

AN ABSTRACT OF THE THESIS OF

Xiaomei Li for the degree of Doctor of Philosophy in Soil Science presented on

April 10, 1997 Title: Effects of Root Temperature and Soil Water Potential on Spring

Wheat Seedlings (Triticum aestivum L. Siete Cerros)

Abstract approved: *Redacted for Privacy*

Larry Boersma

Laboratory experiments were conducted to investigate the physiological mechanisms of plant response to root temperature and soil water stresses by evaluating the growth and the concurrent physiological functions of plants under controlled root temperature and soil water potential. Leaf area, shoot and root dry masses, leaf water potential (ψ_l), osmotic potential (π), and rates of photosynthesis (P_n), transpiration (E), and respiration were measured in the combinations of five soil water potentials ranging from -0.03 to -0.25 MPa and seven root temperatures ranging from 12 to 32°C.

A mathematical description of plant processes based on thermodynamic considerations was used to characterize plant response to water and temperature stresses. The activation energy (B), optimum temperature, and base rates (K_0) were used in the equation.

The B increased with increasing water stress for growth rates and P_n . Increase of B was higher for the growth rates, suggesting that growth is more sensitive to water stress than P_n . The K_0 of growth rates increased linearly with turgor potential (ψ_p). However, K_0 was independent of ψ_p for P_n . This results suggest that the rate of leaf expansion is directly proportional to ψ_p and that the proportionality coefficient was affected by

temperature and water stresses in a similar manner to photosynthesis. This indicated that the extensibility of plant cells is metabolically controlled.

A mathematical model based on mass balance considerations was used in combination with experimental measurements of rate of net photosynthesis, leaf area, and shoot/root dry masses to determine photosynthate allocation between shoot and root. Partitioning of photosynthates to roots was the lowest at 22-27°C root temperature regardless of soil water potential, and increased at both lower and higher root temperatures. Partitioning of photosynthates to the root increased with decreasing soil water potential. Under the most favorable conditions, e.g. at -0.03 MPa soil water potential and 27°C root temperature, the largest fraction, 57%, of photosynthates was allocated to the shoots. Under the most stressed conditions, e.g. at -0.25 MPa and 32°C root temperature, the largest fraction, more than 80%, of photosynthates was allocated to roots.

Effects of Root Temperature and Soil Water Potential on

Spring Wheat Seedlings

(Triticum Acestorum L. Siete Cerros)

by

Xiaomei Li

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 Xiaomei Li

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EFFECTS OF ROOT TEMPERATURE AND SOIL WATER POTENTIAL
ON SPRING WHEAT SEEDLINGS
(TRITICUM AESTIVUM L. SIETE CERRORS)

1. INTRODUCTION

A growing plant experiences two distinct environments: the atmosphere environment above the soil surface and the soil environment below the soil surface. The major variables of the aerial environment which influence growth of plants are temperature, light, relative humidity, and carbon dioxide. The major soil properties which influence growth of the plants are availability of water and mineral nutrients and soil temperature.

This thesis focuses on the responses of plant growth and physiological functioning to soil water and temperature stresses. Plant growth results from a complex system of physical, chemical, and physiological processes. Responses of these processes to soil water and temperature stresses and their interactions are studied from a system perspective rather than studying one or two aspects of the plant.

The influences of water and temperature on overall plant growth process and productivity have received considerable attention in the past (Nobel, 1991; Kramer and Boyer, 1995). Considerable research has been conducted at how plants respond to temperature and water stresses, and particularly, how they adapt to stressed environmental conditions in order to maintain a favorable water status for growth and development. However, a general procedure which can be used to characterize such responses with physiologically meaningful parameters has been lacking. The mechanisms by which water

and temperature stress reduce plant growth and crop yield are unclear. It is not known how much of overall growth reduction is caused by the effects of decreased turgor potential on cell enlargement and stomatal opening, how much results from direct interference with enzyme mediated processes, or how much is due to effects on rates of transport within the plant. Importantly, the inter-relationships between the responses of physiological processes and growth are unclear because plant growth and physiological functioning are rarely studied simultaneously.

Plant processes, such as photosynthesis, respiration, transpiration, and growth, are influenced by plant water potential (Kramer and Boyer, 1995). The leaf water potential, osmotic potential, and turgor potential have been widely used as measures for plant response to water stress (Passioura, 1982). Therefore, measurements of leaf water potential and its components are important to the understanding of the performance of plants under stressed conditions. The leaf water potential is a dynamic quantity, continually changing with soil water potential and root temperature. To understand the physiological processes within a plant, it is necessary to obtain the diurnal progression of plant water potentials and the concurrent physiological functions, such as photosynthesis and transpiration.

The leaf water potential decreases during the day. Water stress causes lower minimum leaf water potential and osmotic potential (Reicosky, Campbell, and Doty, 1975; Ackerson, 1981). However, most of the reports in the literature provide only qualitative descriptions of the general response of leaf water potential to soil water potential. A

quantitative analysis is still lacking. Little information on the response of the daily course of plant water potential to root temperature has been reported.

Turgor has been considered as a major factor influencing plant growth (Kuang, Turner, and Henson, 1990), stomatal aperture, and photosynthesis (Ludlow, Fisher, and Wilson, 1985) under water stressed conditions. There have been controversial conclusions regarding the role of turgor potential in plant growth (Passioura, 1988; Munns, 1988; Kuang et al., 1990). From one perspective, there are reports suggesting that growth is controlled by turgor potential, based on correlation between turgor potential and the growth rate. From a second perspective, there are reports arguing that growth does not depend on turgor, which is a conclusion based on the observed lack of correlation between turgor and growth rate (Passioura, 1988; Munns, 1988).

As water stress increases, plant cells start to dehydrate and lose turgidity. Osmotic adjustment is regarded as one of the important mechanisms that occur in plants in response to decreasing water potential. This mechanism refers to the increase in solute concentrations (Turner, 1986; Munns, 1988). The decrease in osmotic potential arising from the accumulation of solute in the cells causes water to flow into the dehydrating cells. However, the factors that induce solute accumulation in response to increasing water stress are unclear (Kuang et al., 1990).

The rate of plant growth generally increases with increasing root temperature to an optimum and then decreases with further increasing root temperature. Cooper (1973) reported contradictory results and concluded that the shape of the curve of net photosynthetic rate vs. root temperature differed between species, but in all the species

examined there was a broad optimum root temperature band. He suggested that, in general, net photosynthetic rate may be independent of root temperature over a range of 15°C to 35°C, except at the extremes. Similar results were reported by Barlow, Boersma, and Young (1977) for corn seedlings and by Gosselin and Trudel (1984) for tomatoes. The physiological mechanisms underlying the response of the photosynthetic process to root temperature is not well understood.

Cooper (1973) also pointed out that the change in shoot dry mass with unit change at root temperature above the optimum was steeper than below the optimum, possibly because different mechanisms were involved in limiting plant growth in above and below the optimum root temperature. The optimum root temperature varies with plant species. Duke, et al. (1979) reported that root dry mass of soybean grown in a growth chamber with the air temperature of 20°C at a 13°C root temperature was 12 % of the root dry mass of plants grown at a 20°C root temperature. The roots at the lower root temperature also exhibited less branching. Rate of photosynthesis at a 20°C root temperature was approximately three times higher than at a 13°C root temperature. They also found that the rate of respiration at 20°C was higher than at 13°C. They concluded that the root temperature affected the growth of soybean plants by affecting the rates of photosynthesis and respiration. Although the general response of plant growth to root temperature has been recognized, a theoretical analysis which could accurately quantify that response is lacking.

It has been demonstrated that the theory which relates reduction in rate of photosynthesis under water stress conditions to the limited supply of CO₂ due to stomatal

closure is not accurate throughout the range of the photosynthetic rate. A widely accepted fact is that stomatal and non-stomatal factors are responsible for a decreased photosynthetic rate under water stress (Jones, 1976; Boyer, 1976, Kanechi et al., 1996).

Stomata play a pivotal role in controlling assimilation and transpiration. Because stomata are turgor-operated valves, limitation to water uptake by roots and transport within the plant, diminished soil water supply, or high atmospheric demand all result in lowering the plant water status, thus allowing stomatal control of the rate of gas exchange. Stomatal movement provides the leaf with a mechanism to change both the partial pressure of CO_2 at the site of carboxylation and the rate of transpiration. Changes in transpiration rate could indirectly affect the rate of photosynthesis by affecting the leaf water potential and leaf temperature.

Non-stomatal limitations to the rate of photosynthesis can be due to a decrease in chloroplast activity, increased mesophyll resistance, and decreased rate of translocation. The mechanisms of non-stomatal inhibitions remains undetermined. Some authors (Farquhar and Sharkey, 1982) relate the non-stomatal factors to the enzymes catalyzing the biochemical reactions in the photosynthetic process. It was hypothesized that decreased translocation of assimilates from the photosynthetic centers may be the cause of lower net photosynthetic rate under water stress (Ekasingh, 1982).

Water stress develops in a plant when water supply from roots cannot satisfy transpiration loss. Blizzard and Boyer (1980) measured the conductance of the soil and the conductance of a soybean plant. Their results revealed that the conductance of the plant was always less than the conductance of soil, indicating that the water movement

through the soil-plant system was limited more by the plant than by the soil. In the plant, the conductance of the root tissue was always less than that of the leaf. Thus, the water permeability of the root may present a mechanism for controlling the rate of transpiration in addition to stomatal opening under water stressed conditions (Slatyer, 1967).

A primary reason for the inadequate understanding of plant processes under water stress is the failure of many researchers to adequately define the degree of stress imposed in their experiments. Water stress is often treated as stressed and non-stressed. This has made the quantitative comparison of separate experiments difficult, if not impossible. A uniform level of water stress can be applied by growing plants in a nutrient solution with solutes added to produce a desired water potential. Polyethylene glycol (PEG) of high molecular weight has been used for this purpose (Michel and Kaufmann, 1973; Money, 1989). This made it possible to design a series of water stress levels. A semi-permeable membrane separating the plant rhizosphere from the PEG solution was introduced by Zur (1966). This technique was used in many studies to provide a "clean" environment around the root system (Sedgley and Boersma, 1969; Sepaskhah and Boersma, 1979; Ekasingh, 1982).

Soil water stress often interacts with root temperature (Barlow et al., 1977). Few experiments have been performed where both soil water potential and temperature were involved as controlled variables, especially in a series of stress levels.

Because of the importance of these factors to the understanding the plant ecology, A series of laboratory experiments was conducted to quantitatively evaluate the effects of root temperature and soil water potential on plant growth and physiological functions.

Combining water and temperature stresses makes it possible to study the interactive effects of the two environmental factors. The experiments included the measurements of the growth of leaf area, and shoot and root dry masses, the leaf water potential and osmotic potential, and the rates of photosynthesis, respiration, and transpiration of spring wheat seedlings (Triticum Aestivum cv. siete cerros) subjected to different soil water potential and root temperature levels.

The understanding of plant growth responses to the environmental factors should provide an explanation of the responses observed in the experiment. There are at least two purposes for a successful research: first, to test or to prove the hypothesis, and second, to obtain more information by combining current knowledge with the experimental observations.

Mathematical description of plant processes based on thermodynamic considerations can be used to describe the response of plants to soil water and temperature stresses. Johnson and Thornley (1985) developed an equation describing temperature response of plant processes by combining the Arrhenius equation for chemical reactions and the Boltzman distribution of enzymes between the active and inactive states and named it the Arrhenius equation for plant processes. The applicability of this equation to whole plant processes and its potential as a tool for studying the combined effects of root temperature and soil water stress have not been explored. This thesis explores this possibility to provide a quantitative description for observed response of plant processes to water and temperature stresses in terms of the mechanistically meaningful parameters,

which include activation energy of plant processes. The roles of turgor and metabolic control in plant growth are discussed.

Besides providing a quantitative description of the complex interactions among carbon assimilation, translocation and utilization during plant growth, a properly designed mathematical model may also be used, in combining experimental observations, to evaluate parameters that are not readily measurable for the particular experimental techniques (McCoy et al. 1989, 1990). In this study I analyze the effects of soil water potential and root temperature on photosynthate partitioning of spring wheat seedlings. Partitioning of photosynthates is evaluated by fitting a simple plant growth model, derived on the basis of mass balance considerations, to experimental observations of the rate of net photosynthesis, root and shoot dry mass accumulation and leaf area expansion.

