <td>0.026</td> </tr> </tbody> </table>	Source	df	Mean square	Total	7	4	Regression	2	14	Error	5	0.026	
Source	df	Mean square												
Total	7	4												
Regression	2	14												
Error	5	0.026												
24 c	$\ln \text{SDM} = -26.37 + 0.56 x - 0.00239 x^2$	0.989												
	<table border="1"> <thead> <tr> <th>Source</th> <th>df</th> <th>Mean square</th> </tr> </thead> <tbody> <tr> <td>Total</td> <td>8</td> <td>3</td> </tr> <tr> <td>Regression</td> <td>2</td> <td>12</td> </tr> <tr> <td>Error</td> <td>6</td> <td>0.040</td> </tr> </tbody> </table>	Source	df	Mean square	Total	8	3	Regression	2	12	Error	6	0.040	
Source	df	Mean square												
Total	8	3												
Regression	2	12												
Error	6	0.040												

Days after emergence	Observed SDM check [†]	Predicted SDM check	Observed SDM 16c [†]	Predicted SDM 16c	Observed SDM 24c [†]	Predicted SDM 24c
	g m ⁻²					
72	-	-	-	-	4	4.9
79	0.46	0.42	3.2	2.9	28	20
86	3	3	12	16	53	63
93	10	16	69	63	175	159
100	92	61	214	184	340	317
107	200	167	390	393	471	500
114	307	336	577	617	550	623
121	444	491	672	711	575	614
128	460	521	632	602	540	479
135	450	401	-	-	-	-

[†]Average of four replications.

Appendix II-13. Calculated crop growth rate (CGR) for each treatment on selected dates in 1981 and 1982.

Crop growth rate (CGR)							
Days after emergence	1981			Days after emergence	1982		
	Check	16 c	24 c		Check	16 c	24 c
	— gm ⁻² day ⁻¹ —				— gm ⁻² day ⁻¹ —		
10	0.28	0.28	0.32	30	1.12	1.43	1.32
20	0.73	0.94	0.97	37	1.94	2.30	2.40
30	1.81	2.58	2.55	44	3.17	3.96	4.32
40	4.13	6.09	5.79	51	5.54	6.32	6.96
50	8.68	11.98	11.05	58	8.05	9.38	10.36
60	15.86	19.62	17.74	65	10.90	12.90	14.10
70	24.59	26.73	23.50	72	13.65	19.62	17.50
80	30.62	28.07	25.46	79	19.50	23.40	19.56
90	27.35	21.60	19.55	86	21.24	25.32	19.20
100	10.96	6.10	6.67	93	20.64	24.27	18.05
110	-12.14	-11.92	- 8.81	100	19.50	19.54	18.04
				107	19.43	13.36	9.71
				114	11.10	12.00	0.01
				121	4.71	1.22	-
				128	0.5	-	-

Appendix II-14. Calculated net assimilation rate (NAR) for each treatment on selected dates in 1981 and 1982.

Calculated net assimilation rate (NAR)							
1981				1982			
Days after emergence	Treatment			Days after emergence	Treatment		
	Check	16 c	24 c		Check	16 c	24 c
— gm ⁻² day ⁻¹ —				— gm ⁻² day ⁻¹ —			
10	14.10	14.35	15.95	44	9.13	8.03	8.26
20	10.45	11.71	10.81	51	6.90	6.18	6.33
30	7.85	8.61	8.51	58	5.51	5.07	5.18
40	6.56	6.85	6.98	65	4.66	4.41	4.52
50	6.02	5.76	6.00	72	4.15	4.06	4.18
60	5.66	5.03	5.41	79	3.89	3.94	4.05
70	5.42	4.59	4.98	86	3.81	3.98	4.06
80	4.99	4.06	4.64	93	3.87	4.15	4.08
90	3.92	3.29	3.80	100	4.01	4.32	3.80
100	1.66	1.23	1.71	107	4.25	4.23	2.40
110	-2.30	-3.99	-3.69	114	3.90	3.12	-
				121	2.5	-	-

Appendix II-15. Calculated leaf growth rate (LGR) for each treatment on selected dates in 1981 and 1982.

