# INTERACTION OF TEMPERATURE AND $CO_2$ ENRICHMENT ON SOYBEAN: PHOTOSYNTHESIS AND SEED YIELD

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Seed yield and photosynthetic responses of soybean (*Glycine max* L. Merr. 'Ransom') were studied in growth chambers at day/night temperatures of 18/12, 22/16, and 26/20°C and atmospheric $CO_2$ concentrations of 350, 675 and 1000 $\mu$L L$^{-1}$. No seeds were produced at 18/12°C within any of the $CO_2$ concentrations. Numbers of pods and seeds increased with increasing temperature and $CO_2$ levels. Carbon dioxide enrichment increased seed yield of soybean grown at moderately cool temperatures. This increase was associated with an increase in net photosynthetic rate. Leaf photosynthesis in response to $CO_2$ enrichment increased more at 22/16°C than at 26/20°C. Increases in temperature and $CO_2$ levels enhanced total growth of plants but hastened senescence of leaves. The extended photosynthetic capacity at cool temperatures did not result in allocating more dry matter to developing pods. $CO_2$ enrichment at 26/20°C resulted in greater seed yield increases than $CO_2$ enrichment at lower temperatures.

Key words: Soybean yield, low temperature, $CO_2$ × temperature

[Effets d'une interaction entre la température et la teneur en $CO_2$ sur la photosynthèse et le rendement grainier du soja.]
Titre abrégé: Effets du $CO_2$ et de la température sur le soja.
Nous avons étudié les variations du rendement grainier et de la photosynthèse du soja (*Glycine max* L. Merr. 'Ransom') dans des chambres de croissance à des températures (jour/nuit) de 18/12, 22/16 et 26/20°C et à des teneurs en $CO_2$ de l'atmosphère de 350, 675 et 1 000 $\mu$L L$^{-1}$. Aucune semence n'a été produite à 18/12°C aux teneurs en $CO_2$ testées. Le nombre de gousses et de semences a augmenté en même temps que la température et les teneurs en $CO_2$. L'enrichissement en $CO_2$ a provoqué une hausse du rendement grainier du soja cultivé à des températures modérément fraîches. Cette hausse est attribuable à une augmentation du taux net de photosynthèse. L'augmentation de la photosynthèse des feuilles avec l'enrichissement en $CO_2$ a été plus rapide à 22/16°C qu'à 26/20°C. Les hausses de la température et de la teneur en $CO_2$ ont favorisé la croissance des plantes mais hâté la sénescence des feuilles. La capacité accrue de photosynthèse aux températures fraîches n'a pas provoqué d'augmentation de la proportion de la matière sèche contenue dans les gousses en développement. L'enrichissement en $CO_2$ à 26/20°C a donné une augmentation plus importante du rendement grainier que l'enrichissement en $CO_2$ aux températures plus basses.

Mots clés: Rendement du soja, basse température, $CO_2$ × température

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Productivity of seed crops is a function of total photosynthate produced by the source and proportion of the assimilate allocated to reproductive sinks (Kramer 1981). Variability in yield among crop species and cultivars of the same species is due to genetic potential and environmental conditions (Boyer 1982). Environmental factors have been shown to affect the processes of both photosynthesis and dry matter allocation in plants. For example, $CO_2$ concentration in the atmosphere (Kimball 1983; Strain 1985) and temperature regime (Patterson and Flint 1979) are two important factors that regulate gas exchange and growth rates in plants. Net photosynthesis increases while stomatal conductance decreases in leaves with increases in atmospheric $CO_2$ concentration (Allen et al. 1981; Strain and Armentano 1982; Rogers et al. 1983; Sionit et al. 1984; Jones et al. 1985a,b; Valle et al. 1985). Thomas and Raper (1978), and Seddigh and Jolliff (1984) have shown that temperature regime has a significant effect on net $CO_2$ exchange rate of leaves, carbohydrate allocation, and yield of soybean.

Most previous investigations on the effects of atmospheric $CO_2$ enrichment have given little attention to the possible interactions between $CO_2$ and temperature. The vigor and productivity of okra (*Abelmoschus esculentus*) at low temperatures, however, has been shown (Sionit et al. 1981) to be greater when atmospheric $CO_2$ is enriched. The present study was undertaken to analyze the combined effects of increasing atmospheric $CO_2$ concentration and temperature regimes on photosynthesis and production of soybean.

