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The Relationship Between Leaf Area Index and Photosynthetic Temperature Response in Wheat (*Triticum aestivum* L.) Canopies

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THE RELATIONSHIP BETWEEN LEAF AREA INDEX AND

PHOTOSYNTHETIC TEMPERATURE RESPONSE

IN WHEAT (<u>Triticum</u> <u>aestivum</u> L.)

CANOPIES

by

David B. Meek

A thesis submitted in partial fulfillment
of the requirements for the degree

of

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in

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(Crop Physiology)

Approved

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ABSTRACT

The Relationship Between Leaf Area Index and

Photosynthetic Temperature Response

in Wheat (<u>Triticum</u> <u>aestivum</u> L.)

Canopies

by

David B. Meek, Master of Science

Utah State University, 1990

Major Professor: Dr. Bruce G. Bugbee
Department: Plant, Soil, and Biometerology

The objective of this study was to determine the effect
of increasing leaf area index on the photosynthetic
temperature response of a wheat canopy. Hard red spring
wheat (<u>Triticum</u> <u>aestivum</u> L. cv. Veery-10) was grown
hydroponically in a growth chamber, which also served as the
gas-exchange chamber. Gas-exchange parameters were measured
on single leaves and on wheat canopies at various leaf area
indices. The temperature response curves of the canopy
shifted from being steeper with a high temperature optimum
to being flatter with a lower temperature optimum as leaf
area index increased from 0 to 20.0 m^2 m^{-2}. Single-leaf and
canopy measurements show that this shift was primarily a
result of increasing respiration from accumulating stems and
reproductive structures and, to a lesser extent, from lower

temperature optimums associated with lower light levels

within the canopy.

(57 pages)

CHAPTER I

INTRODUCTION

Many studies have focused on the physiology of
photosynthesis, but relatively few have examined
photosynthesis in a continuously growing crop canopy.
Examples of papers on canopy photosynthesis include Fukai
and Silsbury (1977) on the effects of temperature on
photosynthesis in clover canopies, Sionit et al. (1984) on
photosynthesis and stomatal conductance in soybean canopies,
Pierce et al. (1985) and Hatfield and Carlson (1978) on
photosynthesis in soybean canopies, and Woledge and Parsons
(1986) on the effect of temperature on photosynthesis in
ryegrass canopies.

A search of the literature did not find detailed
studies examining the effects of increasing leaf area index
(LAI) on the photosynthetic temperature response of
canopies. This study was conducted to help fill this gap in
our knowledge and to provide techniques to assist in the
prediction of canopy temperature response. This study also
adds to the crop physiology data base needed to refine
existing crop growth models such as those developed by
Johnson and Thornley (1984) and Weir et al. (1984). It may
also elucidate the physiological basis for a system of
phasic temperature control in controlled environments to
enhance photosynthesis and productivity. The most direct

application will be in the high-CO_2, high-light environments of extra-terrestrial farms in the future.

This research was conducted in growth and measurement atmospheres of 1200 μmole CO_2 mole^{-1} of air (ppm) for the canopy and measurement atmospheres of 750 ppm for single leaves. There are two reasons for using high-CO_2 atmospheres. Foremost is our interest in high-input space-based agriculture. Secondly, high CO_2 helps to minimize the effects of stomatal responses, as is explained later.

All measurements were performed at temperatures where physiological effects are reversible (15° to 35°C). Root respiration was not included in the results of this research since the circulating hydroponic solution carried root-respired CO_2 outside of the gas-exchange chamber. Consequently, for conciseness, only subjects pertinent to the growth of crop shoots in such environments are described.

CHAPTER II

LITERATURE REVIEW

The net photosynthetic temperature response of a canopy is the sum of the gross photosynthetic contribution of each leaf minus the respiratory efflux of leaves, stems, and reproductive structures.

TEMPERATURE EFFECTS ON LEAF PHOTOSYNTHESIS

Leaf photosynthesis is temperature dependent. Temperature effects can be the result of growth temperature, measurement temperature, or both (Berry and Björkman, 1980). The use of many different species and varying growth and measurement conditions by investigators make comparison of results difficult, but some generalizations can be drawn.

Optimal photosynthetic temperature tends to be near the prevailing growth temperature at saturating light. As light is lowered, the temperature response curves become flatter and broader and optimal temperature decreases (Berry and Björkman, 1980; Downs, 1970). Temperatures above 27°C tend to increase photosynthesis in 2% oxygen and saturating light, but low temperature tends to cause inhibition of photosynthesis under the same conditions (Cornic and Louason,1980; Sharkey et al., 1986b). In atmospheres of low oxygen, the effect of low temperature is compounded by high CO_2 (Harris et al., 1983). Finally, atmospheres of high CO_2

stimulate photosynthesis, but, in high light, the stimulation is often accompanied by a gradual decline in photosynthesis over time. This decline is more marked at low temperature than at high temperature (Azćon-Bieto, 1983). Many factors influence the leaf responses described above, but they can be separated into two groups-- diffusional and biochemical. Of the diffusional factors, stomatal aperture is probably the most important.

Effects on Stomata

Stomatal response to temperature may affect leaf photosynthesis since stomata regulate intercellular CO_2 concentration (C_i). The effect that a change in C_i will have on photosynthesis is strongly determined by leaf temperature, light intensity, and the magnitude of C_i.

Lösch (1977, 1979) found that stomata respond to temperature independent of other environmental factors; stomata also have an independent response to the vapor pressure deficit (VPD) between leaf and air. This was later confirmed by Küppers et al. (1988). As temperature increases, stomatal aperture tends to increase, and as VPD increases, stomatal aperture tends to decrease. These responses parallel, but appear to be independent of, increasing or decreasing photosynthesis.

Since an increase in temperature usually increases the VPD, difficulties were often encountered in the 1950's,

1960's, and 1970's in sorting out the nature of stomatal response to temperature. Some investigators reported stomates opening with increasing temperature, while others reported stomates closing at higher temperature (Berry and Björkman, 1980; Downs, 1970).

Studies in which temperature or VPD were held constant have clarified the record on stomatal response to temperature. It appears that stomata of well watered plants continue to open as temperature increases (Lösch, 1979). Berry and Björkman (1980) concluded that in the absence of water stress and/or low VPD, stomata respond to photosynthetic demand for CO_2. The following studies help support this hypothesis in grasses and especially in wheat.

Monson et al. (1982) maintained a constant VPD of less than 1 kPa (a low VPD) while measuring single-leaf gas-exchange in Agropyron smithii and detected large changes in photosynthesis over a temperature range from 10° to 50°C. They concluded that stomata aperture did not affect photosynthesis. Several other investigators had similar results when maintaining a constant VPD. Labate and Leegood (1988) examined the effect of temperature change from 5° to 30°C on the photosynthetic rate in leaves of Hordeum vulgare. Their results showed that temperature effects on photosynthesis when C_i was held constant compared closely with photosynthesis when C_i was not controlled but VPD was less than 1 kPa. Finally, Kobza and Edwards (1987) found

that photosynthesis in wheat leaves increased between 15° and 25°C while C_i was maintained unchanged if VPD was kept less than 1 kPa, showing that stomatal contributions to photosynthesis were not significant.

The effect a change in C_i will have on temperature response depends primarily on C_i, and to a lesser extent on temperature. A decrease or increase in C_i caused by a change in stomatal conductance will have a smaller effect at high CO_2 than at low CO_2 concentrations. A typical photosynthesis vs. C_i curve shows a steep slope at lower CO_2 levels and a relatively flat slope at higher CO_2 levels. A change in C_i on the steep portion of the curve will elicit a larger photosynthetic response than an equal change on the flat portion (Hay and Walker, 1989).

Temperature can affect the photosynthesis vs. C_i response by changing the C_i at which photosynthesis is saturated. For instance, von Caemmerer and Farquhar (1981) found that as temperature increased, C_i became saturated in _Phaseolus_ _vulgaris_ at progressively higher CO_2 concentrations; however, the initial slope of the photosynthesis vs. C_i curve remained the same at all temperatures tested. Similar results were obtained by Labate and Leegood (1988).

In conclusion, in high CO_2 atmospheres where VPD is low and/or plants are well watered, biochemical rather than

stomatal change should account for nearly all of the temperature response of photosynthesis in leaves.

Effects on Photosynthetic Biochemistry

Biochemical contributions to the temperature response of leaf photosynthesis can be divided into gross photosynthesis (P_g) and respiration. Because there are both shaded and directly illuminated leaves in a canopy, it is useful to further divide P_g into low light P_g and high light P_g.

The Calvin Cycle

Gross photosynthesis requires CO_2 and ribulose-1,5-bisphosphate (RuBP) as substrates and ribulose-1,5-bisphosphate carboxylase (rubisco) as an enzyme to catalyze the reaction. Assuming CO_2 is not limiting, as in high CO_2 atmospheres, the reaction is dependent on the supply of RuBP and the activity of rubisco (Kirschbaum and Farquhar, 1984; Farquhar et al. 1980).

RuBP is produced in the Calvin cycle by the reaction of ribulose-5-P and ATP. The reaction is catalyzed by ribulose-5-P kinase. Kobza and Edwards (1987) found that ribulose-5-P kinase was not limiting over the temperature range of 15°- 45°C in wheat. Information on the availability of ribulose-5-P was not found in the literature, but it is assumed to be in sufficient quantity.