The experimental procedures are reported in Chapter 2, Materials and Methods. In Chapters 3 through 6, the responses of the leaf water potential, transpiration, photosynthesis, and plant growth to root temperature and soil water potential stresses are discussed. In the Chapters 7 and 8, the interactions between physiological functions are discussed, based on theoretical considerations. The conclusions and recommendations were summarized in the Chapter 9.

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2. MATERIALS AND METHODS

Experimental Design

The experiment was designed to study the effect of root temperature and soil water potential on the growth of spring wheat seedlings (Triticum aestivum cv. siete Cerreros). Seven experiments, one at each root temperature of 12, 14, 17, 22, 27, 29, and 32°C, were carried out. For each experiment, there were five soil water potential treatments -0.03, -0.06, -0.10, -0.17, -0.25 MPa. There were five replicates each consisting of one chamber holding three soil slabs for each soil water potential treatment. This results in a total of 25 experimental units, each with three soil slabs. The 25 experimental units were randomly placed in the 25 experimental chambers in such a way that every possible arrangement would have the same probability of occurring. This was achieved by using a computer algorithm. The five replicates for each soil water potential treatment were sampled in a random sequence. The sampling sequence was predetermined by using the same computer algorithm.

Control of Experimental Conditions

Root Temperature

The chambers containing the osmotic solution were surrounded by a water jacket, which was connected to a constant temperature water bath. Water was constantly pumped from the water bath through this jacket and recirculated to the water bath. The

temperature of the osmotic solution was controlled at the desired treatment level by the recirculating water (Barlow and Boersma, 1976).

Soil Water Potential

Control of soil water potential was achieved by inserting the soil slabs, which were encased in a semi-permeable membrane, into osmotic solutions with pre-determined potentials. The osmotic solutions were prepared by dissolving polyethylene glycol-8000 (PGE) in distilled water (Michel and Kaufmann, 1973; Money, 1989). The water potential of the solution was determined by the amount of PGE dissolved in the water. Nutrients were mixed with the osmotic solution to provide the source of nutrients for the plants during the experiments. The assumption was made that nutrient elements can pass through the cellulose semi-permeable membrane freely, and thus do not affect the water potential. Concentrations of PGE were calculated using the empirical equation reported by Michel (1983):

$$P = 0.129 * [PEG]^2 * T - 14 * [PEG]^2 - 0.4 * [PEG], \quad [2-1]$$

where P is osmotic potential or water potential of the [PGE] solution in MPa; T is temperature expressed in °C; and PEG is the concentration of polyethylene glycol-8000 expressed in kg/kg H₂O.

Nutrient Solution

The same nutrient solution was used during the cultivation and measurement period. The composition of the nutrient solution was designed by considering several

nutrient solutions, used by several workers, for various plant species (Hoagland and Arnon, 1950) and was tested in a preliminary experiment. The compositions and their concentrations of the nutrient solution are showed in Tables 2-1 and 2-2.

Table 2-1. Composition of the nutrient solution used for growing spring wheat seedlings.

Compound	Mol.Wt	Nutrient solution		Stock solution
		-- g --	--mol/L-- --g/L --	
MgSO ₄ .7H ₂ O	246.16	0.002	0.4929	98.58
Ca(NO ₃) ₂ .4H ₂ O	236.16	0.005	1.1808	236.16
KH ₂ PO ₄	136.09	0.003	0.4083	81.65
NH ₄ H ₂ PO ₄	115.03	0.001	0.1150	23.01
K ₂ SO ₄	174.26	0.001	0.1743	34.85
		mmol/L	mg/L	
H ₃ BO ₃	61.80	0.0230	1.4214	0.2843
ZnSO ₄ .7H ₂ O	287.56	0.0019	0.5464	0.1093
MnSO ₄ .H ₂ O	169.01	0.0048	0.8028	0.2605
CaCl ₂ .2H ₂ O	147.00	0.0045	0.6615	0.1323
CuSO ₄ .5H ₂ O	249.49	0.00078	0.1934	0.0387
Na ₂ MoO ₄ .2H ₂ O	241.95	0.00025	0.0605	0.0121
FeEDDHA (6% Fe)	455.90		16.70	3.4

Table 2-2. The concentrations of nutrient elements.

Macroelement (mg/L)		Microelement (mg/L)	
Ca	200.5	Zn	0.150
Mg	48.6	Cu	0.050
K	195.5	Mn	0.250
N	154.0	Mo	0.025
P	124.0	B	0.250
S	96.3	Fe	1.000
		Cl	0.180

Other Environmental Parameters

All experiments were performed in a walk-in growth room where the temperature and relative humidity were controlled. The day and night air temperatures were maintained at 20°C and 19°C, respectively. The relative humidity was controlled at 45 to 50 percent. The light intensity was 210 $\mu\text{mol m}^{-2}$. The light period was controlled at 14 hours. Lights were turned on in four steps at 7:00, 7:30, 7:50, and 8:00 and turned off at 21:00, 21:30, 21:50, and 22:00.

Experimental Procedure

Preparation of the Soil Slabs

Sandy loam soil from the Vegetable Crops Farm of Oregon State University in Corvallis was passed through a 2 mm screen. Before use, the soil was spread in layers approximately 1 cm thick in trays and heated at 95°C for 48 hours. This treatment killed

fungal spores thereby reducing the growth of fungi that attack the semi-permeable membrane. Thus, the treatment helped to lengthen the useful life of the membrane. The soil was packed in lucite frames to form soil slabs 0.8 cm thick, 30 cm long, and 10 cm wide (Sedgely and Boersma, 1969). A vibrating device was used to ensure uniformity of soil packing in the slabs.

Preparation of the Plants

Planting

Spring wheat seeds were soaked in water for one hours, after which the seeds were spread in a tray and covered with wetted filter paper to germinate for two days. The healthy seeds were selected and planted (3 cm deep) into the soil slabs. Eight seeds were planted in each slab. A total of 100 slabs were cultivated. The slabs were saturated with water and placed in a growth chamber. The day and night temperatures of the growth chamber were 20°C and 19°C, respectively. The light intensity was 400 $\mu\text{mol m}^{-2}$ and the light period was 14 hours.

Thinning

Two days after germination, plants were approximately 7 to 8 cm height. Five uniform plants were selected in each slab and the remaining seedlings were removed. After thinning, the planted soil slabs remained in the growth chamber. During germination and the first three days after germination, the surface of the slabs were irrigated with water or

nutrient solution on alternate days. During the remaining of the period before transplanting, the slabs were irrigated by immersing them into a 3 cm deep nutrient solution for 1 hour every other day. The nutrient solution wetted the soil through capillary action.

Transplanting

Two weeks after thinning, 78 slabs were selected for the experiments. Three slabs were used for the measurements of initial leaf area, shoot dry mass, and root dry mass (day 0). The 75 slabs were transferred for the experimental treatments.

The side covers of the soil slabs were removed, leaving the frame with soil and plant roots. The assemblies were inserted into semi-permeable cellulose membrane bags. The lower end of each bag was sealed by folding and clamping the folds with a plastic clip. The upper end of the bag was secured by braces. These braces also supported the assembly when it was placed in the experimental chamber. Next, the assemblies were placed into the chambers containing the osmotic solutions with nutrients in the walk-in room. Three slab assemblies were suspended in each chamber.

Measurements

Leaf Area and Dry Mass:

Plants were harvested on days 0, 2, 3, 4, 5, and 7(6) following exposure to the treatment conditions at 10:00 according to predetermined sampling sequences. One

chamber, holding three slabs, was harvested each day for each treatment. Leaf area was measured with the LI-COR 3100 leaf area meter. Plant roots were washed free of soil using a jet or spray of water aided by hand to remove all the soil. Shoot dry mass was obtained by drying leaves and stems in an oven at 60°C for 48 hours. Root dry mass was obtained by the same method. The three slabs were measured separately as replicates.

The leaf area, shoot and root dry masses were averaged over three replicates for each treatment. Results are showed in tables A1 through A3 in Appendix I.

Leaf Water Potential Components

Daily cycles of the total leaf water potential were measured using the pressure chamber on day 3 and day 5. The samples were taken from plants designated to be harvested later during the same day for leaf area and dry weight measurements. Only third mature leaf from the bottom was used for leaf water potential measurements. This eliminated variation due to leaf position. Leaves were wrapped with several layers of Saran wrap immediately after being excised to prevent water loss. The pressure chamber was pressurized slowly at the rate of 10 s/bar. The end-point was observed with a hand-held magnifying glass. The pressurization ceased when cell sap appeared at the cut end of the leaf. The pressure was allowed to release slowly at less than half of the pressurization rate. The pressure at the end-point was recorded when the sap at the cut end of the leaf just disappeared. This procedure prevented over pressurization. The accuracy of the pressure chamber is ± 0.05 MPa.

Leaf area of each sample was measured after total water potential measurement, adding it into the value of leaf area measured later in the day. The sample leaves were placed into a section of plastic tubing. The ends of the tubing were sealed with rubber stoppers. The tubes were immediately frozen in dry ice for later osmotic potential measurements.

The osmotic potentials were measured with a thermocouple psychrometer (Wescor Vapor Pressure Osmometer Model 5100C). The accuracy of the instrument is ± 0.03 MPa. The osmometer was cleaned and calibrated using standard KCl solutions before each measurements series. The osmometer was rechecked with a standard solution after every three to four hours of operation. The osmometer was cleaned when the measurements were completed.

The samples were thawed at room temperature for at least two hours before measuring of osmotic potential. Cell sap was extracted after thawing by forcing the plastic tubing containing the sample leaf between steel rollers. A filter paper disk with a diameter of 7 mm was placed in the sample holder of the osmometer. Ten microliters of extracted sap were aspirated with a micropipet and placed on the filter paper disk. Care was taken during this process not to spill the sap outside of the sample cup. The osmotic potential of the sap was measured and recorded. Finally the room temperature was recorded, which was used in the later calculations.

The osmotic potential measured by the above method may not represent the true value of osmotic potential of solution in the cytoplasm and vacuole. When cell membranes are disrupted to release cell sap, relative pure apoplastic water in a cell wall or xylem

mixes with cell sap and increases the osmotic potential (Boyer and Potter, 1973; Tyree, 1976; Acock and Grage, 1981). The magnitude of this error is proportional to the ratio of apoplastic water to symplastic water. Apoplastic water fractions ranging from 5 to 30 percent have been inferred in dryland winter wheat (Campbell, Papendick, and Rabie, 1979). Therefore, a factor of 10% was used for correcting this dilution effect of apoplastic water (Boyer and Potter, 1973; Campbell et al., 1979). The corrected values of osmotic potential were calculated by

$$\pi = \pi_m \frac{1}{1 - 0.1} \quad [2-1]$$

where π_m is the measured value of osmotic potential.

The measurements of leaf water potential and the corrected values of osmotic potential are shown tables B1 through B6 in Appendix I. Turgor potentials of the leaves were calculated according to

$$\psi_l = \pi + \psi_p \quad [2-3]$$

where ψ_l is the leaf water potential, MPa, π is the corrected osmotic potential, MPa, and ψ_p is the turgor potential, MPa. Results are also shown in Tables B1 through B6 in Appendix. It was assumed that the matric potentials were negligible.

Photosynthesis and Transpiration

Daily cycles of photosynthesis rate were measured during days 3 and 5 after plants were exposed to the treatment conditions. Measurements were made using a LI-COR 6200 portable photosynthesis system on plants to be harvested the next day for dry mass

and leaf area measurements. The third mature leaf from the bottom was used for these measurements.

The LI-6200 consists of 3 major components: a leaf chamber, the LI-6250 CO₂ analyzer, and a control console. Air temperature, leaf temperature, and relative humidity are measured in the leaf chamber. The pump in the LI-6250 circulates air from the chamber to the analyzer where the CO₂ concentration is measured and then returns the air to the chamber. The rate of photosynthesis, transpiration, and leaf and air temperature are measured simultaneously.

When a plant photosynthesizes, it takes up CO₂. As it respire, it emits off CO₂. The net exchange of CO₂ between the leaf and the atmosphere is measured with the Li-6200 by enclosing the leaf in a closed chamber and monitoring the rate at which the CO₂ concentration in the air changes over a short time interval. The net photosynthesis rate is calculated using the rate of change and other factors, including the amount of leaf area that was enclosed, the volume of the enclosure, leaf and air temperature, and vapor pressure.