## MATERIALS AND METHODS

Soybean (*Glycine max* (L.) Merr. 'Ransom') seeds were germinated in a 1:1:1 (by volume) mixture of gravel:vermiculite:Turface (Jaeger et al. 1981) in 3.5-L plastic pots and grown in controlled environment chambers of the Duke University Phytotron (Kramer et al. 1970). Ransom is a determinate, maturity group VII, cultivar that is widely planted in the southeastern U.S.A. There was one plant in each pot and the pots were watered to the drip point three times every day with modified half-strength Hoagland's solution (Downs and Hellmers 1978). The photoperiod was 12 h. For the 3-wk flower induction period from 21 to 41 d after planting the photoperiod was 9 h. A combination of fluorescent and incandescent lamps at an input wattage ratio of 15:4 provided a photosynthetic photon flux density of $550 \pm 50$ $\mu$mol $m^{-2}$ $s^{-1}$, as measured with a LiCor Quantum sensor at the top of the plant canopy in the chambers. The relative humidity was 70% during the day and close to saturation at night. The day/night temperature regimes were 18/12, 22/16, and 26/20°C. Carbon dioxide was injected into the chambers automatically and its concentration monitored continuously by an infrared gas analyzer (Hellmers and Giles 1979). The injection system provided $CO_2$ concentrations of $350 \pm 40$, $675 \pm 30$, or $1000 \pm 45$ $\mu$L $L^{-1}$ in three different chambers at each temperature regime.

Eight plants were harvested at each of the three $CO_2$ and three temperature environments at 20, 40, 67 and 115 (late senescence to maturity) days after planting for dry weight and leaf area determinations. Numbers of pods and seeds were determined and dry weights of seed per plant and per seed were obtained after drying at 65°C to constant weight. Net assimilation rate (NAR), which is the amount of dry matter produced per unit leaf area per unit time (g $m^{-2}$ $d^{-1}$), was calculated for the harvest intervals of 20–40 and 40–67 d. Net photosynthetic rate and stomatal conductance measurements were made in the respective chambers on four plants on the middle leaflet of the third or fourth trifoliolate leaves from the top of the main stem with a steady state minicuvette system developed by Bingham et al. (1980). Vapor pressure deficit in the cuvette was controlled and maintained at $8.0 \pm 0.15$ g $m^{-3}$ in all measurements. The plants were at early- to late-flowering stage, stages $R_1$ to $R_4$ (Fehr and Caviness 1977), during the measurements. No photosynthetic measurement was made at 18/12°C because of technical difficulties. A two-way analysis of variance was used for $CO_2$ and temperature to determine differences among treatments.

## RESULTS AND DISCUSSION

The number of pods per plant increased with increasing day/night temperature regime from 18/12°C to 26/20°C and increased $CO_2$ concentration from 350 to 675 $\mu$L $L^{-1}$ (Table 1). Further increase in $CO_2$ concentration to 1000 $\mu$L $L^{-1}$ produced little or no

Table 1. Pods per plant of soybean grown at three $CO_2$ concentrations and three day/night temperature regimes

| $CO_2$ Concentration ($\mu L\ L^{-1}$) | Day/night temperature (°C) | | |
|---|---|---|---|
| | 18/12 | 22/16 | 26/20 |
| 350 | 43.9 | 86.4 | 121.6 |
| 675 | 55.6 | 95.4 | 170.0 |
| 1000 | 50.1 | 115.9 | 168.9 |
| *Source of variation* | | | |
| $CO_2$ | ** | | |
| Temp. | ** | | |
| $CO_2$ × Temp. | * | | |

*,**$P<0.05$ and $P<0.01$, respectively.