Therefore, when RuBP regeneration is limiting, ATP is probably the one component that would limit RuBP regeneration.

ATP is produced by the reaction of ADP and orthophosphate (p_i) in photophosphorylation. Assuming ADP is not limiting, the reaction is potentially limited by the rate of photosynthetic electron transport (Salisbury and Ross, 1985) or the availability of p_i. Electron transport is limited by the availability of photons in low light, or by the light harvesting capacity of the leaf as is encountered in high light.

Temperature Effects on
Low Light Assimilation

The energy required to drive electron transport is acquired directly from photons. Consequently, at light levels below those saturating the light harvesting complexes, RuBP regeneration is limited by the availability of photons. Mott et al. (1984) measured the RuBP concentration of Xanthium leaves in response to light levels and concluded that P_g at low light is limited by RuBP regeneration.

If RuBP is the limiting factor at low light, P_g should increase as light intensities increase independent of temperature up to some point. In support of this, Monson et al. (1982) did not find significant temperature effects

on the light response of P_g assimilation in leaves of

Agropyron _smithii_ at temperatures between 20° and 35°C.

Temperature Effects on
High Light Assimilation

At saturating light, RuBP regeneration is limited by

the maximum rate at which electron transport can operate

(Ferrar et al., 1989; von Caemmerer and Farquhar, 1981).

However, the maximum rate of electron transport is

temperature dependent. Kirschbaum and Farquhar (1984) found

that the RuBP regeneration vs. temperature curve peaked near

30°C in snowgum. This response was corroborated by Farquhar

et al. (1980) who found that the electron transport

temperature optimum in barley was also near 30°C.

Also important is the observation of Stidham et al. (1982)

that electron transport and photophosphorylation are

inhibited by temperatures above the optimum for

photosynthesis in _Agropyron_; this fact may explain the drop

in P_g above the optimum. [Studies also show that rubisco

has about the same relation to above-optimum temperature as

electron transport and may be an alternative mechanism.

Monson et al. (1982) found that temperature dependent

changes in rubisco activity may have a role in

photosynthetic limitation at above optimum temperature below

40°C in _Agropyron_. These findings are corroborated by

Ferrar et al. (1989) and Weis (1981)].

The regulation of P_g at high light and high CO_2 by temperature via the electron transport cycle is an attractive hypothesis. If this was the only limiting factor, the magnitude of P_g should remain essentially unchanged during a long photoperiod. However, reports of declining P_g over time in high light and high CO_2 have been reported, suggesting that a time dependent factor also may be limiting.

Inhibition of assimilation by photosynthates

Azćon-Bieto (1983) found that P_g decreased with time after illumination in ambient air at temperatures below 25°C in wheat; the rate of decline increased in atmospheres of 700 to 825 ppm CO_2. At higher CO_2, a decline also occurred at temperatures above 25°C. The presence of a time dependent limitation on P_g became apparent. Accompanying these changes, stimulation of P_g by reducing the O_2 concentration to 2% decreased after several hours of light as did quantum yield. This phenomenon of reduced response to decreasing O_2 concentration, known as O_2-insensitivity, has been reported in several other species (Sharkey, 1985). See Appendix A for further information on O_2 insensitive photosynthesis.

Azćon-Bieto (1983) hypothesized that the reduced quantum yield in wheat attending time dependent reduction of P_g indicates impairment in the production or consumption of

ATP in photosynthesis. The mechanism suggested is a reduced stromal p_i. Reduction of stromal p_i under these conditions is supported by experiments where mannose or other p_i sequestering sugars are fed to leaves. This technique usually results in reduced P_g rates (Harris et al. 1983). Corroborating evidence was obtained by Leegood and Furbank (1986) who restored O_2-sensitivity by feeding leaves orthophosphate. The fact that low p_i can reduce P_g is well documented (see Appendix B for an explanation of the p_i cycle); however, the mechanism by which p_i is reduced and how reduction is detected is less clear.

p_i Limitation

The literature indicates that p_i reduction may originate in one of two processes-- accumulation of sugars, or the synthesis of sucrose. The site of action affected by reduction in p_i is thought to be either the regeneration of RuBP or the activation of rubisco.

Source of Limitation-- Accumulation of Sugars Azćon-Bieto (1983) hypothesized that the accumulation of sugars in the leaves leads to low p_i in the leaf. To test this, translocation of sugars was inhibited in wheat by chilling the leaf base, which produced a marked decline in P_g at 340 and 700 ppm CO_2. Similar results were obtained by Blechschmidt-Schneider et al. (1989) in Amaranthus edulis.

Azćon-Bieto further found that photosynthesis in the upper part of P_g vs. C_i curves usually recovered after a short period of darkness in which sugar was removed from the leaves. Bagnall et al. (1988) found that in peanut reductions in P_g by accumulation of assimilates could be reversed within one hour of rewarming the source to 30°C. Similar phenomena were observed in rice by Huang et al. (1989), in spinach by Sharkey et al. (1986b), and in wheat by Sawada and Miyachi (1984). Azćon-Bieto (1983) believes that accumulation of sugars could sequester cytosolic p_i making it unavailable to the chloroplast.

Source of Limitation-- Low Rate of Sucrose Synthesis
Sharkey et al. (1986b) hypothesized that in spinach, low rates of sucrose synthesis, or triose phosphate utilization (TPU), limited P_g because p_i is a product of sucrose synthesis. In support of this hypothesis, they found that pool size of triose-phosphates increased and ATP/ADP ratios fell dramatically in conditions of O_2-insensitivity.

Site of Action-- Limited RuBP Regeneration Azćon-Bieto (1983) found that P_g vs. C_i curves in high sucrose leaves showed reduction in the upper part of the curve while the initial slope of the curves remained unaffected. This was interpreted as an indication that sugar accumulation, via lowering p_i concentration, led to impaired regeneration

of RuBP. Some literature, however, supports the hypothesis that the site of action of p_i deficiency is in reduced activity of rubisco.

Site of Action-- Limited Rubisco Activity Sharkey et al. (1986b) found that in spinach, RuBP levels in O_2-insensitive conditions actually increased over time to exceed pool sizes measured in ambient conditions. Similar results were obtained by Sawada et al. (1989). These results lead to the conclusion that photosynthesis in O_2-insensitive conditions may not be limited by RuBP regeneration. Sharkey et al. (1986a), instead, suggested that TPU limitation may lead to rubisco deactivation. Low TPU would lead to low p_i. Low p_i leads to low ATP, which increases PGA because of inhibited PGA reduction. PGA is an acid, so for each PGA produced, an H^+ is produced. H^+ is normally consumed during reduction of PGA to triose-P, but without sufficient ATP, PGA and H^+ will increase. The lower pH would then deactivate rubisco.

p_i as the Limiter Another mechanism has been suggested to explain decline in P_g at high CO_2, high light , and low temperature conditions. Leegood and Furbank (1986) suggested the following scenario. Low p_i in the cytosol slows export of triose-phosphate from the stroma and so restricts sucrose synthesis. An increase in the rate of

sucrose synthesis could then come about only by increasing the cytosolic pool of phosphate by slow movement from a vacuole. However, an increase in cytosolic phosphate to export triose-phosphate must be balanced with the requirement for maximum activity of enzymes of sucrose synthesis, which are favored by a high ratio of triose-phosphate and hexose phosphate to phosphate in the cytosol. The mechanism by which low temperature causes p_i limitation may be that low temperature results in a higher cytosolic phosphate optimum for CO_2 fixation.

Inhibition by Photosynthates-- Summary.

Decreasing p_i may cause decreasing P_g rates over time. Low p_i may result from inhibited sucrose translocation or inhibited sucrose production. Low p_i decreases production of ATP needed in regeneration of RuBP and conversion of PGA to triose-phosphate. Large pools of PGA will lead to lower stromal pH, which would decrease rubisco activity. In contrast, low temperature may increase the cytosolic optimum for p_i, which may then cause low rates of triose-phosphate export and sucrose synthesis. One, all, or none of these mechanisms may be responsible for reduction of P_g over time in high input (CO_2 and light) and low temperature environments.

These hypotheses are explanatory, but it is important to realize that almost all of the data was acquired from

short term experiments. The long term significance of these observations is in question. Sage et al. (1989) have recently concluded that in five C_3 species, acclimation (via biochemical adjustments) to high CO_2 levels caused a reduction or elimination in p_i limitations.

Effects on Respiration

Respiration is the efflux of CO_2 from living tissue. In plants it occurs as a result of RuBP combining with O_2 instead of CO_2 (photorespiration), and as a result of the metabolism of carbon compounds via the Krebs cycle (dark respiration).

Photorespiration

At ambient CO_2 concentrations, increase in temperature increases inhibition of P_g by photorespiration. The reduction can range from 10% at 15°C to 45% at 35°C. In high CO_2 environments, however, the effects of photorespiration largely disappear (Monson et al., 1982). For this reason, further references to respiration pertain only to dark respiration.

Dark Respiration

Mitochondrial or "dark respiration" rate (R_d) increases with temperature in darkened leaves (Downton and Slatyer, 1972) and usually has a Q_{10} near two (Amthor, 1989). If R_d

occurs in illuminated as it does in darkened leaves, it could have an important negative effect on the rate of net photosynthesis (P_n), especially at higher temperature. However, the nature and effect of R_d in illuminated leaves remains controversial because methods to measure it directly during photosynthesis have not been developed. Biochemical studies and more recent physiological experiments suggest that R_d may be the same in the illuminated and darkened leaves.