Calculated leaf growth rate (LGR)							
1981				1982			
Days after emergence	Treatment			Days after emergence	Treatment		
	Check	16 c	24 c		Check	16 c	24 c
— gm ⁻² day ⁻¹ —				— gm ⁻² day ⁻¹ —			
20	0.46	0.58	0.58	37	1.42	1.63	1.83
30	1.31	1.64	1.66	44	2.52	3.05	3.71
40	2.67	3.65	3.65	51	4.06	5.03	6.31
50	4.89	6.32	5.95	58	5.95	7.28	8.88
60	7.53	8.24	6.78	65	7.84	9.14	10.01
70	9.24	7.39	4.24	72	9.19	9.72	8.38
80	8.92	3.01	-0.69	79	9.40	8.27	3.78
90	5.34	-3.01	-	86	8.03	4.72	0.00
100	-0.11	-	-	93	5.04	0.00	-
				100	0.95	-	-

Appendix II-16. Calculated stem growth rate (StGR) for each treatment on selected dates in 1981 and 1982.

Calculated stem growth rate (StGR)							
1981				1982			
Days after emergence	Treatment			Days after emergence	Treatment		
	Check	16 c	24 c		Check	16 c	24 c
— gm ⁻² day ⁻¹ —				— gm ⁻² day ⁻¹ —			
20	0.21	0.27	0.30	37	0.53	0.61	0.71
30	0.69	0.92	0.94	44	0.97	1.13	1.24
40	1.81	2.49	2.35	51	1.64	1.89	1.96
50	3.92	5.35	4.63	58	2.50	2.85	2.79
60	6.86	8.77	7.19	65	3.45	3.86	3.54
70	9.51	10.67	8.51	72	4.27	4.62	3.95
80	10.35	8.67	6.60	79	4.65	4.79	3.76
90	6.70	1.93	1.60	86	4.34	4.14	2.83
100	0.41	-5.53	-4.25	93	3.22	2.60	1.28
110	-6.12	-	-	100	1.41	0.46	-0.57

Appendix II-17. Calculated pod growth rate (PGR) for each treatment on selected dates in 1981 and 1982.

Calculated pod growth rate (PGR)							
1981				1982			
Days after emergence	Treatment			Days after emergence	Treatment		
	Check	16 c	24 c		Check	16 c	24 c
— gm ⁻² day ⁻¹ —				— gm ⁻² day ⁻¹ —			
40	0.03	0.05	0.32	65	0.04	0.08	0.15
50	0.15	0.30	1.00	72	0.46	2.36	4.08
60	0.60	0.98	2.40	79	2.07	5.11	7.19
70	1.83	3.80	4.40	86	7.04	8.82	9.73
80	4.28	7.83	5.89	93	14.75	11.78	9.39
90	7.53	10.54	5.24	100	17.16	11.38	5.01
100	9.34	7.68	1.86	107	5.92	6.21	-0.14
110	7.25	-0.96	-2.44	114	-8.07	-0.11	-
120	1.29	-	-				

Appendix II-18. Calculated seed growth rate (SGR) for each treatment on selected dates in 1981 and 1982.

Calculated seed growth rate (SGR)							
1981				1982			
Days after emergence	Treatment			Days after emergence	Treatment		
	Check	16 c	24 c		Check	16 c	24 c
— gm ⁻² day ⁻¹ —				— gm ⁻² day ⁻¹ —			
50	-	-	0.14	72	-	-	1.06
60	0.06	0.28	1.09	79	0.13	0.79	3.61
70	0.53	1.81	5.15	86	0.78	3.47	9.39
80	2.85	7.48	14.85	93	3.40	11.01	18.35
90	9.48	18.68	24.34	100	10.17	23.99	25.94
100	18.64	25.88	17.53	107	20.49	34.00	24.13
110	18.62	13.18	-	114	25.84	26.87	9.17
120	1.75	-	-	121	15.35	0.00	-11.56
				128	-7.46	-	-

Appendix II-19. Analysis of variance for the ratios of final seed dry weight to the maximum dry weight accumulated in other plant components in 1981 and 1982.