A leaf was placed in the (0.25 liter) leaf chamber, assuring there was adequate contact between the leaf and the leaf temperature thermocouple. The chamber was closed and latched. Thirty seconds were allowed to lapse to let the system reach a steady state condition. The instrument was programmed to record the data every 5 seconds. One observation consisted of 4 data readings. Three observations were made for each measurement. After the measurement, the leaf was removed from the chamber and the width of the leaf was measured with a small ruler. At least three measurements were

observed and the average was entered into the instrument. The instrument calculates the leaf area enclosed in the leaf chamber by multiplying the average width of the leaf and the length of the leaf chamber. The rate of net photosynthesis, transpiration, stomatal conductance, and intercellular CO₂ concentration were calculated for each of the three observations. These values can be viewed on the display of the instrument. The data set can be stored in the instrument's memory if desired.

Respiration

Respiration rate measurements were the same as the net photosynthesis rate measurement except that the leaf chamber was covered with a piece of black cloth to exclude light.

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3. LEAF WATER POTENTIAL

Introduction

The leaf water potential and its components: osmotic potential and turgor potential, have been widely used as parameters describing plant water status and as measures for plant response to water stress (Bradford and Hsiao, 1982; Passioura, 1982; Kramer and Boyer, 1995). Positive turgor may not be essential to continued photosynthesis (Jones and Rawson, 1970) but there is no doubt that it is associated with a rapid photosynthesis rate (Turner, 1974). Water potentials are also associated with stomatal conductance and with leaf growth (Kuang et al., 1990; Ludlow et al., 1985). Measurements of leaf water potential and its components are, therefore, crucial to the understanding of the performance of plants in stressed environments.

Soil water potential and root temperature are two of the most important environmental factors to influence plant water potentials. Several studies on the responses of the plant water potential to temperature have been reported in the literature (Kleinendorst and Brouwer, 1972; Frank, Power, and Willis, 1973; Barlow, Boersma, and Young, 1977; Kirkham and Ahring, 1978; Graves, Dona, and Joly, 1989). The results varied with plant species, and experimental procedures, and conditions. Kirkham and Ahring (1978) observed that the leaf water potential and osmotic potential of winter wheat grown in a growth chamber with an air temperature of 25°C increased with increasing root temperature, reached the maximum value at the root temperature of 24.7°C and decreased as the temperature increased. Graves et al. (1989) reported that the leaf water potential of

red maple grown in a greenhouse with an air temperature of 24°C decreased with increasing root temperature from 18°C to 36°C. Barlow et al. (1977) observed an opposite result with corn seedlings.

The effect of soil water potential on the water potential of plants has been studied by many researchers for various plant species (Kramer and Boyer, 1995). Leaf water potential generally decreased with increasing soil water stress. Leaf turgor may be partially conserved by solute accumulation (Turner et al., 1978; Morgan and Cordon, 1984). The water potential of a plant is dynamic, continually changing with soil water potential and root temperature. To understand fully the physiological processes within a plant, it is necessary to observe the diurnal progression of plant water potentials and the concurrent physiological responses. There are several reports in the literature on the response of the daily plant water potentials to water stress for diverse plant species under field conditions (Reicosky et al., 1975; Turner et al., 1978; Acevedo et al., 1979; Byers et al., 1988) and under controlled environmental conditions (McCree, 1974; Ackerson, 1981; Henson et al., 1989). Reicosky et al. (1975) observed that the leaf water potential for corn in the field reached its maximum value of -0.5 MPa at sunrise and then decreased to a minimum value of -1.2 MPa when radiation reached its peak value. The maximum and minimum values of leaf water potential of corn decreased with decreasing soil water potential. Ackerson (1981) studied the effect of water stress on the diurnal course of leaf water potential and its components for cotton grown in controlled conditions. He reported that stressed plants had a lower minimum leaf water potential and lower minimum osmotic potential, but maintained turgor pressure. Similar results were reported by McCree (1974) for sorghum.

Most of these reports provide only qualitative description of the general response of leaf water potential to water stress. A quantitative analysis is lacking. In the meantime, little information on the response of the daily course of plant water potential to root temperature has been reported. In this chapter, the responses of diurnal change of leaf water potential and its components to soil water potential and root temperature are investigated. Quantitative description of these responses was developed based on theoretical considerations.

Results

Leaf water potential of plants is related to osmotic potential and turgor potential as follows:

$$\psi_l = \pi + \psi_p, \quad [3-1]$$

where ψ_l is the total leaf water potential of plants, MPa; π is osmotic potential, MPa; and ψ_p is turgor potential, MPa.

The diurnal trend of total leaf water potential and osmotic potential were measured throughout the light period as described in Chapter 2. Results of the measurements are shown in tables B1 to B6 in Appendix I. The turgor potentials calculated by equation [3-1] are also shown in tables B1 to B6 in Appendix. The daily trends of total leaf water potential and its components were similar for all treatments. An example of diurnal courses of total leaf water potential, osmotic potential, and turgor potential is illustrated in figure 3-1. There were differences between the measurements made on the third and fifth days, especially at the lower soil water potential and higher root temperatures treatments.

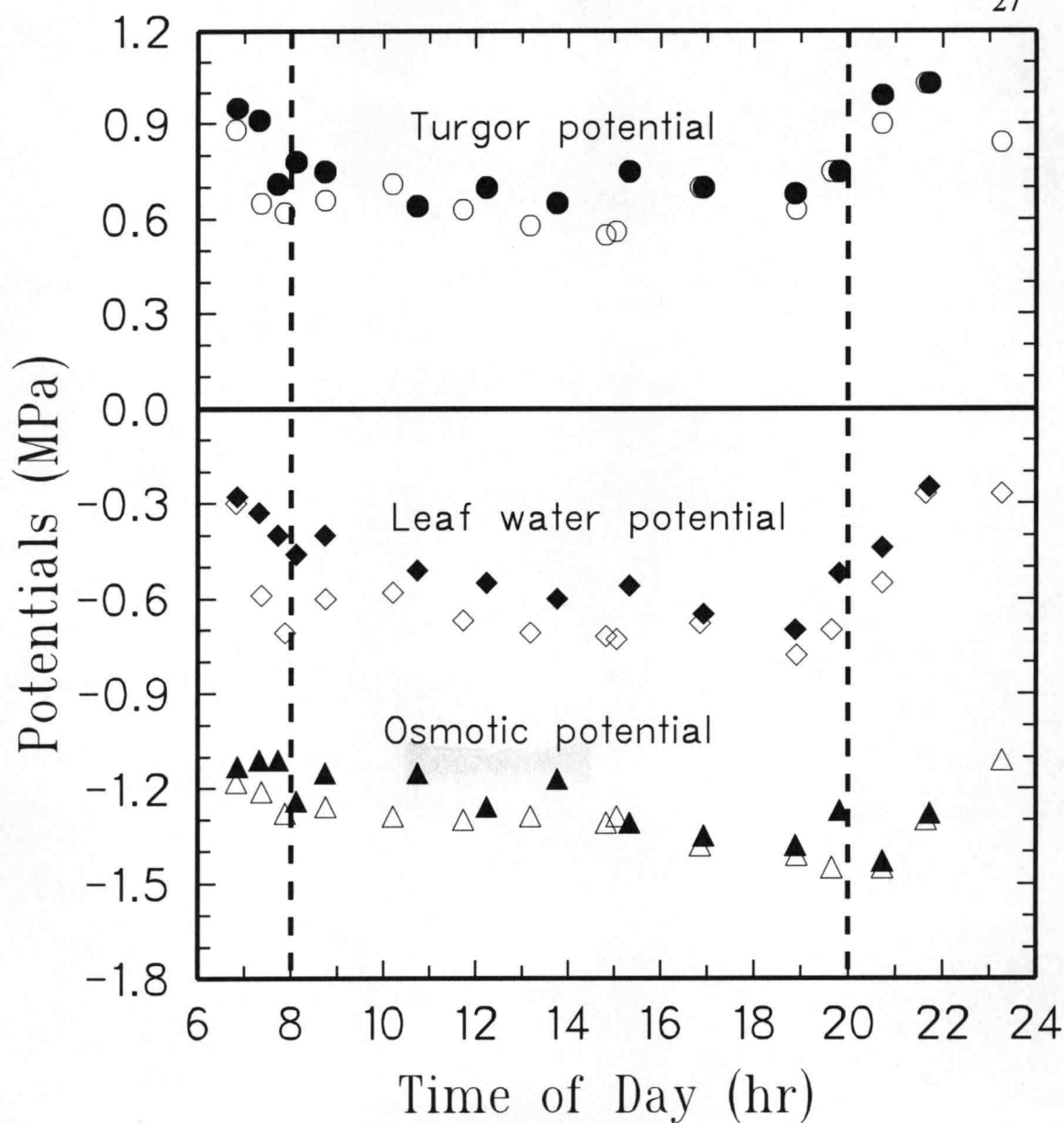


Figure 3-1. Diurnal courses of leaf water potential, osmotic potential, and turgor potential at the soil water potential of -0.03 MPa and root temperature of 22°C . The open and closed symbols represent measurements made on the third and fifth days following exposure to the experimental conditions. All lights were on during the time between the dashed lines.

I will postpone analyzing these differences for the time being. The following analyses are conducted using the measurements made on the third day.

Total Leaf Water Potential

The total leaf water potential decreased rapidly during the few hours after the lights were turned on and thereafter continued to decrease at a lower, but nearly constant rate throughout the remaining light period (Figure 3-1). Once the first light was turned off the total leaf water potential quickly recovered. The total leaf water potential returned to the morning value approximately 30 to 40 minutes after all lights were turned off. The diurnal trend of leaf water potential was similar for all treatments but the magnitude varied. To describe the change of leaf water potential during the light period, a mathematical equation was developed based on theoretical considerations.

Mathematical description

The total water potential of plant leaves during a day-night cycle is viewed as the response of the plant as a simple system to its environmental factors without consideration of the detailed mechanisms involved.

The total water potential of the plant leaves depends on an interaction between the evaporative demand and the water supply to the roots. The external driving force, or evaporative demand, is directly related to radiation intensity, temperature, and humidity. Water supply to the leaves depends on the plants resistance to water movement as well as soil water potential.

Under given and constant environmental conditions and soil-plant combinations, the system approaches a steady state. The exact value of leaf water potential at this steady state depends on the balance between the evaporative demand and the ability to supply water to the leaves. For the experiments of this study, the air temperature, humidity, and radiation intensity were controlled so that they remained constant after all lights were turned on. Thus, the evaporative demand was constant for all the treatments during the full light period. Define E_p as the potential evaporation rate dictated by external demand. E_p has the units of transpiration rate, $\text{mol m}^{-2} \text{s}^{-1}$.

While the water supply depends on the water potential gradient through the soil-plant system and the conductance of the system to water flow expressed as

$$E_{\text{sup}} = L(\psi_{\text{soil}} - \psi_l) \quad [3-2]$$

where E_{sup} is the rate of water supply with the same units as E_p , L is the conductance of soil-plant, $\text{mol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$, ψ_{soil} is the soil water potential, MPa, and ψ_l is the leaf water potential, MPa. When lights are turned on L is larger but its value decreases slowly until a steady state condition is reached.

At steady state, the supply and the demand is equal to one another and the leaf water potential approaches a lower value, referred to as a minimum value, ψ_{min} , written as:

$$\psi_{\text{min}} = \psi_{\text{soil}} \frac{E_p}{L} \quad [3-3]$$

If a plant is considered as a system and the leaf water potential as the system response to its environment, it is assumed that under constant environmental conditions, the rate at which the system moves toward the steady state is proportional to the

difference between its current state and the steady state. For the change of the total leaf water potential as time can be written:

$$\frac{d\psi_l}{dt} = \frac{-(\psi_l - \psi_{min})}{k}, \quad [3-4]$$

where k is a proportionality constant. The k has the same unit as time, t , and is considered the time constant of the system response. Integration of this equation with the initial condition, (when $t=0$),

$$\psi_l = \psi_{l,0}, \quad [3-5]$$

where ψ_0 is the predawn leaf water potential, produces:

$$\psi_l = \psi_{min} + (\psi_{l,0} - \psi_{min})e^{-t/k} \quad [3-6]$$

Setting

$$\psi_d = \psi_{l,0} - \psi_{min},$$

equation [3-6] becomes,

$$\psi_l = \psi_{l,0} - \psi_d(1 - e^{-t/k}) \quad [3-7]$$

where k is a time constant, which is related to the half- time, $t_{0.5}$, of the exponential decrease of leaf water potential represented by

$$t_{0.5} = -k \ln(0.5) \quad [3-8]$$

Equation [3-7] describes the total leaf water potential as a function of time during the period between 7:00 to 20:00, under the conditions in the growth room.