Graham (1980), in a comprehensive review of the literature, found biochemical evidence supporting continued operation of the Krebs cycle in the light in both green algae and leaves of higher plants. In some instances, rates were comparable with those in the dark. Unfortunately, physiological evidence in the past has not been so convincing, but recent investigations support the biochemical evidence.

Since R_d produces ATP, it was felt that high cytosolic ATP/ADP ratios resulting from photosynthesis might be inhibiting R_d, and measurement showed up to 75% inhibition of R_d in light (Graham, 1980). Kirschbaum and Farquhar (1984) concluded that R_d in snowgum in the light was 60% of R_d in dark. These conclusions are also supported by Massacci et al. (1986). However, Ciccarelli and Brown (1988) showed that photosynthesis actually decreased ATP in Asparagus mesophyll cells 24-34% and so high ATP levels

could not be affecting respiration rates. Weger et al. (1988), in studies with mass spectrometric analysis of O_2 and CO_2 exchange in green algae, concluded that R_d is not inhibited in light. Their results show that the Krebs cycle and the mitochondrial electron transport chain are capable of operation in the light. Rates of respiration in light and dark were similar since O_2 consumptions were similar. Azćon-Bieto and Osmond (1983) arrived at the same conclusion by analyzing CO_2 compensation points and carbohydrate fractions in the leaf.

Whether R_d is 75% or 40% inhibited or not inhibited at all in light, however, may be less important than the temperature response of R_d, which appears to be the same in light and dark (Kirschbaum and Farquhar, 1984; Azćon-Bieto and Osmond, 1983). Gealy (1989) concluded that increases in dark respiration at higher temperature contributed significantly to the decline in P_n in goatgrass leaves.

TEMPERATURE EFFECTS ON CANOPY PHOTOSYNTHESIS

Temperature effects on leaves in a canopy are partly determined by the light levels the leaves are exposed to. Light levels, in turn, are a function of leaf area index. Leaf area index also estimates the relative amount of respiring tissue in the canopy. The rate of respiration is an important determiner of canopy P_n.

Interaction of Light and Temperature

Berry and Björkman (1980) concluded that as light intensity is lowered, P_g vs. temperature curves in leaves become flatter and broader. Since the light required to saturate photosynthesis at low temperature is lower than at high temperature, a reduction in light has little effect on photosynthesis until the light becomes limiting at that temperature. When light is low enough to limit over the entire temperature range, the temperature curve is flat and linear and P_n declines with increasing temperature because of increasing respiration. Similar conclusions were reached by Monson et al. (1982) and Gealy (1989). Since the interaction of light, temperature, and respiration is potentially a significant contributor to canopy assimilation, light gradients in the canopy become important factors.

Leaf Area Index and Light Gradients

Light gradients in a canopy are a result of attenuation of light or PPF (photosynthetic photon flux) as it passes through the canopy. This attenuation is a function of LAI as expressed in the Lambert's-Beer's Law analog, as developed by Monsi and Saeki (1953)

$$\phi = \phi_o e^{-k*LAI}$$

where ϕ is the PPF at some point in the canopy, ϕ_o is the PPF incident at the top of the canopy, and k is the foliar absorption coefficient. This equation shows that LAI, through its attenuating effect on PPF, is an important characteristic in canopy temperature response. On the average throughout the canopy, as LAI increases, PPF and P_g per unit area of leaf decreases. The lower photosynthetic rate is further decreased by increased R_d from concomitant increases of photosynthetic and non-photosynthetic tissues.

Respiration

R_d subtracts only a small percentage of P_g in saturating light in leaves, especially at low temperature. However, it becomes a large factor in determining net photosynthetic response to low and high temperature in canopies where up to 70% of the biomass is non-photosynthetic tissue (stems, roots, lower leaves, and seeds). Also, since most leaves in a mature canopy are shaded, the effects of light on the biochemistry of respiration of a canopy would decrease during its life cycle.

Integration of Light, Temperature,
and Respiration

In young canopies (LAI < 1), the percentage of light saturated leaves is very high, and canopy photosynthesis should be essentially determined by the principles governing high light photosynthesis in single leaves, i.e., limited by the maximum rate of electron transport, highly dependent on temperature, and with a photosynthetic optimum near 30°C. The canopy could also be subject to O_2-insensitive (p_i limited) photosynthesis and show a noticeable decrease in photosynthesis over time.

Mature canopies (LAI > 6) have a low percentage of light saturated leaves; they would be mostly ruled by the principles governing low light P_g in leaves, i.e., restricted by the light-limited rate of electron transport, which results in limited RuBP regeneration. Consequently, P_g in mature canopies would be less dependent on temperature, and P_n would be mostly limited by the rate of R_d.

SUMMARY

The photosynthetic response of a canopy to temperature is governed by the physiology of its respective leaves as affected by light intensity and respiration. The physiology of the canopy is constantly changing. Light intensity on

leaves within the canopy, as determined by LAI, is constantly changing, and the amount of non-photosynthetic tissue is increasing. The objective of this research is to determine the temperature response of a wheat canopy in high CO_2 atmospheres as the canopy grows from seedling stage to maturity.

CHAPTER III

MATERIALS AND METHODS

PLANT MATERIAL

Dwarf spring wheat (<u>Triticum</u> <u>aestivum</u> L. cv. Veery 10) was used in this research. Plants were grown hydroponically in a sealed growth chamber, which also served as the open gas-exchange chamber.

CULTURAL TECHNIQUES

Planting density was 920 seeds per m^{-2}. Plants were germinated and grown in 4 specially designed plastic growing flats, 0.2 m^{-2} each (see Appendix C). The flats were designed to minimize nutrient solution evaporation but allow free access of roots to nutrient solution. Seeds were germinated in mist at 25°C with periods of no mist as needed to promote downward root growth. Seedlings were thinned to 470 plants per m^{-2} and equidistantly spaced. Flats were placed over the tubs in the growth chamber when roots had grown 5 - 8 cm below the growing flats (long enough to reach the nutrient solution).

ENVIRONMENTAL CONTROL

Plants were grown at 23°C day and night with 12 hours of light per day. Temperature was controlled in the chamber

by use of a water cooled heat exchange coil through which chamber air was circulated by high output fans. In addition, long wave radiation from the light source was absorbed by a water bath under the lights (see Bubenheim et al., 1988). Water for the heat exchanger and water bath was cooled with freon in an external reservoir. Temperature was monitored with chromel - constantan (type E) thermocouples shaded from direct light with aluminum foil cups.

Light was provided by four 400-watt HPS (high pressure sodium), two 1000-watt HPS, and four 400-watt metal halide lamps. Plants were grown at a PPF (photosynthetic photon flux) of 1500 μmol m^{-2} s^{-1}. PPF level at the canopy top was measured with a series of 8 gallium arsenide photodiodes (GASP-Hamamatsu G1118) calibrated against an integrating quantum sensor (Licor LI-188B).

HYDROPONIC SYSTEM

The hydroponic system consisted of a 100-L reservoir outside the growth chamber (EGC) and four 20-L black plastic tubs inside. Nutrient solution was supplied continuously to the 4 tubs by an epoxy coated magnetic drive pump which moved solution through PVC pipe and Tygon tubing. Solution was pumped through a manifold inside each tub for uniform distribution. Solution was aerated as it returned to the reservoir through a drain in the middle of each tub and cascaded into the reservoir (see Bugbee and Salisbury,

1989). Appendix D shows the concentration of nutrients in "starter" and "refill" solutions.

Solution pH was maintained between 5.5 and 5.8 by a pH controller (Omega) and a varying pH control solution consisting of HNO_3 and NH_4NO_3. The pH control solution was used as follows: 100 mM HNO_3 for first 2 weeks of growth. At 20 days, use a 1:1 molar ratio of NH_4NO_3 and HNO_3. At 30 days use a 2:1 molar ratio of NH_4NO_3 and HNO_3. This pH control method provided about 25% of the total N as ammonium in the first 30 days of growth.

Electrical conductivity was kept between 100 and 150 mS m^{-1} (1.0 and 1.5 mmhos cm^{-1}; see Bugbee and Salisbury, 1989). Deionized water was added as necessary to maintain E.C.

GAS-EXCHANGE SYSTEM

Open gas-exchange techniques were used in this research. Carbon dioxide concentration was monitored with an infra-red gas analyzer (Model ADC 225), dew points with a dew point hygrometer (Bingham Innerspace model BI-5Ed), mass flow of air into the chamber with a mass flow meter (Sierra Instruments model MFM-1-1511215-11-742-12-1), and air flow into the gas analyzer with rotometers (Cole-Parmer).

The large amount of CO_2 enriched air needed-- up to 1300 l min^{-1} -- was supplied by a rotary vane blower (Sutorbilt model 3 HVF). The intake to the system was at the top of a 10-m pole, which was 30 m away from the building

housing the growth chamber. Taking the air from the tower minimized fluctuations in CO_2 concentration. Air was pumped through a 240-L buffering chamber, then through 100 kg of calcium alumino-silicate clay desiccant (Desi Pak--United Desiccants), which effectively buffered water vapor fluctuations. CO_2 was added at this point by metering in pure CO_2 with a rotometer. The mixture then passed through a 100 L mixing/buffering chamber. The IRGA was used in differential mode and reference and analysis air was buffered such that fluctuations were insignificant. Enough air was provided at all times to maintain a positive pressure throughout the growth chamber and air lines.