Year	Trait	Source of variation	df	Mean square	F
1981	<u>Seed wt.</u> Leaf wt. + stem wt.	Replications	3	0.013	12.1**
		Treatments	2	0.121	
		Error	6	0.010	
	<u>Seed wt.</u> Pod wt.	Replications	3	0.060	83.26**
		Treatments	2	0.816	
		Error	6	0.0098	
	<u>Seed wt.</u> Total wt. - seed wt.	Replications	3	0.0029	9.75*
		Treatments	2	0.0527	
		Error	6	0.0054	
	<u>Seed wt.</u> Total wt.	Replications	3	0.0029	6.13*
		Treatments	2	0.0141	
		Error	6	0.0023	
1982	<u>Seed wt.</u> Leaf wt. + stem wt.	Replications	3	0.035	13.91**
		Treatments	2	0.668	
		Error	6	0.048	
	<u>Seed wt.</u> Pod wt.	Replications	3	0.143	6.21*
		Treatments	2	0.236	
		Error	6	0.038	
	<u>Seed wt.</u> Total wt - seed wt.	Replications	3	0.193	14.75**
		Treatments	2	0.236	
		Error	6	0.016	
	<u>Seed wt.</u> Total wt.	Replications	3	0.0011	5.63**
		Treatments	2	0.0107	
		Error	6	0.0019	

*, ** Significant at the 0.05 and 0.01 level, respectively.

A P P E N D I X I I I

Appendix III-1. Diurnal measurement of CO₂ exchange rate[†] for each treatment on selected dates in 1981.

Date	Time (hours)	Treatment		
		Check	16 c	24 c
		————— $\mu\text{ mol m}^{-2} \text{ s}^{-1}$ —————		
30 July	0700	12.34	14.72	11.88
	0930	19.41	18.31	21.22
	1200	21.48	22.69	23.43
	1450	21.15	21.65	21.26
	1700	20.57	19.51	19.89
	1950	11.20	13.17	10.59
	14 August	0700	13.70	14.44
0930		13.80	20.23	19.52
1200		17.33	18.76	18.93
1450		18.16	16.98	21.25
1700		9.20	8.30	9.15
1950		4.46	3.57	6.03
27 August		0700	6.19	11.67
	0930	17.20	18.90	20.89
	1200	12.10	13.78	16.15
	1450	16.23	16.31	15.23
	1700	13.63	11.62	15.02
	1950	6.17	6.88	9.23

[†]Average of four replications.

Appendix III-2. Diurnal measurement of stomatal diffusive resistance[†] for each treatment on selected dates in 1981.

Date	Time (hours)	Treatment		
		Check	16 c	24 c
		$s\ m^{-2}$		
30 July	0700	102	120	152
	0930	63	78	54
	1200	46	44	46
	1450	56	44	46
	1700	64	71	76
	1950	124	150	141
14 August	0700	110	150	206
	0930	69	51	46
	1200	70	43	51
	1450	84	77	86
	1700	185	148	107
	1950	254	364	291
27 August	0700	142	173	191
	0930	100	78	66
	1200	220	245	98
	1450	156	156	105
	1700	195	170	191
	1950	333	412	265

[†]Average of four replications.

Appendix III-3. Diurnal measurement of transpiration rate[†] for each treatment on selected dates in 1981.

Date	Time (hours)	Treatment		
		Check	16 c	24 c
		m mol m ⁻² s ⁻¹		
30 July	0700	2.24	1.94	1.45
	0930	6.89	5.08	5.59
	1200	11.11	10.67	11.37
	1450	13.09	15.91	14.75
	1700	11.49	10.36	9.81
	1950	5.22	4.11	4.65
14 August	0700	1.55	2.02	1.04
	0930	4.95	6.52	6.75
	1200	14.59	18.69	16.28
	1450	13.04	14.88	12.75
	1700	4.37	7.00	8.67
	1950	3.60	2.74	2.84
27 August	0700	2.48	2.39	1.42
	0930	4.66	5.97	6.72
	1200	4.47	5.10	9.25
	1450	7.57	6.93	9.67
	1700	5.94	6.71	6.59
	1950	3.04	2.38	3.67

†Average of four replications.

Appendix III-4. Diurnal measurement of CO₂ exchange rate[†] for each treatment on selected dates in 1982.