additional increase in number of pods at all temperatures. Greater increases in number of pods per plant were observed in response to $CO_2$ enrichment from 350 $\mu L\ L^{-1}$ to 675 $\mu L\ L^{-1}$ at high temperatures than at low temperatures. The temperature × $CO_2$ interaction for pod production was statistically significant (Table 1). Seddigh and Jolliff (1984) reported that pod production in a field-grown indeterminate soybean cultivar was increased during the early reproductive stage by warmer night temperatures (24°C as compared to 16 or 10°C), but due to differences in rates of pod abortion the final number of pods at maturity was not affected by warm night temperatures. Thomas and Raper (1978) recorded a two-fold increase in pod number of a phytotron-grown determinate soybean cultivar by increasing night temperature from 14°C to 18°C at day temperature of 22°C. In another study, Thomas and Raper (1976) reported that increasing pod production at 30/26°C was dependent upon the number of consecutive short-day photoperiods and morphological development stage at floral induction. Carbon dioxide treatment complicated the temperature effect on pod production because it produced differences in the size of plants at flower induction (Sionit et al. 1987). This plus the direct effect of $CO_2$ enrichment on subsequent growth (Sionit et al. 1987) resulted in more branches and more nodes on the main stem, causing a greater potential for pod production.

All pods produced at 18/12°C in each of the $CO_2$ treatments were small, parthenocarpic and abnormal in shape. No seeds were developed in these pods; however, $CO_2$ enrichment up to 675 $\mu L\ L^{-1}$ increased the number of pods. Such a cold-induced pod abnormality in soybean has been observed by Thomas and Raper (1981) at 18/18°C and 22/14°C and by Lawn and Hume (1985) at 20/12°C and at 20/8°C. The physiological basis for production of abnormal pods at cool temperatures has partly been investigated. Thomas and Raper (1981) proposed that the events occurring during floral development were responsible for abnormal pods because successive development after floral initiation seemed to have "increasingly stricter temperature requirements". Lawn and Hume (1985) found that absence of normal pod set at low night temperatures in several soybean lines of temperate and tropical origins was related to reduction in pollen formation and reduced pollen vigor resulting in curled and distorted pollen tubes.

Sionit et al. (1981), in a phytotron study, observed that $CO_2$ enrichment at suboptimal temperature of 20/14°C compensated for the adverse effect of cool temperature on pod number for okra.

Increasing $CO_2$ concentration from 350 to 675 $\mu L\ L^{-1}$ at high temperatures caused a greater percentage increase in seed yield than it did at 22/16°C (Fig. 1). The increase in total seed yield in response to increasing $CO_2$ concentration and temperature regime was mainly associated with the increased numbers of pods (Table 1) and seeds (Fig. 1) and not with the weight of individual seeds (Fig. 1). Seddigh and Jolliff (1984) observed that soybean grown under ambient day temperature in the field produced smaller seeds at night temperatures of 10 or 16 than at 24°C. These investigators concluded that production of assimilates was unaffected by cool nights but growth rate of seeds was limited by the direct effect of low night temperature. The growth rate of individual seeds appears to be insensitive to a range of variation in the supply of assimilate (Egli and Leggett 1976). Although we did not measure rates of trans-