DATA ACQUISITION

All sensors and thermocouples were read with a Campbell Scientific datalogger (model CR10). The CR10 was programmed to give one second updates of all measured parameters and ten second averages of several calculated parameters including transpiration, assimilation, intercellular CO_2 concentration, and stomatal conductance. Data points reported are 1 to 10 minute averages of the ten second updates.

EXPERIMENTAL PROCEDURE

Two types of data were collected from the wheat canopy and single wheat leaves: 1) net photosynthesis as affected by temperature and light, and 2) respiration as affected by temperature. Other data collected on the canopy included PPF absorbance and leaf area index at various stages in canopy development.

Canopy

Gas-Exchange

Net photosynthesis vs. temperature and respiration vs. temperature experiments were conducted by starting at 35°C and reducing the temperature by 2½° or 5° increments to 15°. This method was chosen after several experiments that demonstrated that decreasing temperature from a high starting point gave more repeatable results that increasing temperature from a low starting point. The inability to obtain the same response when starting from a cold temperature may be the result of accumulated photosynthates that have been shown to inhibit photosynthesis. Data was taken at each temperature when stomatal conductance and photosynthetic rates had stabilized.

Light Absorbance

Light absorbance by the canopy was determined by measuring incident PPF at the top of the canopy (Q_o), PPF at the bottom of the canopy (Q_b), and PPF reflected (Q_r) from the growing medium (white plastic flats). Absorbed PPF (Q_a) was then calculated from the following equation :

$$Q_a = Q_o - Q_r - Q_b + (Q_b * .734),$$

where the value .734 is the fraction of light reflected by the growing flats (see Gallo and Daughtry, 1986; Hipps, 1983).

Leaf Area Index
Determination

Leaf area index was determined by selecting four representative plants, one from each flat, measuring their leaf area with an LI-300 Leaf Area Meter (LICOR), and calculating LAI based on the number of plants covering the growing surface. Since this was done several times during the life of the canopy, larger samples were not collected because doing so would affect other results.

Single-leaf Gas Exchange

Plants were taken from the growth chamber at the flag leaf stage. Two leaves were chosen for single-leaf

measurements: the flag leaf and one leaf down the stem from the flag leaf (2nd leaf). These measurements were done in two identical open gas-exchange chambers (one leaf per chamber). The design and methods employed in this dual system were similar to those used in the canopy system. Exceptions are that air is provided by precisely mixing N_2, O_2, and CO_2; the light source was a single 1000-watt metal halide lamp; and gas-exchange was measured on about 7 cm^2 of leaf in each chamber. Light levels were reduced by placing aluminum screens between the light source and the chambers. For further information concerning this gas-exchange system see Mott (1988).

CHAPTER IV

RESULTS AND DISCUSSION

The results of this study confirm the hypothesis that the shift in the photosynthetic temperature optimum in developing canopies is the result of respiration rates increasing exponentially with increasing temperature ($Q^{10} \approx$ 2), and increasing respiration resulting from the accumulation of non-photosynthetic plant structures.

The effect of this increase in respiration is illustrated in Fig. 1, which shows the light response of net (P_n) and gross photosynthesis (P_g) in wheat leaves and a wheat canopy at 17° and 25°C. In Fig. 1a, P_n was highest in single leaves at 25°C but highest in the canopy (about Haun Stage 7.0) at 17°C. Subtracting the respiration rates from the single leaf and canopy data (estimated by respiration in dark) produces Fig. 1b. Note that subtracting respiration has little effect on the single leaf data (discussed more later), but has a large effect on the canopy data. Also note that temperature had little effect on canopy P_g (also discussed more later). These data clearly show that respiration is the primary source of variation in the photosynthetic temperature response of wheat canopies.

Stomatal effects do not appear to be responsible for the changes observed in these experiments. Accumulation of photosynthates, however, may play a minor role. Data
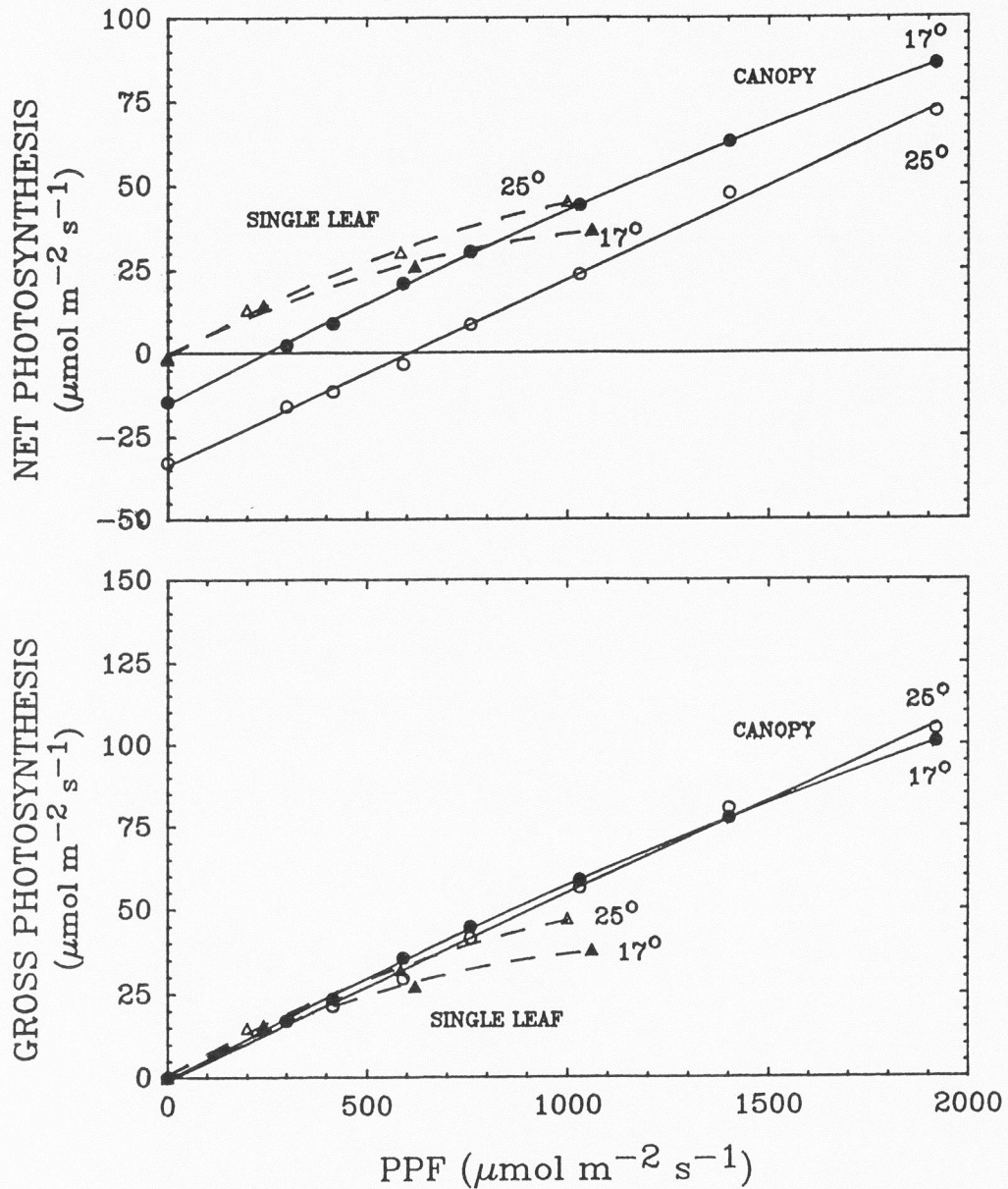
Fig. 1. Effect of temperature on the light
response of photosynthesis in single wheat
leaves and a wheat canopy. 1a shows the effect
on Pn. 1b shows the effect on Pg, which is Pn
minus the respiration component determined in
the dark in 1a.

presented here on the photosynthetic temperature response of wheat was replicated, but the replicate data is not shown.

RELATIONSHIP BETWEEN STOMATA AND PHOTOSYNTHESIS

Photosynthesis requires CO_2 as a substrate to manufacture carbohydrate. Typically, photosynthesis increases rapidly as intercellular CO_2 concentration (C_i) increases up to approximately 400 ppm. Above 400 ppm CO_2, however, the photosynthesis vs. CO_2 response becomes relatively flat (von Caemmerer and Farquhar, 1981).

C_i is regulated by the stomatal conductance (g), which is determined by the size of the stomatal aperture. If stomatal aperture decreases, g decreases, CO_2 diffusion into the stomata is inhibited, and C_i drops.

Figure 2a shows the response of g to temperature in single wheat leaves at 1500 μmol m^{-2} s^{-1} photosynthetic photon flux (PPF). Stomatal conductance increased as temperature decreased from 35° to 25°C. This indicates that stomata opened as the vapor pressure deficit between the leaf and the air decreased.