Date	Time (hours)	Treatment		
		Check	16 c	24 c
————— $\mu \text{ mol m}^{-2} \text{ s}^{-1}$ —————				
19 July	0730	17.15	16.55	23.37
	0900	20.81	27.86	29.71
	1130	27.65	24.86	27.86
	1300	21.82	23.91	25.05
	1430	24.48	26.22	25.28
	1600	23.55	26.50	22.50
	1730	19.91	22.82	19.58
	1900	18.38	15.36	20.47
4 August	0730	12.87	18.38	16.09
	0900	12.17	18.98	22.16
	1130	15.89	14.21	19.94
	1300	17.97	16.77	17.18
	1430	10.88	15.87	15.33
	1600	9.27	15.76	9.44
	1730	12.93	8.35	11.81
	1900	5.52	6.60	7.28
17 August	0730	13.86	17.61	20.17
	0900	12.90	20.61	22.50
	1130	7.23	15.30	23.96
	1300	12.46	12.98	18.82
	1430	6.61	9.00	21.22
	1600	8.92	10.48	15.36
	1730	7.43	8.07	12.52
	1900	5.46	5.18	8.82

[†]Average of four replications.

Appendix III-5. Diurnal measurement of stomatal diffusive resistance[†] for each treatment on selected dates in 1982.

Date	Time (hours)	Treatment		
		Check	16 c	24 c
		s m ⁻²		
19 July	0730	32	21	21
	0900	23	18	18
	1130	17	16	15
	1300	15	19	14
	1430	18	15	17
	1600	15	23	17
	1730	37	37	30
	1900	31	61	53
4 August	0730	90	86	42
	0900	64	27	43
	1130	59	91	44
	1300	62	58	69
	1430	69	96	70
	1600	160	113	58
	1730	128	173	99
	1900	194	160	196
17 August	0730	163	100	164
	0900	261	109	113
	1130	254	115	88
	1300	194	228	154
	1430	448	328	160
	1600	221	287	167
	1730	385	178	124
	1900	370	814	357

[†]Average of four replications.

Appendix III-6. Diurnal measurement of transpiration rate[†] for each treatment on selected dates in 1982.

Date	Time (hours)	Treatment		
		Check	16 c	24 c
		m mol m ⁻² s ⁻¹		
19 July	0730	10.57	11.97	12.90
	0900	14.83	15.44	16.04
	1130	26.39	23.61	23.76
	1300	26.95	26.89	30.81
	1430	32.49	33.00	32.24
	1600	38.55	31.27	35.52
	1730	29.85	25.90	31.80
	1900	18.26	17.40	20.93
4 August	0730	3.13	6.75	4.70
	0900	5.21	9.99	10.83
	1130	9.36	6.28	10.44
	1300	11.54	10.57	10.36
	1430	13.54	23.83	12.52
	1600	9.29	11.87	16.10
	1730	7.32	5.23	8.03
	1900	4.55	6.13	4.34
17 August	0730	1.51	2.24	1.45
	0900	1.76	3.64	3.92
	1130	3.70	6.36	8.15
	1300	5.74	5.32	8.07
	1430	4.05	4.80	8.10
	1600	5.93	4.81	9.54
	1730	3.66	6.32	7.68
	1900	8.72	1.24	3.10

[†]Average of four replications.

Appendix III-7. Analysis of variance for CO₂ exchange rate
in 1981 and 1982.

Source of variation	df	Mean square	F
<u>1981</u>			
Rep	3	13.32	
Trmt	2	43.47	4.01
Error A	6	10.83	
Date	2	525.92	51.07**
Date x Trmt	4	6.83	0.66
Error B	18	10.28	
Time	5	724.04	79.43**
Time x Trmt	10	12.89	1.41
Time x Date	10	81.41	8.93**
Time x Date x Trmt	20	7.76	0.85
Error C	135	9.15	
<u>1982</u>			
Rep	3	43.23	
Trmt	2	507.41	15.18**
Error A	6	33.42	
Date	2	2873.02	57.95**
Date x Trmt	4	106.03	2.13
Error B	18	49.56	
Time	7	413.14	18.89**
Time x Trmt	14	40.02	1.83
Time x Date	14	51.07	2.35
Time x Date x Trmt	28	22.85	1.04
Error C	189	21.86	

**Significant at 0.01 level

LSD for treatment means at 0.05 level:

within times in 1981 = 2.41

within dates in 1981 = 1.81

within times in 1982 = 3.74

within dates in 1982 = 3.44

Appendix III-8. Analysis of variance for stomatal diffusive resistance in 1981 and 1982.