Fitting procedures

Values of $\psi_{l,0}$, ψ_d , and k were obtained by fitting equation [3-7] to the experimental data set, consisting of 260 measurements representing all combinations of five root temperature and five soil water potential treatments. The statistical method used was a non-linear least square procedure. The assumption was made that root temperature and soil water potential treatments affect leaf water potential by altering $\psi_{l,0}$, ψ_d , and k in equation [7],

$$\psi_{l,0} = \psi_{l,0}(\psi_{\text{soil}}, T_{\text{root}}) \quad [3-9a]$$

$$\psi_d = \psi_d(\psi_{\text{soil}}, T_{\text{root}}) \quad [3-9b]$$

$$\text{and } k = k(\psi_{\text{soil}}, T_{\text{root}}) \quad [3-9c]$$

where ψ_{soil} (MPa) is the soil water potential, and T_{root} ($^{\circ}\text{C}$) is the root temperature. Both ψ_{soil} and T_{root} were imposed by treatment. It was further assumed that $\psi_{l,0}(\psi_{\text{soil}}, T_{\text{root}})$, $\psi_d(\psi_{\text{soil}}, T_{\text{root}})$, and $k(\psi_{\text{soil}}, T_{\text{root}})$ are be approximated by polynomial functions. The functions, which best approximated the data set, were chosen on the basis of estimated standard errors of the parameters and R^2 . The final results are

$$\psi_{l,0} = a_0 + b_1 \psi_{\text{soil}}, \quad [3-10a]$$

$$\psi_d = a_d + b_2 \psi_{\text{soil}}^2 + c_1 T_{\text{root}}, \quad [3-10b]$$

$$\text{and } k = a_k \quad [3-10c]$$

where the parameters and corresponding estimated standards are:

$$a_0 = -0.27 \pm 0.03 \text{ MPa},$$

$$a_d = 0.10 \pm 0.04 \text{ MPa},$$

$$a_k = 1.80 \pm 0.29 \text{ hr},$$

$$b_1 = 0.79 \pm 0.15 \text{ MPa/MPa},$$

$$b_2 = 1.64 \pm 0.65 \text{ MPa/MPa}^2,$$

$$c_1 = 0.010 \pm 0.001 \text{ MPa/}^\circ\text{C},$$

and $R^2 = 0.784$.

The time constant of 1.80 hr is equivalent to a half-time of 1.25 hr, according to equation [3-8]. The total leaf water potential during the light period is characterized by three values: 1) the pre-dawn value, $\psi_{l,0}$, before the first light was on, 2) the value at 8:00 achieved with full lights on, and 3) the value at 20:00 just before the first light was turned off. The values at 8:00 a.m and at 20:00 p.m. are referred to as the morning leaf water potential, $\psi_{l,morning}$, and the evening leaf water potential, $\psi_{l,evening}$, respectively. These values are calculated using equations [3-7] and [3-10].

Pre-dawn leaf water potential

Equation [3-10a] demonstrates that the pre-dawn leaf water potential was a function soil water potential but independent of root temperature. The values of pre-dawn leaf water potential at different soil water potentials were calculated by equation [3-10a] and shown in table 3-1.

Table 3-1. The pre-dawn total leaf water potential, $\psi_{l,0}$, calculated by equation [3-10a] as a function of soil water potential, ψ_{soil} .

ψ_{soil} (MPa)	-0.03	-0.06	-0.10	-0.17	-0.25
$\psi_{l,0}$ (MPa)	-0.29	-0.31	-0.34	-0.39	-0.45

Morning leaf water potential and evening leaf water potential

Morning leaf water potentials and evening leaf water potentials for all treatments were calculated using equations [3-7] and [3-10] at 8:00 and 20:00. Results are shown in tables 3-2 and 3-3.

Table 3-2. Morning leaf water potential, $\psi_{l,morning}$, calculated by equations [3-7] and [3-10] at the indicated combinations of soil water potential and root temperature.

Soil water potential	Root temperature °C					avg
	14	17	22	27	32	
---MPa-----	-----MPa-----					
-0.03	-0.40	-0.42	-0.44	-0.46	-0.48	-0.44
-0.06	-0.43	-0.44	-0.46	-0.48	-0.51	-0.46
-0.10	-0.46	-0.47	-0.49	-0.52	-0.54	-0.50
-0.17	-0.52	-0.53	-0.56	-0.58	-0.60	-0.56
-0.25	-0.60	-0.62	-0.64	-0.66	-0.68	-0.64
avg	-0.48	-0.50	-0.52	-0.54	-0.56	-0.52

Table 3-3. Evening leaf water potential, $\psi_{l, \text{evening}}$, calculated by equations [3-7] and [3-10] at the indicated combinations of soil water potential and root temperature.

Soil water	Root temperature °C					
potential	14	17	22	27	32	avg
---MPa---	----- MPa -----					
-0.03	-0.60	-0.64	-0.69	-0.74	-0.79	-0.69
-0.06	-0.63	-0.66	-0.71	-0.77	-0.82	-0.72
-0.10	-0.67	-0.70	-0.75	-0.81	-0.86	-0.76
-0.17	-0.75	-0.78	-0.83	-0.89	-0.94	-0.84
-0.25	-0.86	-0.89	-0.95	-1.00	-1.05	-0.95
avg	-0.70	-0.73	-0.79	-0.84	-0.89	-0.79

Osmotic Potential

Unlike total leaf water potential, the osmotic potential decreased at a constant rate during the full light period (Figure 3-1). After illumination was stopped, the recovery rate of osmotic potential was much slower than that of total leaf water potential. To quantitatively describe the daily change of osmotic potential, a mathematical equation was developed.

Mathematical description

The accumulation of photosynthesis products in the leaf lowers osmotic potential. The rate at which the osmotic potential decreases depends on the balance of net rate of photosynthesis, rates of translocation, utilization, and storage. The storage carbohydrates mainly are starches which do not contribute to the osmotic potential. Letting C be the concentration of sugar in the leaf,

$$\frac{dC}{dt} = \left[\begin{array}{c} \text{rate} \\ \text{of} \\ \text{production} \end{array} \right] - \left[\begin{array}{c} \text{rate} \\ \text{of} \\ \text{translocation} \\ \text{utilization} \end{array} \right] - \left[\begin{array}{c} \text{rate} \\ \text{of} \\ \text{storage} \end{array} \right] \quad [3-11]$$

The rate of carbohydrate production is directly proportional to the rate of net photosynthesis according to

$$\left[\begin{array}{c} \text{rate} \\ \text{of} \\ \text{production} \end{array} \right] = \frac{P_n}{\alpha} \quad [3-12]$$

where α is the volume of the symplast per unit leaf area, $\text{m}^3 \text{m}^{-2}$, and P_n is the net photosynthetic rate, expressed in $\text{mol m}^{-2} \text{s}^{-1}$. For simplicity, it was assumed that the rates of translocation, utilization, and storage at any given time are proportional to the carbohydrate concentration at that time:

$$[\text{trans} + \text{util} + \text{storage}] = \beta(C - C_{\min}), \quad [3-13]$$

where β is a proportionality constant and C_{\min} is the minimum solute concentration maintained by the plant. C_{\min} is assumed to be equal to the solute concentration in the early morning before the lights were turned on. Combining equation [3-11] to [3-13] yields,

$$\frac{dC}{dt} = \frac{Pn}{\alpha} - \beta(C - C_{\min}) \quad [3-14]$$

Integration of equation [3-14] with the initial condition,

$$C = C_{\min} \text{ when } t=0,$$

produces

$$C = C_{\min} + \frac{Pn}{\alpha\beta}(1 - e^{-\beta t}) \quad [3-15]$$

According to the van't Hoff law, the osmotic potential, π , can be calculated from the concentration of solutes

$$\pi = - CRT, \quad [3-16]$$

where R is the universal gas constant and T is the Kelvin temperature. Substituting equation [3-15] into equation [3-16] yields:

$$\pi = \pi_{\max} - K(1 - e^{-\beta t}), \quad [3-17]$$

where

$$K = PnRT/\alpha\beta.$$

In this equation, π_{\max} is obtained from the solute potential measurements in the early morning. For simplicity, equation [3-17] can be linearized by expanding it, according to Lagrange's theorem, resulting in

$$\pi = \pi_{\max} + \frac{[d\pi(\theta)]}{[dt]} * t, \quad 0 < \theta < t, \quad [3-18]$$

where θ is a moment during the light period whose value is unknown. As an

approximation, θ is related with t corresponding to the time when $\pi = \pi_{\text{avg}}$. Thus, equation

[3-18] becomes

$$\pi = \pi_{\max} + \frac{d\pi}{dt}|_{\pi=\pi_{\text{avg}}} * t, \quad [3-19]$$

Differentiating equation [3-17] yields:

$$\frac{d\pi}{dt} = -K\beta e^{-\beta t}. \quad [3-20]$$

Rearrangement of equation [3-17] yields:

$$e^{-\beta t} = 1 - (\pi_{\max} - \pi)/K. \quad [3-21]$$

Substituting equation [3-21] into equation [3-20] results in

$$\frac{d\pi}{dt} = -K\beta \left(1 - \frac{\pi_{\max} - \pi}{K}\right), \quad [3-22]$$

and if $\pi=\pi_{\text{avg}}$ then,

$$\frac{d\pi}{dt}|_{\pi=\pi_{\text{avg}}} = -K\beta \left(1 - \frac{\pi_{\max} - \pi_{\text{avg}}}{K}\right). \quad [3-23]$$

Substituting equation [3-23] into equation [3-19] yields

$$\pi = \pi_{\max} - K\beta \left(1 - \frac{\pi_{\max} - \pi_{\text{avg}}}{K}\right) t, \quad [3-24]$$

or

$$\pi = \pi_{\max} - \beta[K - (\pi_{\max} - \pi_{\text{avg}})]t, \quad [3-25]$$

which may be written in the form,

$$\pi = \pi_{\max} - St, \quad [3-26]$$

where

$$S = \beta[K - (\pi_{\max} - \pi_{\text{avg}})],$$

and S has units of MPa hr⁻¹.

Equation [3-26] describes the change of osmotic potential during the full light period between 8:00 and 20:00. The parameters, π_{\max} and S, are obtained by fitting equation [3-26] to experimental data using a least square technique. The osmotic potential, π , at any time during the full light period is calculated using equation [3-26] with the parameters, π_{\max} and S. The parameter π_{\max} , is referred to as the morning osmotic potential.

Corresponding to the total leaf water potential, the osmotic potential during the light period can be characterized by the pre-dawn osmotic potential, π_0 , the morning osmotic potential, π_{morning} at 8:00, and the evening osmotic potential, π_{evening} at 20:00.

Pre-dawn osmotic potential

Fully recovered values of osmotic potential obtained early in the morning before the lights were turned on were averaged and referred to as pre-dawn osmotic potential. Results are shown in table 3-4a. The analysis of variance for table 3-4a is shown in table 4b. These results indicate that the pre-dawn osmotic potential was independent of soil water potential but was strongly influenced by root temperature (0.01 significance level).

Table 3-4a. The pre-dawn osmotic potential, π_0 , at the indicated combinations of soil water potential and root temperature. The numbers reported are averages of two observations.

Soil water	Root temperature °C					
potential	14	17	22	27	32	avg
---MPa---	----- MPa -----					
-0.03	-1.05	-1.09	-1.15	-1.16	-1.00	-1.09
-0.06	-1.07	-1.10	-1.16	-1.09	-1.03	-1.09
-0.10	-1.06	-1.07	-1.12	-1.14	-1.04	-1.09
-0.17	-1.07	-1.05	-1.15	-1.13	-1.02	-1.08
-0.25	-1.03	-1.04	-1.16	-1.14	-1.02	-1.08
avg	-1.06	-1.07	-1.15	-1.13	-1.02	-1.09

Table 3-4b. ANOVA for data reported in table 3-4a.