Figure 2b shows the temperature response of C_i corresponding to the conductances reported in Fig. 2a. C_i increased with decreasing temperature from 500 ppm at 35°C to 700 ppm at 15°C. The ambient air was kept at 750 ppm CO_2 throughout the temperature range. C_i does not appear to
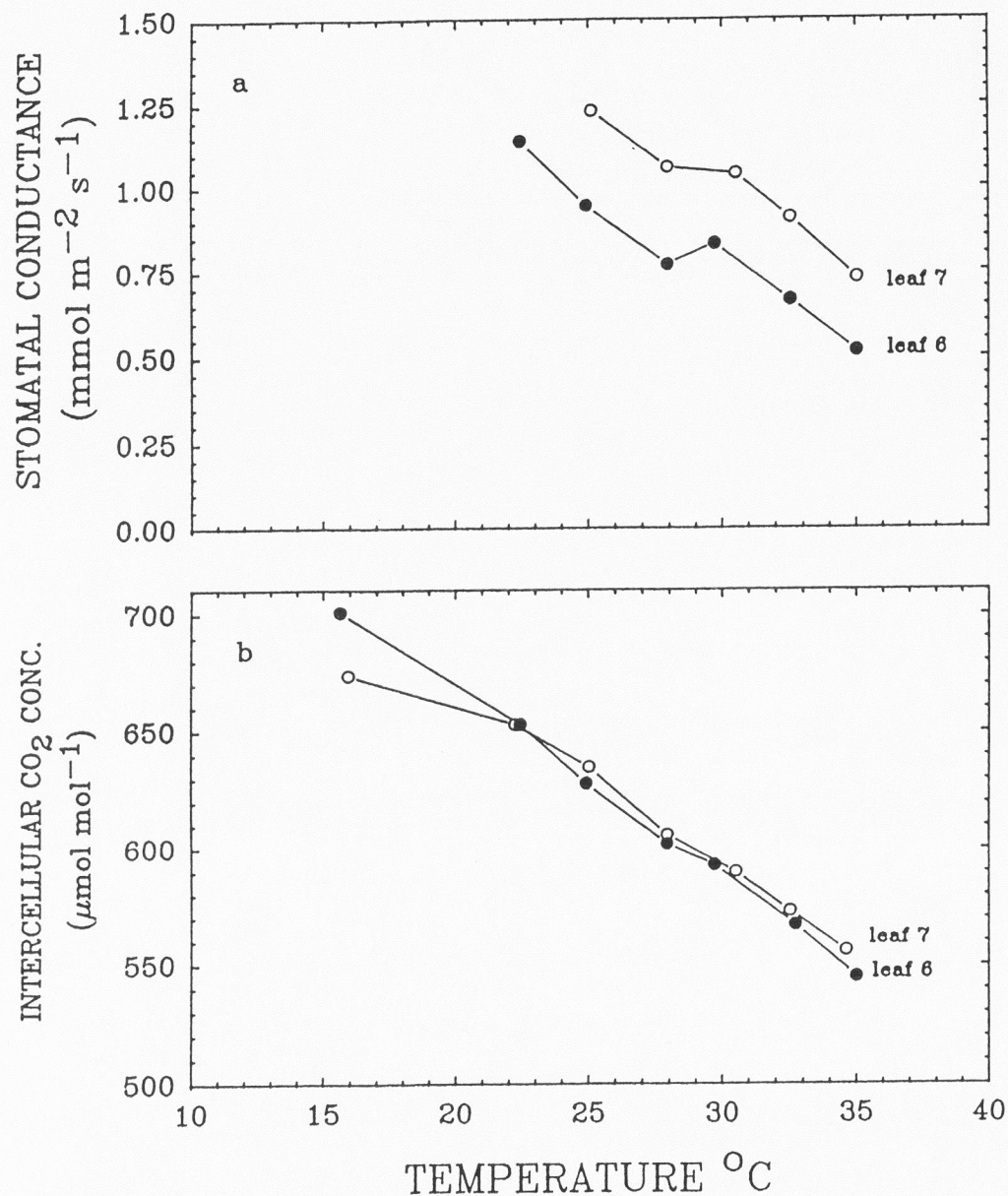
Fig. 2. Response of stomatal conductance (g) and
    intercellular CO$_2$ (Ci) to decreasing
    temperature in wheat leaves. 2a shows the
    response of g for leaves six and seven (flag
    leaf). 2b shows the response of Ci for the
    same leaves.

have been affected by the sharp decrease in g at temperatures below 22°C.

The effect the increase in C_i had on net photosynthesis is probably small. Von Caemmerer and Farquhar (1981) found that increasing C_i above 400 ppm at 1400 μmol m^{-2} s^{-1} PPF had no effect on P_n in Phaseolus vulgaris. Evans (1983) and Azćon-Bieto (1983) both found that this was also the case in wheat at 1800 μmol m^{-2} s^{-1} and 1000 μmol m^{-2} s^{-1} PPF respectively. Based on these findings, it is assumed that changes in C_i had no significant effect on the P_n vs. temperature data.

TEMPERATURE RESPONSE OF SINGLE LEAVES

Figure 3a shows the net photosynthesis (P_n) vs. temperature response of two leaves, a flag leaf (leaf 7) and leaf 6 at 1500 μmol m^{-2} s^{-1} PPF. Both leaves had a similar response to temperature from 35° to 15°C. This indicates that leaves of different ages may have similar P_n vs. temperature responses, which is an important point to establish when predicting canopy physiology since leaves in a canopy are various ages.

Figure 3a also shows that the photosynthetic temperature optimum in these leaves was near 32°C at saturating light (1500 μmol m^{-2} s^{-1} PPF). This optimum probably reflects the temperature optimum for photosynthetic electron transport, which was reported to be near 30°C in
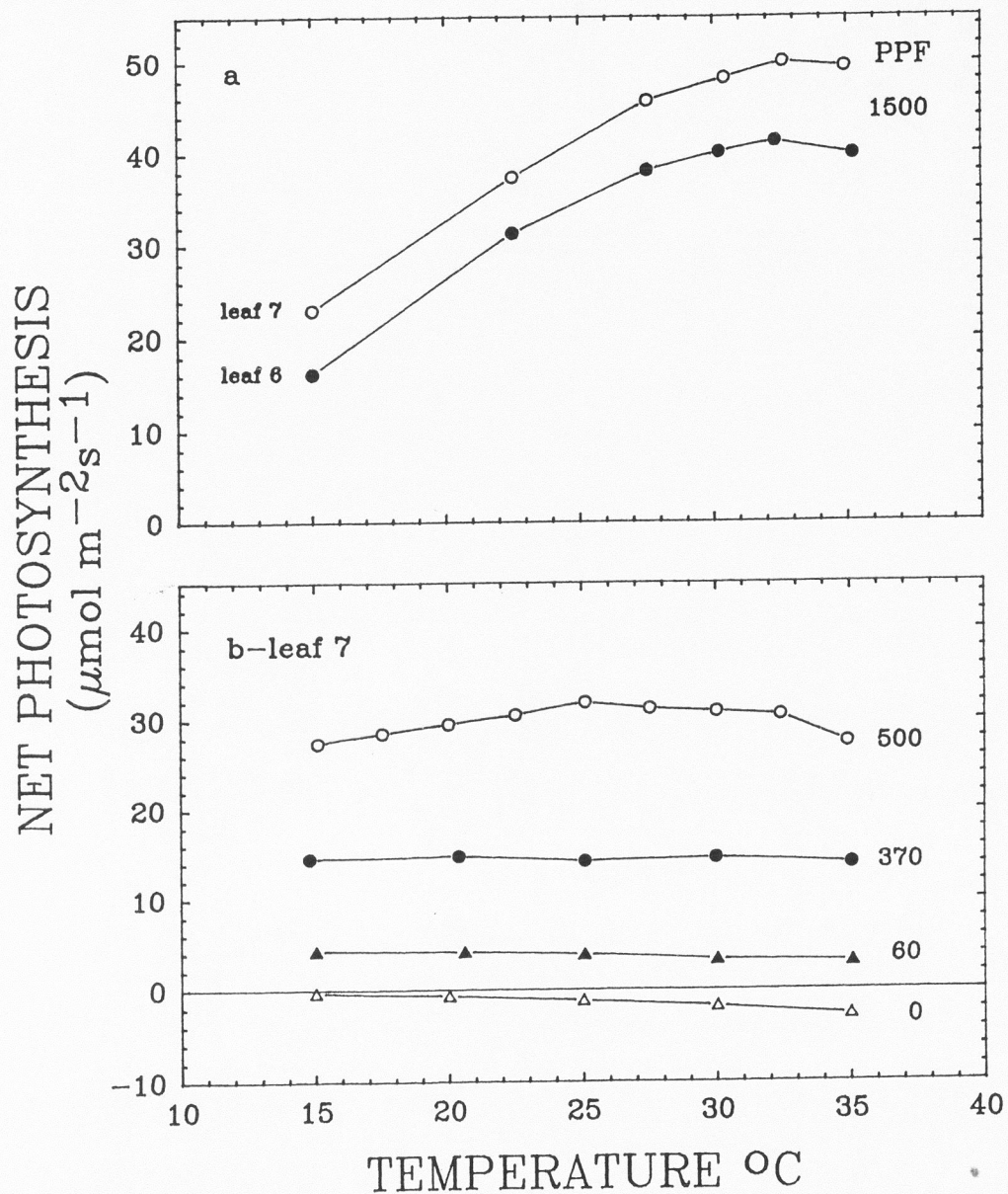
Fig. 3. Response of net photosynthesis to
temperature in wheat leaves at several light
intensities. 3a shows the response for leaves
six and seven at 1500 μmol m-2 s-1 PPF. 3b shows
the response for leaf seven at 500, 370, 60, and
0 μmol m-2 s-1 PPF.

barley (Farquhar et al. 1980). Kirschbaum and Farquhar (1984) also found that the optimum for RuBP regeneration, which is dependent on electron transport, is near 30°C in snowgum.