Source of variation	df	Mean square	F
<u>1981</u>			
Rep	3	5572	
Trmt	2	7177	0.80
Error A	6	8915	
Date	2	184226	48.89**
Date x Trmt	4	6178	1.64
Error B	18	3767	
Time	5	1715	36.29**
Time x Trmt	10	8148	1.72
Time x Date	10	6178	4.29**
Time x Date x Trmt	20	2759	0.58
Error C	135	4725	
<u>1982</u>			
Rep	3	26522	
Trmt	2	68720	5.53*
Error A	6	12424	
Date	2	1173750	84.96
Date x Trmt	4	37485	2.71
Error B	18	13813	
Time	7	119140	15.38**
Time x Trmt	14	16590	2.14*
Time x Date	14	44846	5.79**
Time x Date x Trmt	28	20316	2.62**
Error C	189	7742	

*,**Significant at 0.05 and 0.01 level, respectively.

LSD for treatment means at 0.05 level:

within times in 1981 = 55.0

within dates in 1981 = 34.7

within times in 1982 = 67.0

within dates in 1982 = 57.2

Appendix III-9. Analysis of variance for transpiration rate
in 1981 and 1982.

Source of variation	df	Mean square	F
<u>1981</u>			
Rep	3	2.62	
Trmt	2	9.90	6.97*
Error A	6	1.41	
Date	2	179.02	33.45**
Date x Trmt	4	11.91	2.22
Error B	18	5.35	
Time	5	606.27	136.39**
Time x Trmt	10	4.57	1.02
Time x Date	10	72.08	16.21**
Time x Date x Trmt	20	5.17	1.12
Error C	135	4.44	
<u>1982</u>			
Rep	3	30.29	
Trmt	2	59.21	2.78
Error A	6	21.24	
Date	2	100705.00	412.95**
Date x Trmt	4	31.27	1.28
Error B	18	24.38	
Time	7	693.56	32.08**
Time x Trmt	14	23.92	1.10
Time x Date	14	185.78	8.59**
Time x Date x Trmt	28	20.96	0.97
Error C	189	21.24	

*,**Significant at 0.05 and 0.01 level, respectively.

LSD for treatment means at 0.05 level:

within times in 1981 = 26.0

within dates in 1981 = 23.5

within times in 1982 = 67.0

within dates in 1982 = 57.0

Appendix III-10. Analysis of variance for starch content of leaves sampled in the morning of selected dates in 1981.

Date	Source of variation	df	Mean square	F
30 July	Replications	3	0.0675	2.43
	Treatments	2	0.1829	
	Error	6	0.0752	
14 August	Replications	3	0.0018	47.31**
	Treatments	2	0.1832	
	Error	6	0.0032	
27 August	Replications	3	0.0399	10.34**
	Treatments	2	0.0837	
	Error	6	0.0080	

**Significant at 0.01 level.

Appendix III-11. Diurnal measurement of leaf water potential (ψ)[†] for each treatment on selected dates in 1981.

Date	Time (hours)	Treatment		
		Check	16 C	24 c
		M Pa		
30 July	0700	-0.20	-0.24	-0.21
	0930	-0.63	-0.64	-0.58
	1200	-0.97	-1.00	-0.99
	1450	-1.00	-1.05	-0.99
	1700	-0.84	-0.67	-0.85
	1950	-0.49	-0.46	-0.39
14 August	0700	-0.20	-0.26	-0.24
	0930	-0.62	-0.68	-0.82
	1200	-1.16	-1.19	-1.31
	1450	-1.25	-1.21	-1.31
	1700	-1.06	-1.18	-1.67
	1950	-0.69	-0.80	-0.84
27 August	0700	-0.13	-0.19	-0.23
	0930	-0.64	-0.81	-0.89
	1200	-1.07	-1.09	-1.032
	1450	-1.27	-1.14	-1.20
	1700	-1.02	-1.13	-1.23
	1950	-0.83	-0.91	-0.99

[†]Average of four replications.