Source of variation	SS	d.f	MSS	F
Soil temperature	0.066394	4	0.016598	16.69869**
Soil water potential	0.001286	4	0.000321	0.323440
Error	0.015904	16	0.000994	
Total	0.083584	24	0.003482	

Morning and evening osmotic potentials

The experimental data of osmotic potential during the full light period were fitted to the linear equation [3-26]. The morning osmotic potential, π_{morning} , at 8:00, and the rate of osmotic potential decreases with time, S , were obtained from this fitting for each treatment and are shown in tables 3-4a and 3-5a. The evening osmotic potentials, π_{evening} at 20:00 pm were calculated by equation [3-26] with the parameters, π_{morning} and S , and are shown in table 3-6a.

The analysis of variance for π_{morning} , S , and π_{evening} are shown in tables 3-4b to 3-6b. All of these parameters depend on the root temperature but not on the soil water potential. These results are similar to the pre-dawn osmotic potential.

Turgor Potential

Diurnal course of turgor potential, p , plotted figure 3-1, indicated that turgor potential decreased rapidly after the lights were turned on, as a result of the decrease in total leaf water potential. Total leaf water potential decreased rapidly, while osmotic potential decreased at a lower rate. During the first hour with lights were, the turgor potential remained almost constant because leaf water potential and osmotic potential decreased at the same rate (Figure 3-1). The recovery of turgor potential was rapid once the first light was turned off. The rapid recovery was the result of cessation of evaporative loss of water while the osmotic potential remained unchanged. Turgor potential reached its maximum value when total leaf water potential reached the pre-dawn leaf water potential, after which it declined and reached the pre-dawn turgor value as osmotic

Table 3-5a. Morning osmotic potential, π_{morning} , obtained by fitting equation [3-26] to experimental data during the full light period from 8:00. and 20:00 at the indicated combinations of soil water potential and root temperature.

Soil water	Root temperature °C					
potential	14	17	22	27	32	avg
---MPa---	----- MPa -----					
-0.03	-1.09	-1.10	-1.17	-1.14	-1.04	-1.11
-0.06	-1.10	-1.12	-1.25	-1.13	-1.06	-1.13
-0.10	-1.08	-1.12	-1.26	-1.12	-1.02	-1.12
-0.17	-1.13	-1.17	-1.19	-1.16	-1.03	-1.14
-0.25	-1.16	-1.12	-1.23	-1.17	-1.07	-1.15
avg	-1.11	-1.13	-1.22	-1.14	-1.04	-1.13

Table 3-5b. ANOVA for data reported in table 3-5a.

Source of variation	SS	d.f	MSS	F
Soil temperature	0.086881	4	0.021720	24.7662 **
Soil water potential	0.006706	4	0.001676	1.90335
Error	0.014042	16	0.000877	
Total	0.107631	24	0.004484	

Table 3-6a. Rate of decrease in osmotic potential, S , obtained by fitting equation [3-26] to experimental data during the full light period from 8:00 and 20:00 at the indicated combinations of soil water potential and root temperature.

Soil water	Root temperature °C					
potential	14	17	22	27	32	avg
---MPa---	----- MPa /Htr-----					
-0.03	0.010	0.016	0.014	0.015	0.016	0.014
-0.06	0.006	0.019	0.008	0.015	0.013	0.012
-0.10	0.009	0.014	0.011	0.010	0.021	0.013
-0.17	0.008	0.006	0.012	0.007	0.020	0.011
-0.25	0.001	0.007	0.012	0.015	0.019	0.011
avg	0.007	0.012	0.012	0.012	0.017	0.013

Table 3-6b. ANOVA for data reported in table 3-6a.

Source of variation	SS	d.f	MSS	F
Soil temperature	0.000306	4	0.000076	4.870505**
Soil water potential	0.000045	4	0.000011	0.727966
Error	0.000251	16	0.000015	
Total	0.000603	24	0.000025	

Table 3-7a. Evening osmotic potential, π_{evening} , obtained by fitting equation [3-26] to experimental data during the full light period from 8:00 and 20:00 at the indicated combinations of soil water potential and root temperature.

Soil water	Root temperature °C					
potential	14	17	22	27	32	avg
---MPa---	----- MPa -----					
-0.03	-1.25	-1.30	-1.34	-1.32	-1.23	-1.28
-0.06	-1.24	-1.35	-1.35	-1.31	-1.21	-1.29
-0.10	-1.26	-1.29	-1.39	-1.24	-1.28	-1.29
-0.17	-1.27	-1.24	-1.33	-1.24	-1.27	-1.27
-0.25	-1.91	-1.20	-1.38	-1.35	-1.29	-1.28
avg	-1.24	-1.28	-1.36	-1.29	-1.26	-1.29

Table 3-7b. ANOVA for data reported in table 3-7a.

Source of variation	SS	d.f	MSS	F
Soil temperature	0.034945	4	0.008736	4.929538**
Soil water potential	0.002085	4	0.000521	0.294217
Error	0.028356	16	0.001772	
Total	0.065387	24	0.002724	

potential recovered. The pre-dawn, $\psi_{p,0}$, morning, $\psi_{p,morning}$, and evening, $\psi_{p,evening}$ turgor potentials were calculated (tables 3-8, 3-9, and 3-10), using equation [3-1].

Table 3-8. Pre-dawn turgor potential, $\psi_{p,0}$, calculated by equation [3-1] using data reported in tables 3-1 and 3-4 at the indicated combinations of soil water potential and root temperature.

Soil water	Root temperature °C					
potential	14	17	22	27	32	avg
---MPa---	----- MPa -----					
-0.03	0.76	0.80	0.86	0.87	0.71	0.80
-0.06	0.76	0.79	0.85	0.78	0.72	0.78
-0.10	0.72	0.73	0.78	0.80	0.70	0.75
-0.17	0.68	0.66	0.76	0.74	0.63	0.69
-0.25	0.58	0.59	0.70	0.69	0.57	0.63
avg	0.70	0.71	0.79	0.78	0.67	0.73

Table 3-9. Morning turgor potential, $\psi_{p,morning}$, calculated by equation [3-1] using data reported in tables 3-2 and 3-5 at the indicated combinations of soil water potential and root temperature.

Soil water	Root temperature °C					
potential	14	17	22	27	32	avg
---MPa---	----- MPa -----					
-0.03	0.69	0.68	0.79	0.68	0.56	0.68
-0.06	0.67	0.68	0.77	0.65	0.55	0.66
-0.10	0.62	0.65	0.73	0.60	0.48	0.62
-0.17	0.61	0.64	0.63	0.58	0.43	0.58
-0.25	0.56	0.50	0.59	0.51	0.39	0.51
avg	0.63	0.63	0.70	0.60	0.48	0.61

Table 3-10. Evening turgor potential, $\psi_{p, \text{evening}}$, calculated by equation [3-1] using data reported in tables 3-3 and 3-7 at the indicated combinations of soil water potential and root temperature.

Soil water	Root temperature °C					
potential	14	17	22	27	32	avg
---MPa---	----- MPa -----					
-0.03	0.62	0.65	0.65	0.58	0.45	0.59
-0.06	0.60	0.65	0.66	0.52	0.46	0.58
-0.10	0.53	0.61	0.64	0.43	0.41	0.52
-0.17	0.50	0.47	0.51	0.36	0.34	0.43
-0.25	0.32	0.32	0.41	0.36	0.25	0.33
avg	0.51	0.55	0.58	0.45	0.38	0.49

Discussion

Total Leaf Water Potential

According to equation [3-10a], the pre-dawn leaf water potential, ψ_0 , decreased linearly with increasing soil water stress but was independent of the root temperature. The pre-dawn leaf water potential decreased from -0.29 to -0.45 MPa as the soil water potential decreased from -0.03 to -0.25 MPa (Table 3-1). During the night period, there was no net water loss. Leaf water potential remained at a constant value. Root temperature had no effect on the pre-dawn leaf water potential as discussed earlier.

However, root temperature had an effect on leaf water potential during the light period. Equation [3-10b] shows that leaf water potential during the light period depended on both the soil water potential and the root temperature. The parameter, ψ_d , as a measure of leaf water potential decrease during the light period was a quadratic function of soil water potential and a linear function of root temperature.

The leaf water potential was plotted as a function of time of day, using equation [3-7], for the -0.03 MPa and -0.25 MPa soil water potential treatments at three different root temperatures in figure 3-2. Once the lights were turned on, the leaf water potential decreased quickly in response to the increase of evaporative demand. The leaf water potential achieved 50% of total daily decrease at 8:25 for each treatment according to the half time, $t_{0.5}$. After reaching the full light intensity, the evaporative demand became constant. The exact values of leaf water potential during the full light period depended on the ability of the system to supply water to the leaves, which was related to the soil-plant resistance to water movement as well as soil water potential. When the water potential gradient in the soil-plant system was established, the leaf water potential started to decrease with a lower rate. The difference between the pre-dawn and evening leaf water potential increased with increasing root temperature and soil water stress (Figure 3-3). This confirmed the observations by Barlow et al. (1977). For the soil water potential of -0.03 MPa, the difference increased from 0.31 to 0.50 MPa as root temperature increased from 14°C to 32°C. But for the soil water potential of -0.25 MPa, the difference increased from 0.41 to 0.60 MPa at the same conditions.

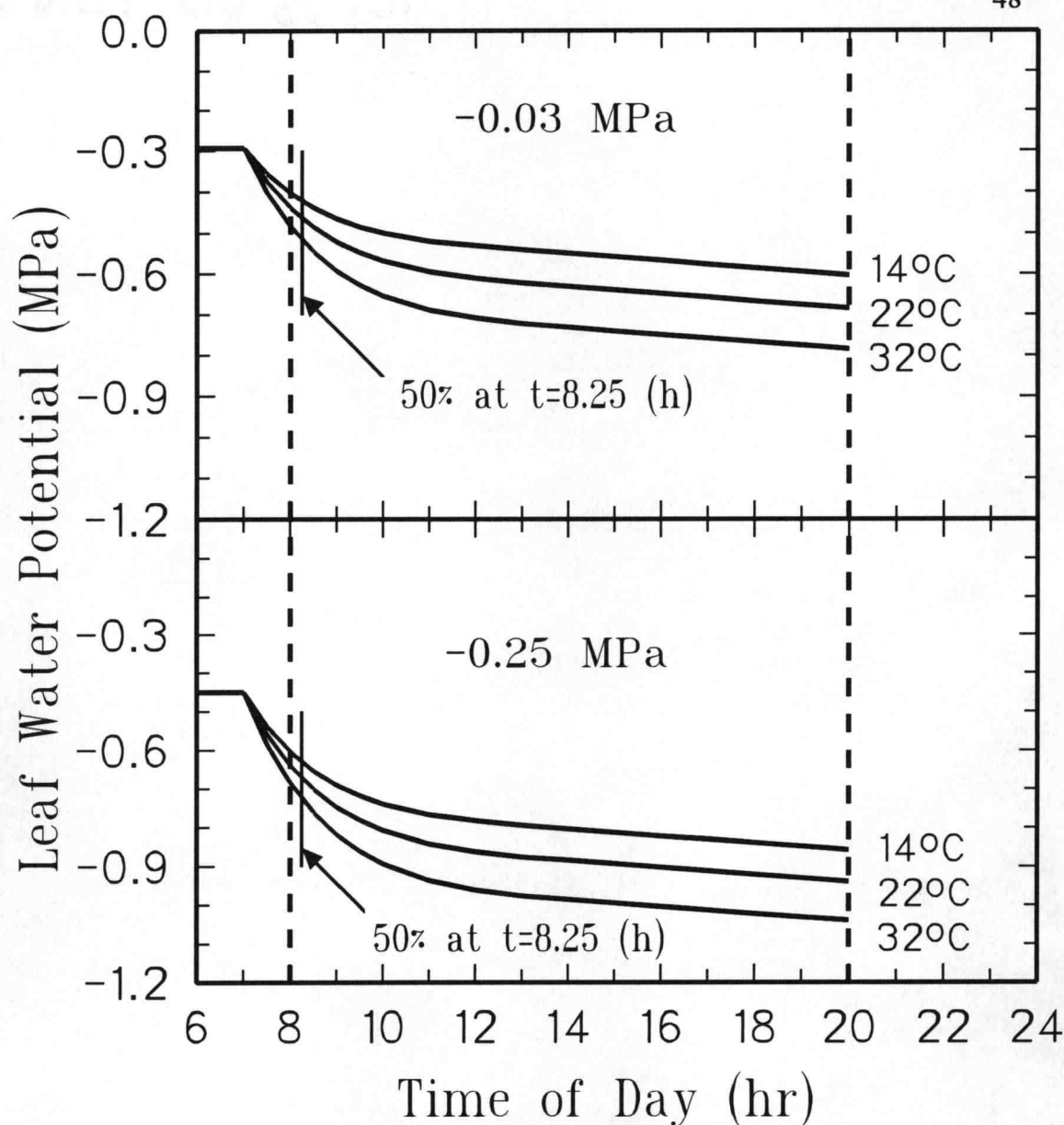


Figure 3-2. Total leaf water potential plotted as a function of time of day at the indicated treatments of soil water potential and root temperature. Data were calculated using equations [3-7] and [3-10]. All lights were on during the time between the dashed lines. The top is the soil water potential at -0.03 MPa and the bottom is the soil water potential at -0.25 MPa.