The sharp decrease in P_n in Fig. 3a at the lower temperature may be a result of limited orthophosphate (p_i) in the stroma. P_i limited photosynthesis is often accompanied by O_2-insensitivity as discussed by Sharkey (1985). When p_i limitation occurs, it usually does so in conditions of high light, high CO_2, and low temperature, all of which are conditions in which data for Figs. 3a and 3b were taken. The important role of this inhibition is evident when comparing Figs. 3a and 3b. In Fig. 3a, P_n at 1500 μmol m^{-2} s^{-1} PPF at 15°C was less than P_n at 500 μmol m^{-2} s^{-1} PPF at 15°C in Fig. 3b.

Figure 3b shows P_n vs. temperature responses for single wheat leaves at 500, 370, 60, and 0 μmol m^{-2} s^{-1} PPF. The temperature optimum appears to decrease and the response becomes flatter as the PPF level decreases. Similar observations were reported by Berry and Björkman (1980) who concluded that when light intensity was decreased, P_n vs. temperature curves in leaves became flatter and broader. Since the light required to saturate P_n at low temperature is lower than at high temperature, a reduction in light has little effect on photosynthesis until the light becomes limiting at that temperature. When the light intensity is

low enough to limit over the entire temperature range, the
temperature curve is flat and linear and P_n declines with
increasing temperature because of increasing respiration.
Similar results were obtained by Woledge and Parsons (1986)
in ryegrass.

TEMPERATURE RESPONSE OF THE CANOPY

Figure 4a shows the LAI dependence of the P_n
temperature response in a wheat canopy. At low LAI, the
temperature response is similar to that of single leaves in
high light, having a steeper response and a higher
temperature optimum. At progressively higher LAI's, up to
20 m^2 m^{-2} (high LAI's in wheat canopies grown in high-input
environments are common [Bugbee and Salisbury, 1988]), the
response becomes flatter and the optimum temperature is
lower. Fukai and Silsbury (1977) obtained comparable
results by measuring the temperature response of
subterranean clover communities at several light
intensities, but at a single LAI of 6.9. The effect of
decreasing light intensity on gross photosynthesis (P_g) is
probably similar to increasing LAI; however, this technique
does not include the effect of the increasing biomass and
concomitant increase in dark respiration (R_d) associated
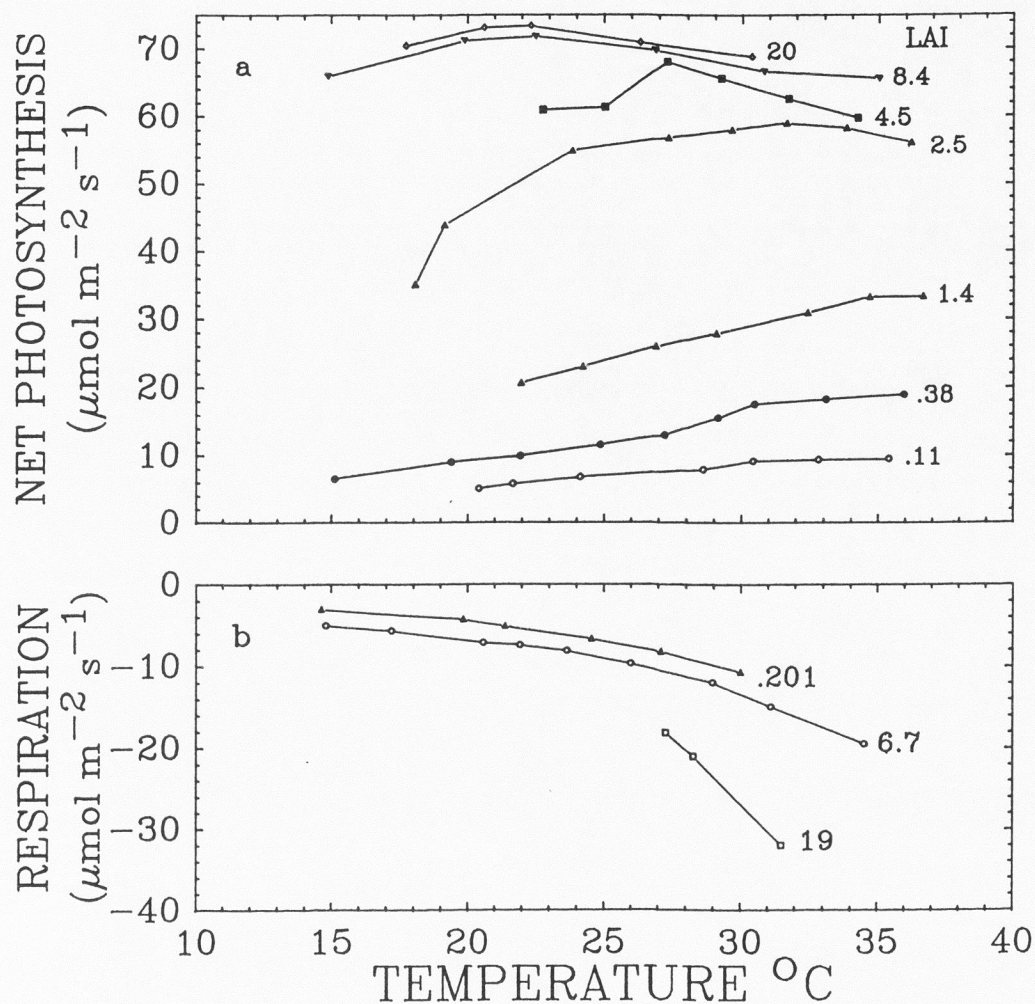with increasing LAI.

Fig. 4. Response of net photosynthesis and
  respiration to temperature in a wheat canopy.
  4a shows the response of net photosynthesis at
  several leaf area indices; incident PPF is 1950
  μmol m-2 s-1. 4b shows the response of
  respiration at three leaf area indices.

Component Responses

Figures 5a and 5b have been constructed to assist in explaining why optimum temperature for canopy P_n decreases as LAI increases. Data used to construct these graphs was based on data found in Figs. 3 and 4. The following reasoning applies to Figs. 5a and 5b: P_n is equal to the difference between P_g and R_d. Canopies are made up of leaves, stems, and reproductive structures. Leaves are entirely responsible for the magnitude of P_g, and leaves, stems, and reproductive structures responsible for the magnitude of R_d.

Gross Photosynthesis Component

P_g of the canopy is the sum of the P_g of all leaves (photosynthesis from other plant part is assumed to be negligible). P_g of the leaves is dependent on light which diminishes in intensity as it passes through the canopy. As the canopy accumulates leave, the amount of light reaching lower leaves is continually reduced, thus continually changing the temperature vs. P_g response of lower leaves.