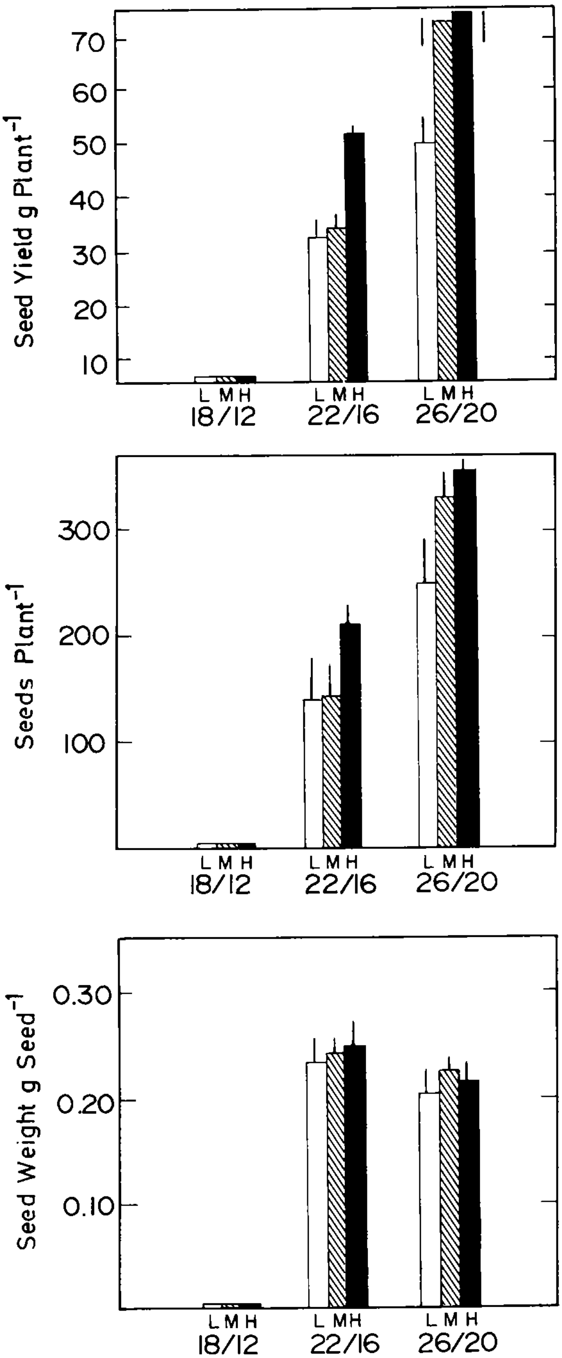


Fig. 1. Seed yield, number of seeds/plant and seed weight of Ransom soybean at three $CO_2$ concentrations (L=350, M=675 and H=1000 $\mu$L L$^{-1}$) and three day/night temperature regimes (18/12, 22/16 and 26/20°C).

Table 2. Mean and standard error for stomatal conductances and photosynthetic rates of leaves of soybean grown at three $CO_2$ concentrations and two day/night temperature regimes

| $CO_2$ concentration ($\mu L\ L^{-1}$) | Stomatal conductance ($cm\ s^{-1}$) | | Net photosynthetic rate ($\mu mol\ m^{-2}\ s^{-1}$) | |
|---|---|---|---|---|
| | Day/night temperature, °C | | | |
| | 22/16 | 26/20 | 22/16 | 26/20 |
| 350 | 0.56+0.04 | 0.26+0.03 | 14.3±0.9 | 22.8±0.4 |
| 675 | 0.25+0.07 | 0.17+0.02 | 17.7±1.1 | 26.1±2.0 |
| 1000 | 0.27+0.02 | 0.14+0.02 | 19.8±1.2 | 21.8±1.1 |

location of assimilates to the seeds, data of Fig. 1 suggest that production and translocation of assimilates to individual seeds probably were not limited at 22/16°C at any $CO_2$ concentration. It might be that 22/16°C temperature regime is optimum, or close to optimum, for maximum seed size as indicated by no statistical differences obtained in seed size between 22/16°C and 26/20°C treatments. Atmospheric $CO_2$ enrichment had little or no effect on seed size at these temperature regimes. Therefore, the differences in seed yield per plant at different atmospheric $CO_2$ and temperature levels were due to differences in number of pods per plant and not due to the weight of individual seeds. Numbers of seeds per pod were unaffected by the $CO_2$ and temperature treatments. Sionit et al. (1987) reported increasing growth of different vegetative plant parts in response to increasing levels of atmospheric $CO_2$ and temperature. It appears that most of the yield differences obtained in the present experiment were due to morphological differences (Sionit et al. 1987) in growth of the plants. The overall influence of temperature and $CO_2$ treatments, therefore, was such that the sink size was probably partly adjusted in response to cool temperature and $CO_2$ enrichment. Thus, in most instances, when plants were grown in 1000 $\mu L\ L^{-1}$ $CO_2$ at 22/16°C the high $CO_2$ compensated for the deleterious effect of low temperature in producing pods and seed mass.

As expected, leaves of soybeans at high $CO_2$ concentrations or high temperatures had lower stomatal conductance than leaves of plants grown at low $CO_2$ or low temperature levels (Table 2). While stomatal conductance decreased, leaf photosynthetic rates increased with increasing $CO_2$ and temperature levels except for 1000 $\mu L\ L^{-1}$ $CO_2$ at 26/20°C (Table 2). Carbohydrate accumulation in plant leaves has been suggested to be a cause of decreased photosynthesis in 1000 $\mu L\ L^{-1}$ compared to lower $CO_2$ concentrations (Clough et al. 1981; Wulff and Strain 1982). The decrease in photosynthesis in response to 1000 $\mu L\ L^{-1}$ $CO_2$ was not observed in our experiment at the lower temperature regime (22/16°C). This may partially be due to a reduced rate of production of assimilates at lower temperatures.