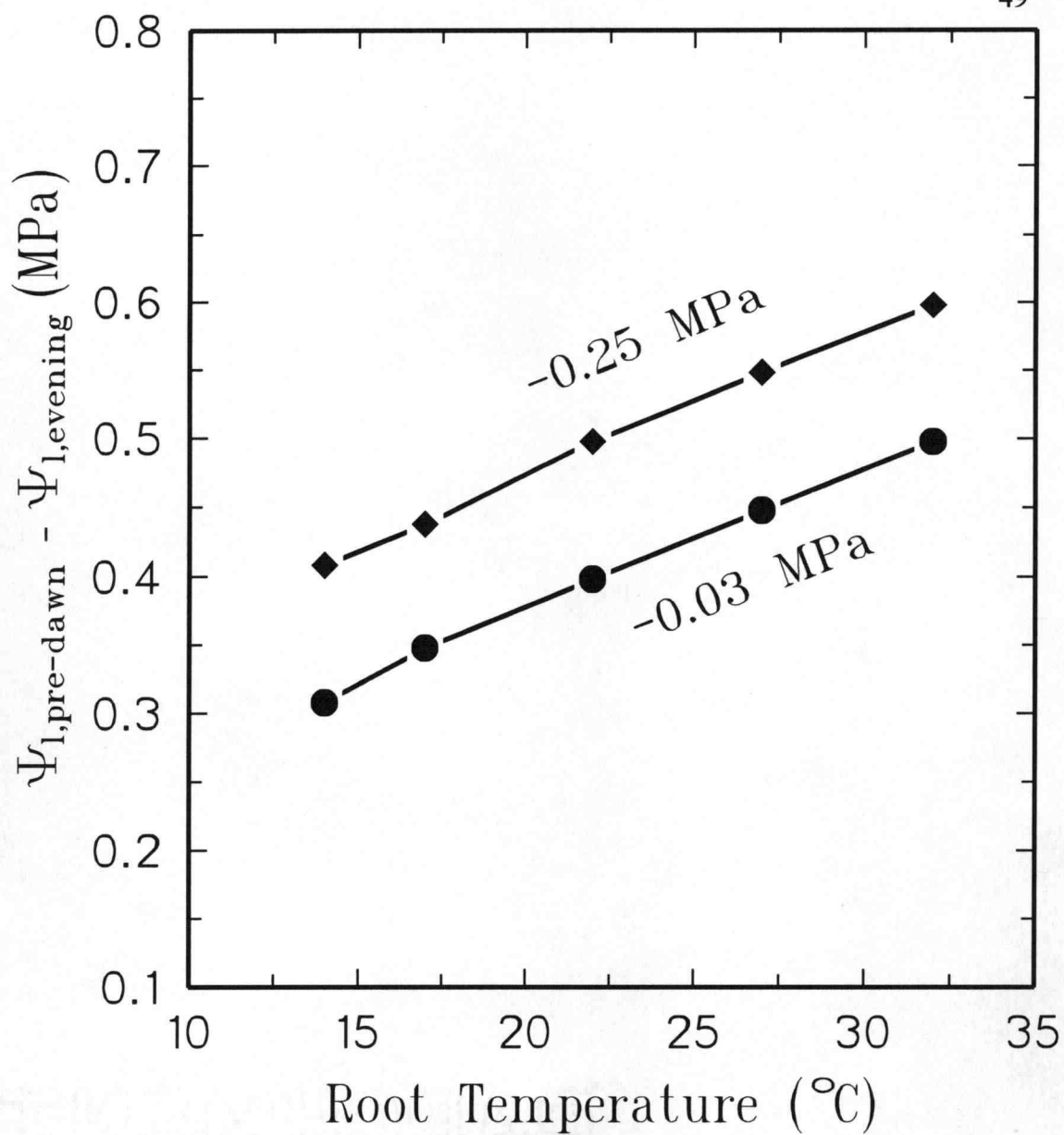


Figure 3-3. Difference between $\psi_{l,0}$ and $\psi_{l,evening}$ plotted as a function of the root temperature at the indicated soil water potential treatments.

Differences between soil water potential, ψ_{soil} , and leaf water potential, ψ_l , for pre-dawn, morning, and evening conditions were plotted as functions of root temperature at the indicated treatments of soil water potential in figure 3-4. The graph shows that for each soil water potential treatment the differences between ψ_{soil} and $\psi_{l,0}$ remained constant as root temperature increased. But the differences between ψ_{soil} and $\psi_{l,\text{morning}}$ and differences between ψ_{soil} and $\psi_{l,\text{evening}}$ increased as root temperature increased. The increase was more rapid in the evening than that in the morning. The greater increase could be a result of the effect of root temperature and soil water potential relation. During the light period the stress in the plant developed progressively. The plant recovered more or less from stress during the night period, thus, the plants were stressed the least in the morning and stressed the most in the evening. The differences between ψ_{soil} and $\psi_{l,0}$ decreased with decreasing soil water potential, which is illustrated in figure 3-4 by noting the change in the differences between ψ_{soil} and $\psi_{l,0}$ at each root temperature. However, the differences were independent of the soil water potential for both in the morning and evening. The differences between ψ_{soil} and ψ_l remained almost constant with decreasing soil water potential during the day time except for the soil water potential of -0.25 MPa at the evening. This illustrates that the water potential gradient across the soil-plant water system decreased during the night and remained the same during the day as soil water stress increased.

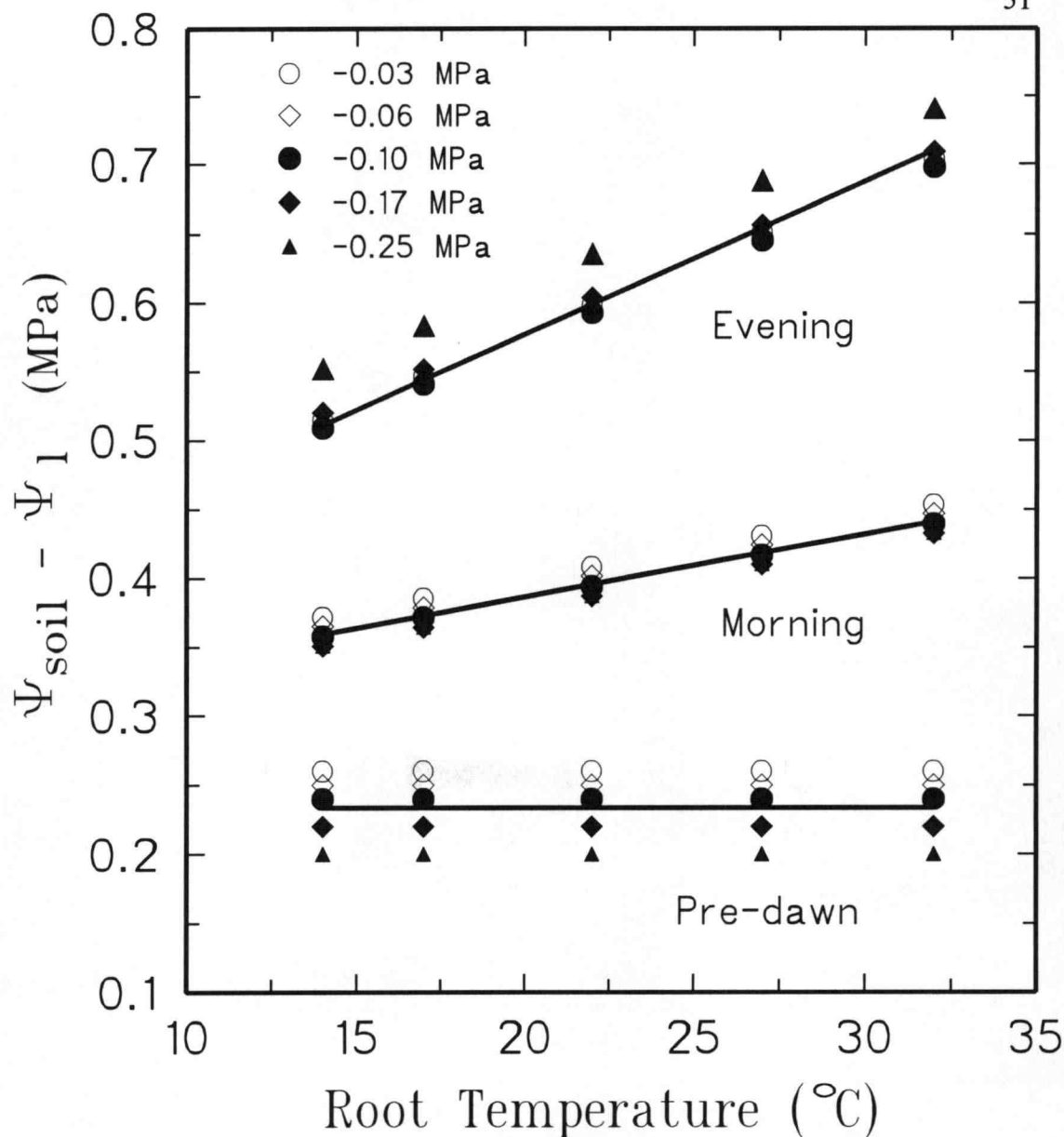


Figure 3-4. Difference between soil water potential and leaf water potential, $\Psi_{\text{soil}} - \Psi_l$, for the pre-dawn, morning, and evening conditions plotted as a function of root temperature at the indicated treatments of soil water potential. Solid lines represent the average values of five soil water potentials at each root temperature treatment.

Osmotic Potential

Analyses of variance for the pre-dawn, morning, and evening osmotic potentials (Tables 3-4b, 3-5b, and 3-7b) demonstrated that these three values depended on the root temperature but were independent of soil water potential. It was concluded that the daily change of osmotic potential was independent of soil water potential. Therefore, the osmotic potential averaged over five soil water potentials was plotted as a function of time of day at the indicated root temperature treatments in figure 3-5. During the first hour of the light period the osmotic potential decreased rapidly in response to the rapid increase in light intensity. During the full light period, the osmotic potential decreased with a similar rate for all root temperature treatments, except at 32°C. The decrease in osmotic potential for the 32°C treatment during the full light period was greater. The diurnal behavior of osmotic potential differed from that of leaf water potential. The concentration of solutes is a balance between rates of net photosynthesis and translocation and utilization. The decreases of osmotic potential during the light period indicated that there was an accumulation of solutes in the leaves, which resulted from lower rates of translocation and utilization of solutes compared to the rate of net photosynthesis.