The accumulation of leaves in the canopy is measured by leaf area index (LAI), which is the ratio of leaf area to ground area. Although a simplification, especially in canopies containing vertical leaves as wheat does, the canopy can be thought of as having leaf layers. Each full leaf "layer" can be thought of as completely covering the
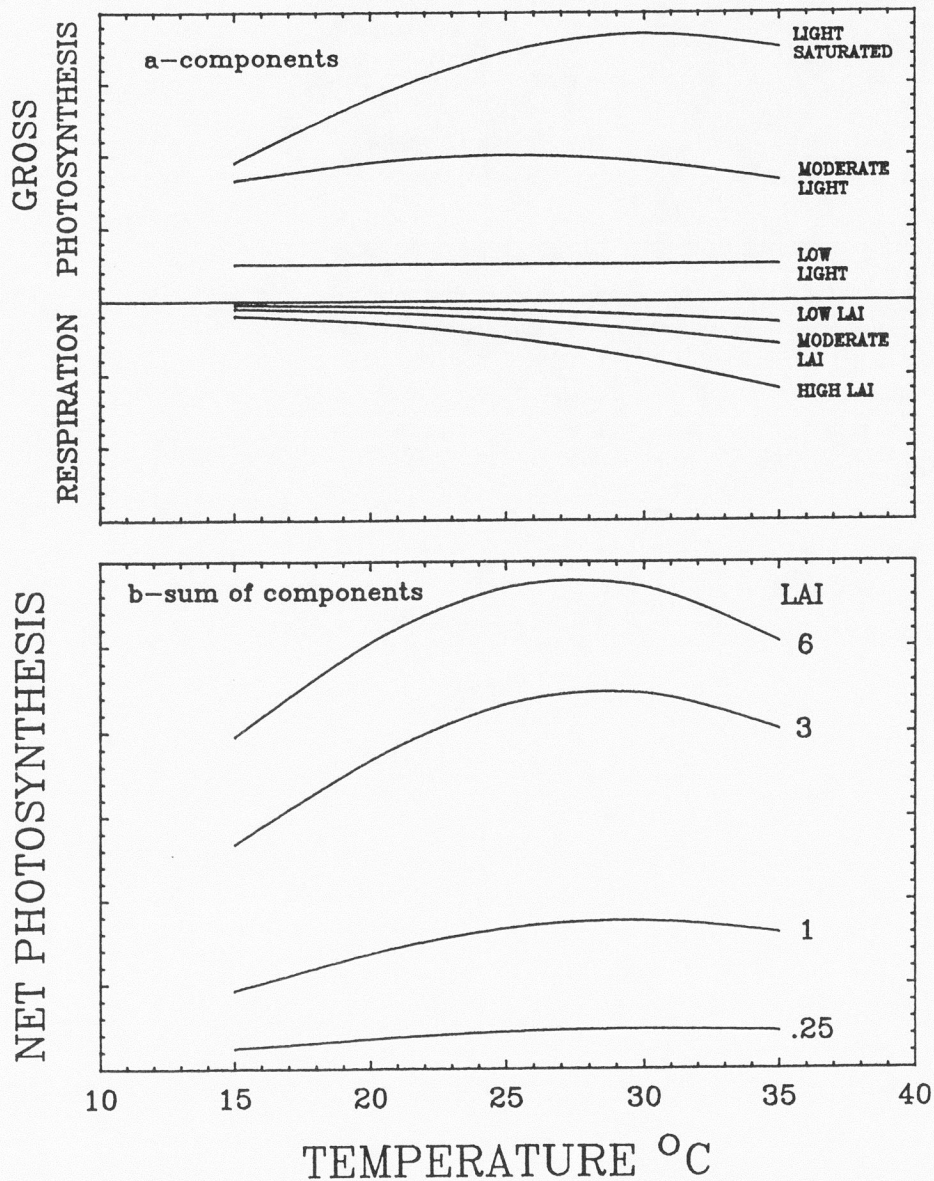
Fig. 5. Derived curves illustrating the effect of
  increasing respiration on the photosynthetic
  temperature response of a wheat canopy. 5a
  shows curves representing typical Pg responses
  at three light groupings and typical respiratory
  responses at three LAI groupings. 5b shows
  curves that represent the sum of one or more
  curves from 5a. The summation curves illustrate
  the change in net photosynthetic temperature
  response in the canopy as LAI increases.

ground and having uniform light intensity. Therefore, the temperature response curves at the various light levels should be identical in shape and magnitude to single-leaf curves at the same light intensities (same in shape because of uniform light over the entire leaf layer, and same in magnitude since the units in single-leaf and canopy photosynthesis are same if the leaf layer covers the entire canopy).

By using the Beer's- Lambert's law analogue as developed by Monsi and Saeki (1953), the light intensity on each leaf layer can be calculated. This has been done in Table 1. For simplicity, the calculated light intensities are assigned to one of three groups: "saturating light" (1100+ μmol m^{-2} s^{-1} PPF--see Monson et al. [1982] for light response curves in <u>Agropyron</u> <u>smithii</u>), "moderate light" (400 - 1100 μmol m^{-2} s^{-1} PPF), and "low light" (0 - 400 μmol m^{-2} s^{-1} PPF). These groups correspond to the empirically derived temperature response curves in Fig. 5a. which have been given corresponding designations. Similar curves were reported by Berry and Björkman (1980).

Table 1. Theoretical PPF[*] on six leaf layers at leaf area indices of 1 to 6 m^2 m^{-2}.

		LEAF LAYER					
		1	2	3	4	5	6
	1.0	**1950**					
	2.0	**1158**	**1950**				
CANOPY	3.0	688	**1158**	1950			
LAI	4.0	409	688	**1158**	1950		
	5.0	**243**	409	688	**1158**	1950	
	6.0	**144**	**243**	409	688	**1158**	1950

PPF (μmol m^{-2} s^{-1})

[*]Intensities are calculated using the Lambert's-Beer's Law analogue. Incident PPF is 1950 μmol m^{-2} s^{-1}, and the extinction coefficient is .521. Intensity groups are "saturating light" (1100+), "moderate light" (400-1100), and "low light" (0-400), and correspond to the empirical curves in Fig. 5a.

Respiration Component

R_d in the canopy is the sum of the R_d of leaves, stems, and reproductive structures. As can be inferred from Fig. 3b, the contribution of leaf respiration to canopy respiration is probably minimal since it had a minimal effect on leaf photosynthesis. In contrast, especially in more developed canopies, the respiration of stems and reproductive structures appears to contribute a large respiratory component to canopy P_n as seen in Fig. 4b, which shows high respiratory rates at higher LAI's. The empirical respiration curves in Fig. 5a reflect the fact that respiration in canopies is low at low LAI's, when the canopy is mostly leaves, and high at high LAI's, when a large

percentage of canopy biomass is stems and reproductive structures. The exponential form of the respiration curves is important in determining the temperature vs. P_n response of the canopy. The exponential form of a temperature vs. R_d response, as seen in Fig. 4b, were reported by Amthor (1989) and attributed to a Q_{10} of about 2.

Combining the Component Curves

Figure 5b shows the result of combining the curves in Fig. 5a based on the light intensity data in Table 1. For instance, if the canopy LAI is 7, Table 1 shows that the first layer of leaves from the ground has a "low light" intensity of 144 μmol m^{-2} s^{-1} PPF (one "low light" curve is added to the sum); the second layer of leaves has a "moderate light" intensity of 409 μmol m^{-2} s^{-1} PPF (one "moderate light" curve is added to the sum; and the third and fourth layers have "high light" intensities of 1158 and 1950 μmol m^{-2} s^{-1} PPF (two "high light" curves are added to the sum).

The LAI = .25 curve is .25 the magnitude of the "saturating light" curve in Fig. 5a (the "saturating light" curve represents the temperature vs. P_g response for one layer of leaves [which has a LAI of 1], so a LAI of .25 has a temperature vs. P_g response .25 that of an LAI of 1). No respiration component was added to this curve because the canopy at LAI = .25 consists almost entirely of leaves, so

respiration would probably be negligible, as it was in single leaves in Fig. 3b.

The LAI = 1 curve is the sum of the "saturating light" photosynthesis and "low LAI" respiration curves in Fig. 5a. The LAI = 2 curve is the sum of the "saturating light" curve (the top layer of leaves is light saturated according to Table 1), the "moderate light" curve (one layer of leaves is in moderate light), and the "moderate LAI" respiration curve. The LAI = 4 curve is the sum of the "saturating light" curve, the "moderate light" curve, two "low light" curves (two layers of leaves are in low light), and the "high LAI" respiration curve.

Summary

Figs. 5a and 5b demonstrate why the optimum shifts to lower temperature as LAI increases. The respiration component is essential to this shift. Without the exponential character of the respiration curves as discussed earlier, the change in temperature optimum would result only from the "moderate light" curve, and the effect would be small. These observations confirm the hypothesis that the shift in the temperature optimum observed in developing canopies is primarily a result of respiration rates increasing exponentially with increasing temperature ($Q^{10} \approx 2$) and overall increases in respiring non-photosynthetic plant tissues.

INHIBITION OF PHOTOSYNTHESIS BY

PHOTOSYNTHATES

Inhibition was noted in single-leaf photosynthesis at low temperature as seen in Fig. 3a as already discussed. Inhibition was also observed in canopy photosynthesis. When canopy photosynthesis was monitored over an entire photoperiod, P_n decreased over time with the most rapid decrease early in the photoperiod, and a progressively slower decrease as the photoperiod continued. As the canopy matured, the effect became less pronounced and eventually became imperceptible toward the end of canopy life (data not shown).