Temperature regime and $CO_2$ enrichment influenced net assimilation rate (NAR), but the interaction of these treatments did not produce statistically significant effects (Table 3). The NAR was always higher at high than at low $CO_2$ concentrations. Soybean plants grown at high $CO_2$ levels were larger, produced more branches and greater leaf area than plants grown at lower $CO_2$ levels (Sionit et al. 1987). Self shading did not influence the NAR at high $CO_2$ levels in our study as has been demonstrated by Flint and Patterson (1983). Ransom soybean had higher NAR values at 22/16°C than at either 18/12°C or 26/20°C. NAR reflects a long-term assimilation by the whole plant between two sampling dates but net photosynthesis is a measure of $CO_2$ uptake by a single, unshaded, and relatively young leaf. Therefore, NAR (Table 3) is dependent upon the phenology and size of the plants, whereas leaf photosynthesis (Table 2) is related to stomatal conductances of the measured leaves. These

Table 3. Net assimilation rates ($g\ m^{-2}\ d^{-1}$) of soybean during the 20- to 40-d and 40- to 67-d harvest intervals at three $CO_2$ concentrations and three day/night temperature regimes

| | 20–40 day | | | 40–67 day | | |
|---|---|---|---|---|---|---|
| $CO_2$ concentration ($\mu L\ L^{-1}$) | Day/night temperature °C 18/12 | 22/16 | 26/20 | 18/12 | 22/16 | 26/20 |
| 350 | 7.7 | 9.3 | 6.8 | 6.3 | 10.7 | 6.6 |
| 675 | 10.8 | 11.7 | 8.9 | 8.4 | 13.7 | 9.5 |
| 1000 | 11.9 | 13.3 | 10.8 | 9.0 | 14.6 | 10.0 |
| *Source of variation* | | | *20–40 day* | *40–67 day* | | |
| $CO_2$ | | | ** | ** | | |
| Temp. | | | ** | ** | | |
| $CO_2$ × Temp. | | | NS | NS | | |

*,**$P<0.05$ and $P<0.01$, respectively.

factors may have contributed to different trends of changes observed in NAR and net photosynthesis in response to increasing temperature from 22/16°C to 26/20°C.

Although seed yield of Ransom soybean at 22/16°C and 1000 $\mu L\ L^{-1}$ $CO_2$ was equal to that at 26/20°C and ambient $CO_2$ (Fig. 1), the photosynthetic rates were different (Table 2). $CO_2$ enrichment increased net photosynthesis at low temperature but did not completely compensate for the low-temperature effects. Increasing the temperature from 22/16°C to 26/20°C increased net photosynthesis by 59, 46 and 10% at 350, 675 and 1000 $\mu L\ L^{-1}$ $CO_2$, respectively. Increasing $CO_2$ concentration from 350 to 675 $\mu L\ L^{-1}$ and from 675 to 1000 $\mu L\ L^{-1}$ increased net photosynthesis by 23.8 and 11.4%, respectively, at 22/16°C and by 14.1% and −16.5%, respectively, at 26/20°C. The data suggest that leaf photosynthesis in soybean benefited from $CO_2$ enrichment more at a moderately low temperature regime than at a high temperature regime.

The increase in temperature and $CO_2$ hastened the time of flowering, appearance of pods, and senescence of leaves. Plants grown at the combination of high $CO_2$ and high temperatures approached the full seed development stage about 19 d earlier than those grown at low levels of temperature and ambient $CO_2$. Although the low temperature regime at all $CO_2$ levels prolonged the duration of efficient photosynthesis of plants by postponing senescence of the leaves, the extended photosynthetic capacity did not result in allocating more dry matter to developing pods. This may have been due to significantly lower rates of net photosynthesis and of subsequent translocation of substrates at low temperatures.

The data show that amelioration of low-temperature effects on soybean yield by atmospheric carbon dioxide enrichment is limited to moderately low temperatures and at a $CO_2$ level of 1000 $\mu L\ L^{-1}$. The projected global increase in carbon dioxide concentration for the next 50 yr and the resultant climatic warming are most likely to increase soybean yields in areas which will have moderately warm to warm climates.

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