The values of pre-dawn, morning, and evening osmotic potential were plotted as a function of root temperature in figure 3-6. As root temperature increased from 14°C to 22°C the osmotic potentials decreased, then approached a minimum value. Further root temperature increase caused osmotic potentials to increase. The values of osmotic potential at 22°C root temperature was approximately 0.1 MPa lower than the values at

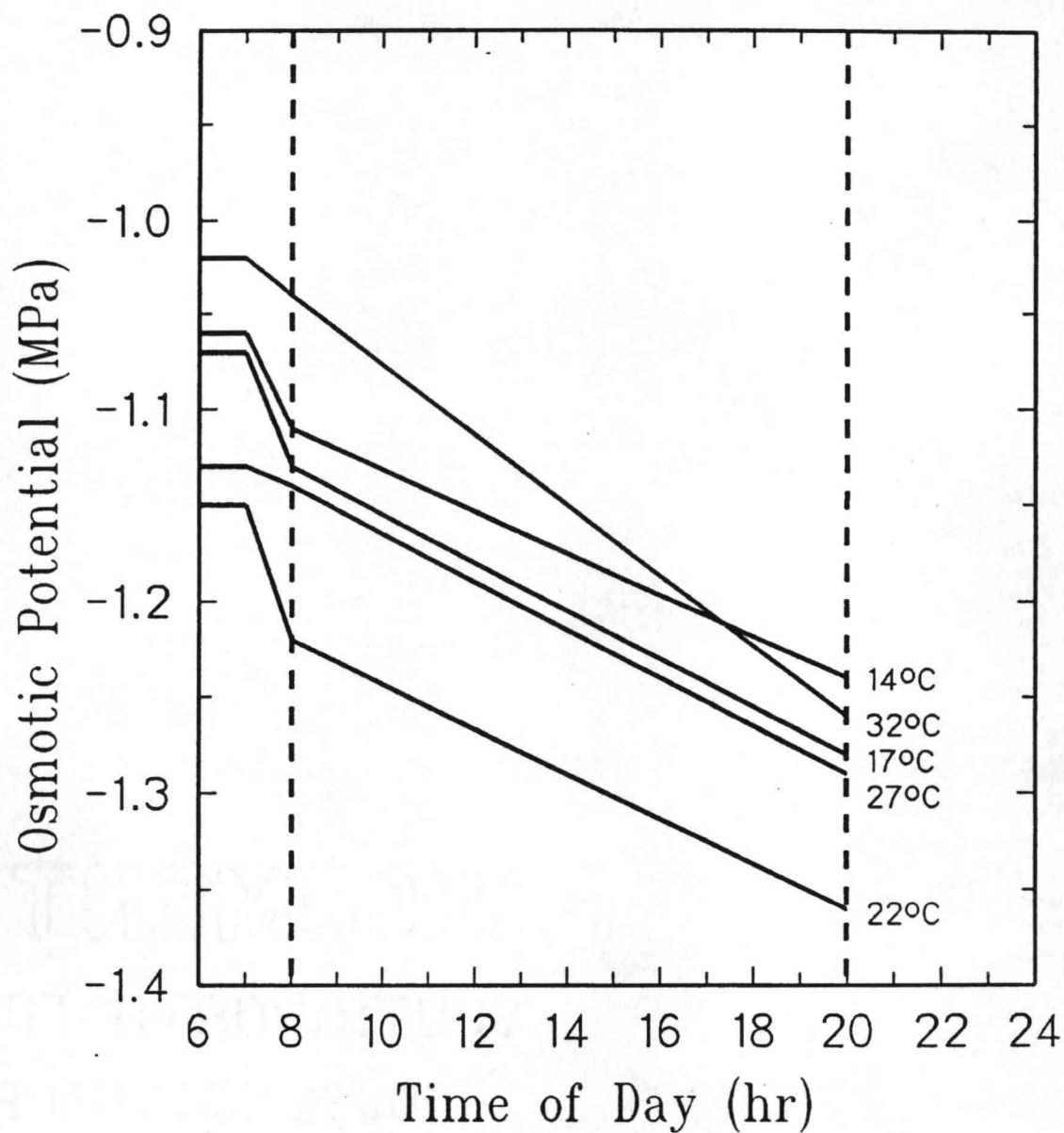


Figure 3-5. Osmotic potential plotted as a function of time of day at the indicated root temperature treatments. Pre-dawn values were from table 3-4a and the values during the full light period were calculated using equation [3-26] with data in tables 3-5a and 3-6a. All lights were on during the time between the dashed lines.

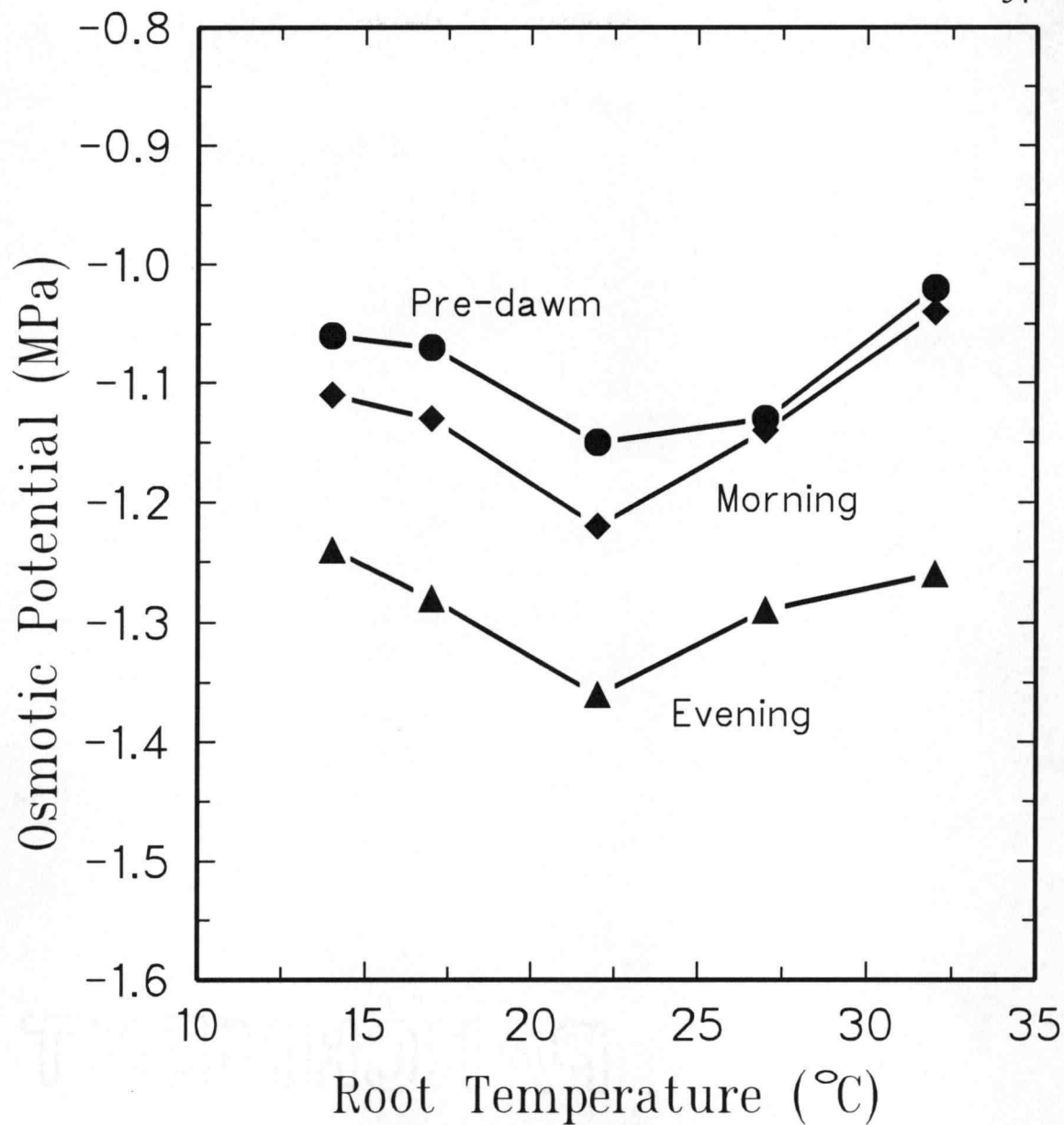


Figure 3-6. Pre-dawn, morning, and evening osmotic potentials plotted as a function of the root temperature.

either 14°C or 32°C. This indicated that turgor potential was maintained best at the optimum temperature for the photosynthetic processes (see next section).

Osmotic adjustment is usually defined as an increase in osmotic pressure of cells resulting from the accumulation of solute molecules (Munns, 1988). The difference between the pre-dawn and evening osmotic potential indicated that leaves of spring wheat seedlings adjusted osmotically during the day approximately (Figure 3-7). This osmotic adjustment did not change with increasing soil water stress and remained constant as root temperature increased.

The trends of leaf water potential and osmotic potential in response to root temperature during the full light period was similar to results reported by Graves et al. (1989) for red maple grown under controlled conditions with a 24°C air temperature. This observation disagreed with the reports by Kirkham and Ahring (1978) for wheat grown under controlled conditions with an air temperature of 24.7°C. They observed that leaf water potential and osmotic potential increased with increasing root temperature and reached high values at 24.7°C, then decreased with further decreasing the root temperature. The reasons for the differences are unclear.

Turgor Potential

Turgor potential as a function of time of day at the indicated treatments is indicated in figure 3-8. When the lights were turned on, the turgor potential decreased because the leaf water potential decreased rapidly while the osmotic potential decreased at a relatively lower rate. Especially, for the root temperature of 32°C, rapid declines were

observed for all soil water potential treatments. A small increase in turgor potential occurred after 12:30. This resulted from a relatively larger decrease in osmotic potential compared to leaf water potential during this period. The turgor potentials remained the highest values at the root temperature of 22°C for each soil water potential treatment. With either increasing or decreasing root temperature, the turgor potential decreased for all experimental treatments. This occurred because that the osmotic potential had a lowest value at the root temperature of 22°C at all times, indicating that plants had a better osmotic adjustment capability at the root temperature of 22°C.

The turgor potential decreased with increasing soil water stress at each root temperature, because the daily change of osmotic potential was independent of the soil water potential. The differences between $\psi_{p,0}$ and $\psi_{p,\text{evening}}$ increased with increasing root temperature from 14°C to 27°C and remained almost constant with further increasing temperature to 32°C (Figure 3-9). The differences also increased as soil water potential decreased from -0.03 MPa to -0.25 MPa. However, this increase decreased with increasing root temperature, which indicates that the higher root temperature overcome certain effect of soil water stress.

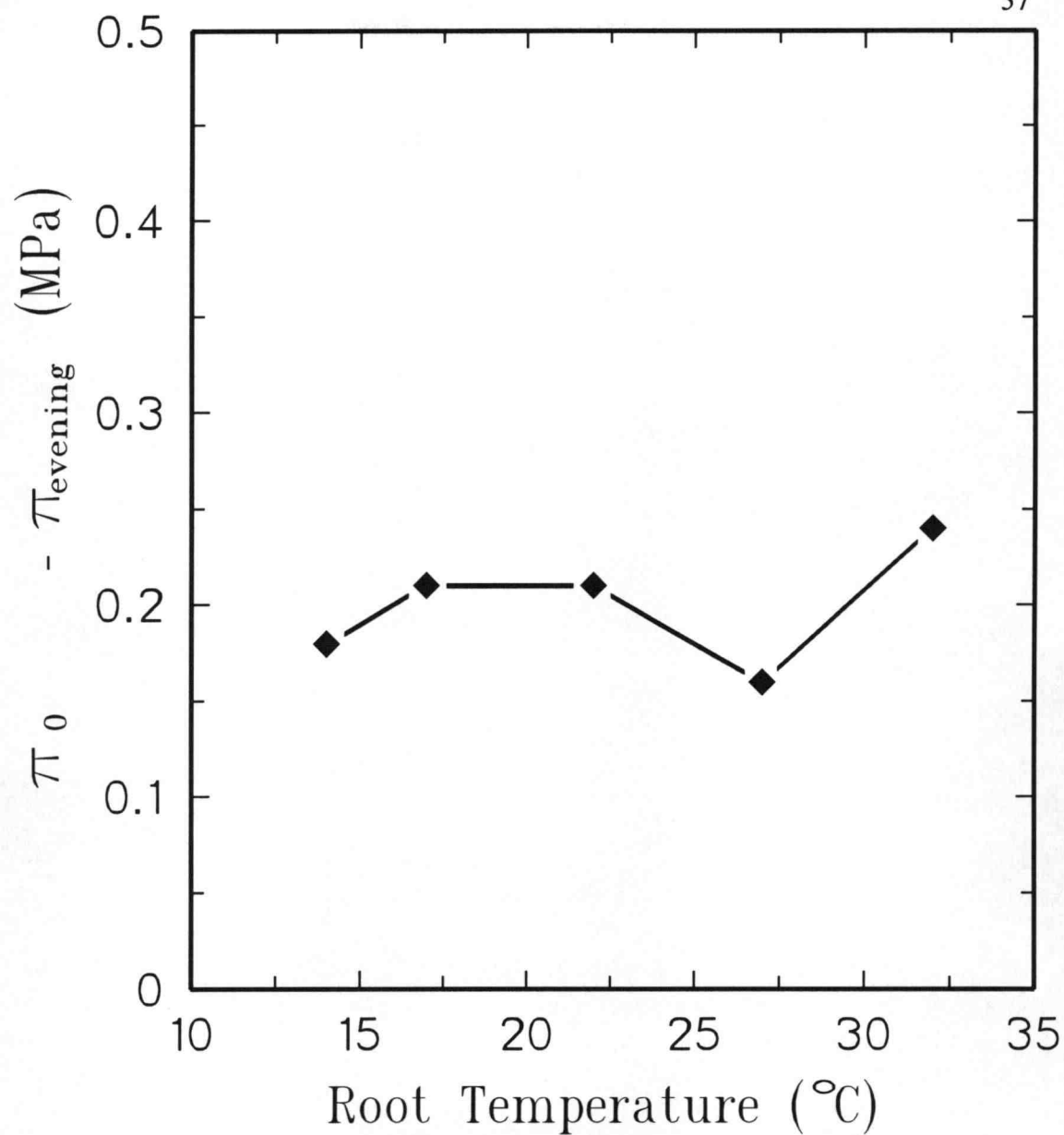


Figure 3-7. Differences between π_0 and π_{evening} plotted as a function of root temperature.