Appendix III-12. Diurnal measurement of leaf osmotic potential (Ψ_{11})[†] for each treatment on selected dates in 1981.

Date	Time (hours)	Treatment		
		Check	16 c	24 c
— M Pa —				
30 July	0700	-1.14	-1.07	-1.10
	0930	-1.26	-1.18	-1.14
	1200	-1.30	-1.24	-1.16
	1450	-1.32	-1.30	-1.30
	1700	-1.37	-1.31	-1.42
	1950	-1.37	-1.39	-1.31
14 August	0700	-0.95	-1.03	-1.09
	0930	-1.07	-1.15	-1.16
	1200	-1.24	-1.24	-1.35
	1450	-1.34	-1.34	-1.44
	1700	-1.27	-1.25	-1.29
	1950	-1.15	-1.19	-1.22
27 August	0700	-0.83	-0.92	-0.95
	0930	-1.09	-1.07	-1.12
	1200	-1.31	-1.24	-1.39
	1450	-1.36	-1.41	-1.40
	1700	-1.28	-1.25	-1.29
	1950	-1.26	-1.18	-1.16

[†]Average of four replications.

Appendix III-13. Diurnal measurement of leaf turgor potential (ψ_p)[†] for each treatment on selected dates in 1981.

Date	Time (hours)	Treatment		
		Check	16 c	24 c
		M Pa		
30 July	0700	0.95	0.83	0.89
	0930	0.60	0.54	0.56
	1200	0.33	0.24	0.16
	1450	0.32	0.25	0.29
	1700	0.54	0.64	0.58
	1950	0.89	0.94	0.92
14 August	0700	0.75	0.77	0.85
	0930	0.45	0.47	0.34
	1200	0.08	0.10	0.05
	1450	0.09	0.12	0.13
	1700	0.21	0.07	0.13
	1950	0.46	0.39	0.38
27 August	0700	0.70	0.73	0.72
	0930	0.44	0.25	0.25
	1200	0.25	0.15	0.08
	1450	0.09	0.26	0.20
	1700	0.26	0.12	0.06
	1950	0.43	0.27	0.17

[†]Average of four replications.

Appendix III-14. Analysis of variance for leaf water potential (ψ) in 1981.

Source of variation	df	Mean square	F
Rep	3	0.0037	
Trmt	2	0.12	10.0*
Error A	6	0.012	
Date	2	1.09	75.85**
Date x Trmt	4	0.048	3.34*
Error B	18	0.014	
Time	5	4.59	299.66**
Time x Trmt	10	0.014	0.94
Time x Date	10	0.105	6.91**
Time x Date x Trmt	20	0.013	0.85
Error C	135	0.015	

*,**Significant at 0.05 and 0.01 level, respectively.

LSD for the treatment means at 0.05 level:

within times = 0.100

within dates = 0.018

Appendix III-15. Analysis of variance for leaf osmotic potential (ψ_H) in 1981.

Source of variation	df	Mean square	F
Rep	3	2.44	
Trmt	2	1.17	0.50
Error A	6	3.39	
Date	2	7.67	7.74**
Date x Trmt	4	3.11	3.14
Error B	18	0.99	
Time	5	58.93	61.46**
Time x Trmt	10	0.64	0.67
Time x Date	10	5.26	5.48**
Time x Date x Trmt	20	0.68	0.71
Error C	135	0.95	

**Significant at 0.01 level.

LSD for the treatment means at 0.05 level:

within times = 0.78

within dates = 0.60

Appendix III-16. Analysis of variance for leaf turgor potential (ψ_p) in 1981.

Source of variation	df	Mean square	F
Rep	3	1.03	
Trmt	2	6.70	4.70
Error A	6	1.42	
Date	2	173.78	139.84**
Date x Trmt	4	1.46	1.18
Error B	18	1.24	
Time	5	208.70	142.00**
Time x Trmt	10	1.82	1.24
Time x Date	10	16.62	11.32**
Time x Date x Trmt	20	1.71	1.16
Error C	135	1.46	

**Significant at 0.01 level.

LSD for the treatment means at 0.05 level:

within times = 0.96

within dates = 0.39