CHAPTER V

SUGGESTIONS FOR FURTHER RESEARCH

Figures 6a and b show the relationship that was found between LAI and optimum temperature, and PPF absorbance and optimal temperature, respectively, in the wheat canopy. These data indicate that optimal photosynthetic temperature is more closely related to PPF absorbance than to LAI. If further research confirmed this relationship, the advantage to the future prediction of optimal temperatures would be significant since light absorbance is more easily measured than LAI.
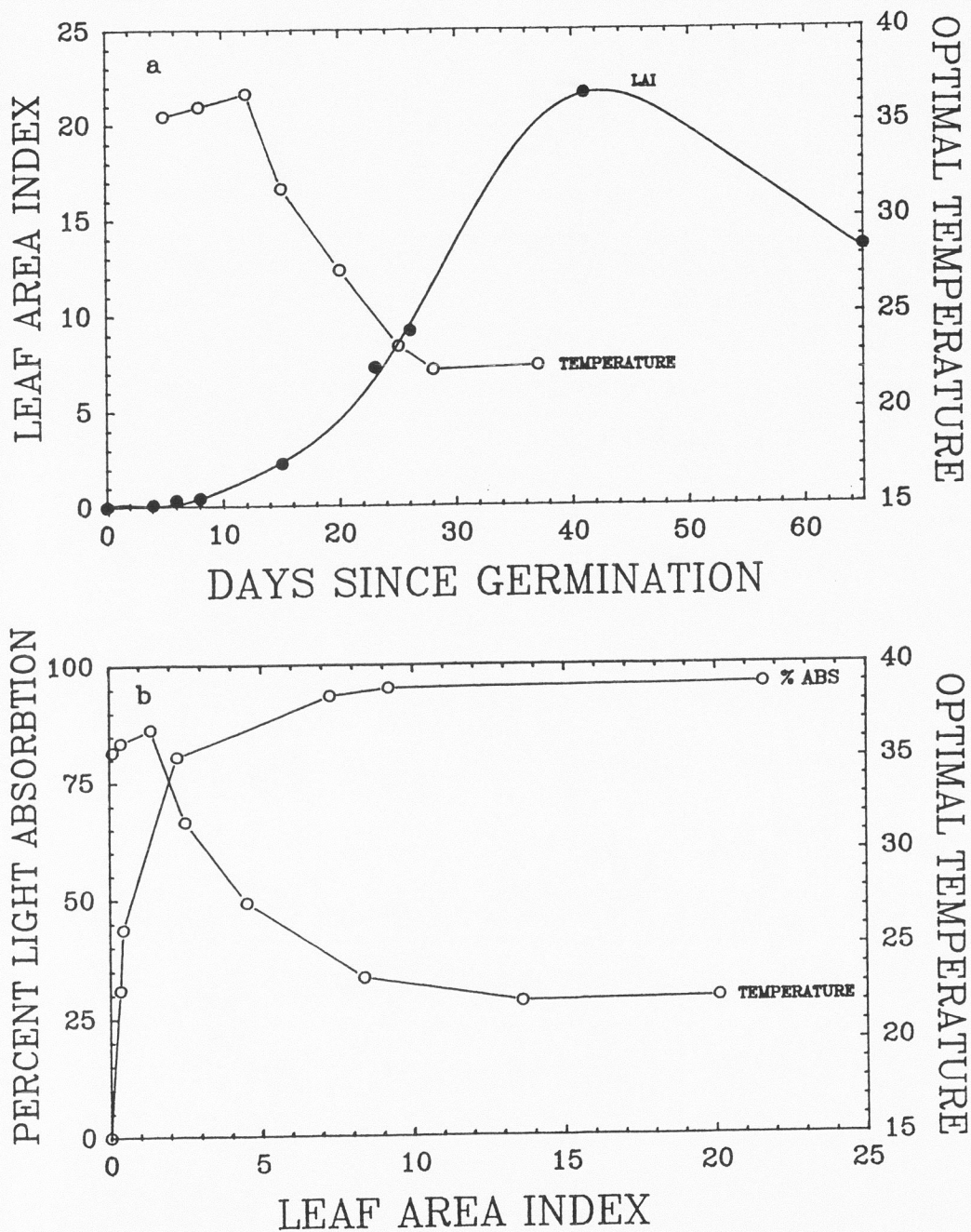
Fig. 6. The relationship between LAI, percent PPF absorbance, and optimum photosynthetic temperature in a wheat canopy. 6a shows the relationship between LAI and optimum temperature. 6b shows the relationship between percent PPF absorbance and optimum temperature.

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APPENDICES

APPENDIX A-- O_2-INSENSITIVE PHOTOSYNTHESIS

O_2-insensitive photosynthesis is defined as a state wherein a decrease in O_2 concentration or an increase in CO_2 concentration does not increase P_g. Most investigators agree that it is caused by limited supplies of phosphate in the stroma. It has been reported in several species, is usually associated with a decrease in photosynthesis, and occurs when C_i is about 700 ppm and light is saturating (Sharkey, 1985). Azćon-Bieto (1983) found that O_2-insensitivity increased after several hours in the light. He also found that it was associated with low temperature (<25°C) in ambient air, and with higher temperature (>25°C) in CO_2 enriched air (700 - 825 ppm). Similar conclusions were reached by Leegood and Furbank (1986).

Sharkey (1985, p. 71) concluded that

"...O_2 and CO_2 insensitivity occurs when the concentration of phosphate in the chloroplast stroma cannot be both high enough to allow photophosphorylation and low enough to allow starch and sucrose synthesis at the rates required by the rest of the photosynthetic component process...."

APPENDIX B-- PHOSPHATE CYCLE IN PHOTOSYNTHESIS

Two-thirds of the ATP and all the NADPH in the Calvin
cycle is used to convert PGA to triose-phosphate. This
reaction releases 8/9 of the phosphate incorporated into ATP
by photophosphorylation. The ninth is imported from the
cytosol in exchange for exported triose-phosphate. Sucrose
synthesis from triose-phosphate frees p_i, making it
available for importation into the stroma (Weis, 1981).

APPENDIX C-- CONSTRUCTION OF
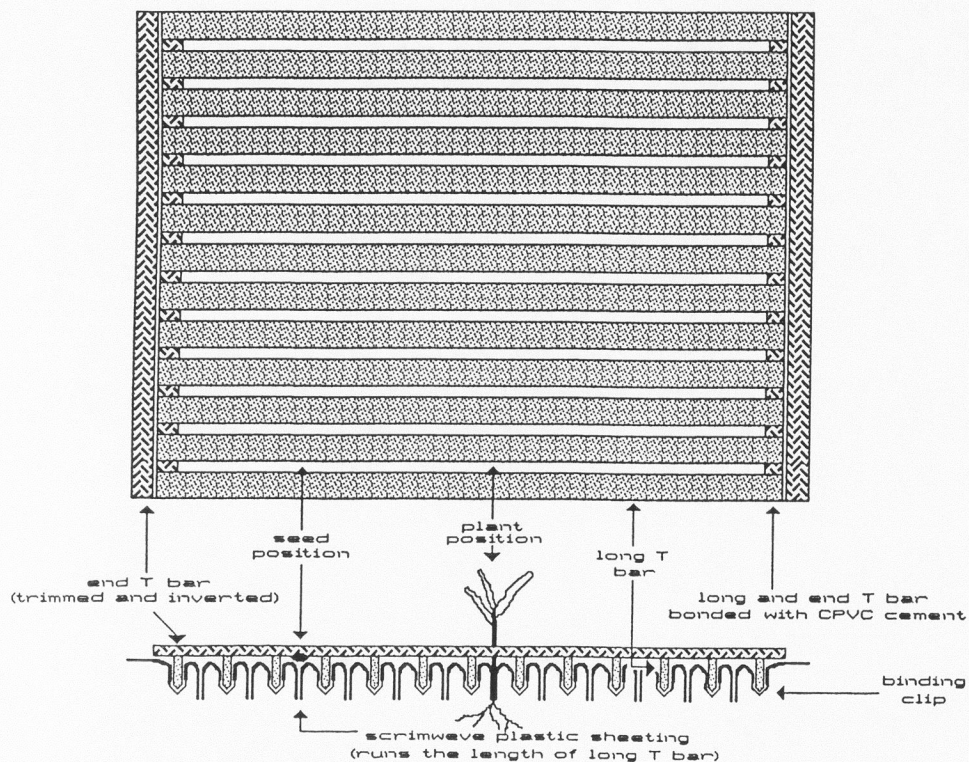
PLASTIC GROWING FLATS

Fig. 7. Top and cross sectional views of growing
    flats. Flats are constructed of white plastic T-bars
    (Cross Tee, KSH, INC., 10091 Manchester Road, St.
    Louis, Mo., 800-325-9577), woven polyolefin plastic
    ("Scrimweve", Sto-Cote Products, Inc., P.O. Drawer
    310, Richmond, Il., 800-435-2621), plastic binding
    clips, and CPVC cement (PVC cement did not bond).

APPENDIX D-- HYDROPONIC NUTRIENT SOLUTIONS

Table 2. Hydroponic starter solution.

Stock Concentration	Name	ml/100 l	Final Concentration
2 M	$Ca(NO_3)_2$	250	5 mM
2 M	KNO_3	200	4 mM
2 M	$MgSO_4$	100	2 mM
1 M	KH_2PO_4	50	.5 mM
25 mM	FeEDDHA	200	50 μM
50 mM	$Fe(NO_3)_3$	50	25 μM
*	Micro-nutrients	20	*
30 mM	$MnCl_2 \cdot 4\ H_2O$	20	6 μM
.5 M	$Na_2SiO_3 \cdot 9\ H_2O$	60	300 μM
5.5 mM	H_3BO_3	180	10 μM
100 mM	FeHEDTA	50	50 μM

*See Table 4.

Table 3. Hydroponic refill solution.

Stock Concentration	Name	ml/100 l	Final Concentration
2 M	$Ca(NO_3)_2$	75	1.5 mM
2 M	KNO_3	200	4 mM
2 M	$MgSO_4$	25	.5 mM
1 M	KH_2PO_4	100	1.0 mM
25 mM	FeEDDHA	20	5 μM
50 mM	$Fe(NO_3)_3$	10	5 μM
*	Micronutrients	20	*
30 mM	$MnCl_2 \cdot 4\ H_2O$	20 (2 after anthesis)	6 μM
.5 BM	$Na_2SiO_3 \cdot 9\ H_2O$	14	70 μM
5.5 mM	H_3BO_3	50	2.75 μM

*See Table 4.

Table 4. Hydroponic micronutrient solution.

Stock Concentration	Name	Final Concentration
10 mM	$ZnSO_4 * 7\ H_2O$	2.0 μM
0.3 mM	$CuSO_4 * 5\ H_2O$	.06 μM
0.15 mM	$Na_2MoO_4 * 2\ H_2O$	.030 μM