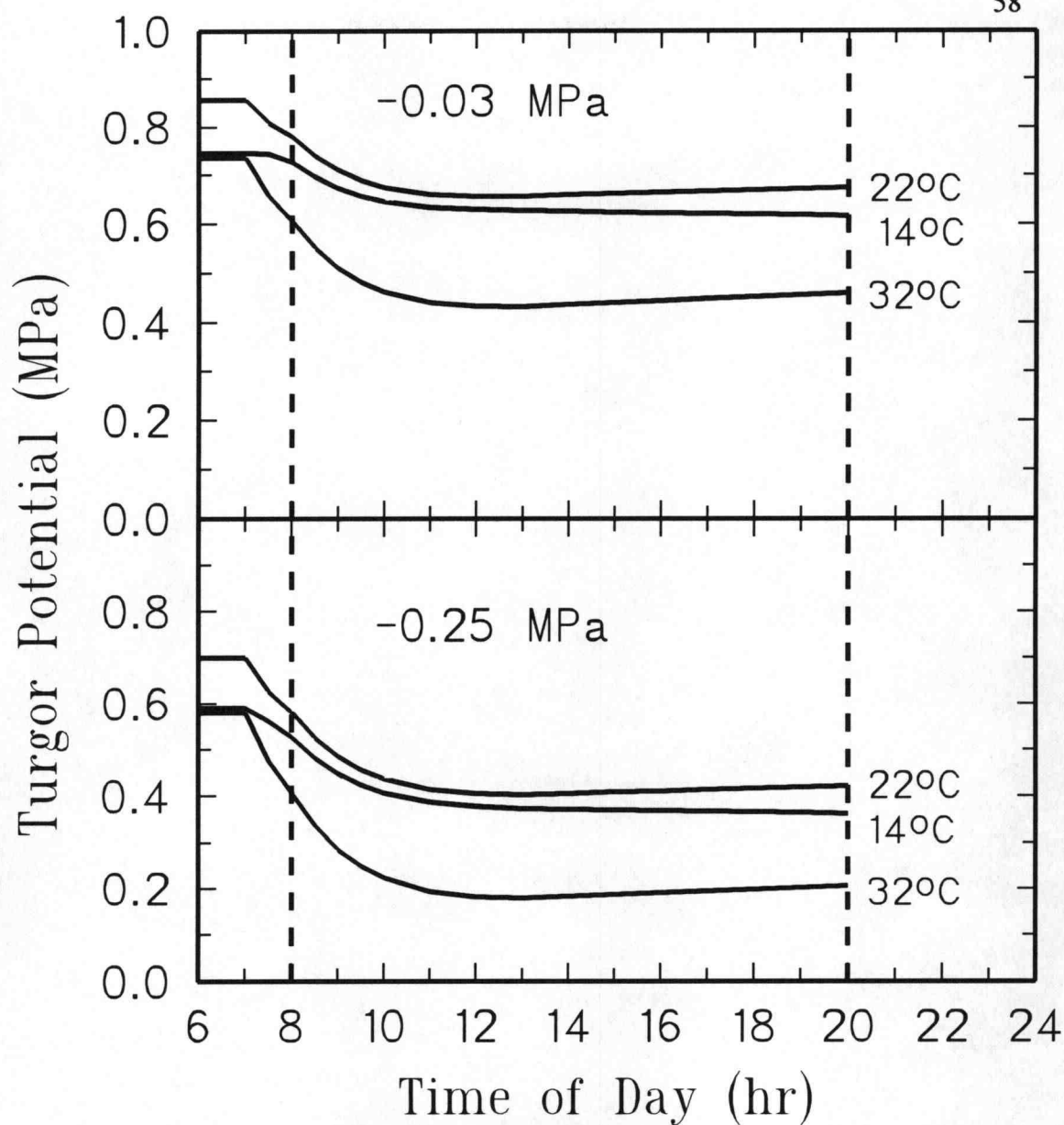


Figure 3-8. Turgor potential plotted as a function of time of day at the indicated treatments of soil water potential and root temperature. Values of turgor potential are calculated using the data drawn from Figures 3-2 and 3-5. All lights were on during the time between the dashed lines.

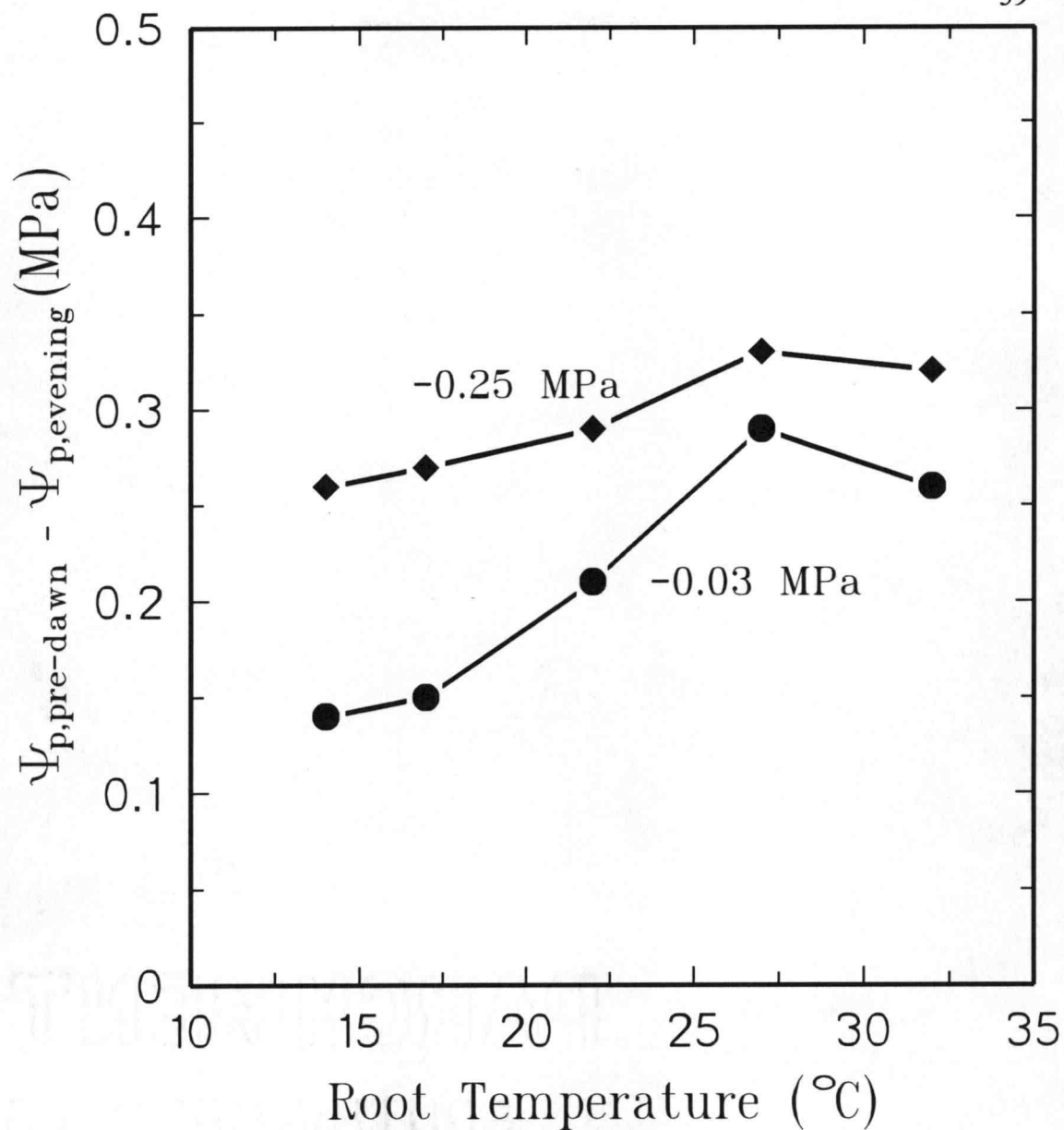


Figure 3-9. Difference between $\Psi_{p,pre-dawn}$ and $\Psi_{p,evening}$ plotted as a function of the root temperature at the indicated soil water potential treatments.

Summary

Quantitative description of the daily trends of total leaf water potential and osmotic potential were developed based on theoretical considerations. Total leaf water potential and osmotic potential decreased during the light period. The daily decrease of total leaf water potential increased with decreasing soil water potential and increasing root temperature. There was little difference in daily change of osmotic potential between -0.03 MPa and -0.25 MPa soil water potential treatments despite the large difference in leaf water potential. This indicates that the spring wheat lacks the osmotic adjustment capability. As a result, the leaf turgor potential changed widely between -0.03 MPa and -0.25 MPa soil water potential treatments, almost in parallel with the change in total leaf water potential.

The osmotic potential during the light period decreased with increasing root temperature and reached the lowest values at the root temperature 22°C, followed by a increase with further increasing root temperature. This resulted in a higher turgor potential at 22°C.

References

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4. TRANSPIRATION AND STOMATAL CONDUCTANCE

Introduction

The process of transpiration is controlled by demands of evaporation, which are external to plants, water availability in the soil, and physiological and anatomical properties of the plant. Characteristics of these three components combine to determine the rates of water absorption and movement in plants. For controlled environmental conditions, where the external demand is constant, the rate of transpiration depends on plant characteristics and soil water potential. Both soil water potential and root temperature govern the soil water availability and modify plant characteristics (Slatyer, 1967; Cooper, 1973; Boyer, 1985).

Cooper (1973) summarized the studies on the effects of root temperature on plant growth and suggested that there is a wide optimum root temperature band for transpiration rate when the whole plant is considered. Since that review, few additional studies have been reported on the effects of changes in root temperature on transpiration rate (Turner, 1975; Küpper, Hall, and Schulze, 1982). Küpper et al. (1982) studied the response of plant functioning to root temperature under controlled conditions. They observed that the rate of transpiration slowly increased with increasing root temperature from 15°C to 30°C and reached a maximum value at 30°C. The transpiration rate rapidly decreased with further increasing root temperature. Root temperature influences the permeability of cell tissue to water absorption. Thus, the water permeability of a cell membrane presents a mechanism to control the rate of transpiration in addition to stomatal

opening (Slatyer, 1967). At excessively high root temperature, limited water uptake may be attributed to the inhibition of plant metabolic activity by high temperature (Slatyer, 1967; Küpper et al., 1982).

Under the soil water stress condition, the limitation of soil water supply to the absorbing root surface and corresponding stomatal closure become apparent and the decrease in transpiration rate occurs (Boyer, 1985). This occurs in plants because the conductance of the soil decreases as water withdraws from the pores, decreasing the cross-sectional area for water flow. Furthermore, shrinkage may occur both in the soil and in the roots (Huck, Klepper, and Taylor, 1970) which decreases the soil contact with the root. Consequently, the entire path through the soil to the surface of the root becomes less conductive. Blizzard and Boyer (1980) compared the conductance of the soil and the conductance of soybean plants by directly measuring the rate of water movement and water potential in both segments of the flow path as the soil dried. The results revealed that the conductance of the plant was always less than the conductance of soil regardless of the soil water content, indicating that water movement through the soil-plant system was limited more by the plant than by the soil. In the plant, the conductance of the root tissue was always less than that of the leaf.

The responses of transpiration rate to root temperature and soil water stress depend on the stomata in response to these two factors (Küppers et al., 1982; Schulze, 1986). Stomata respond directly to a signal from the roots under soil water stress conditions (Schulze, 1986; Davies et al., 1986). It appears that the signal is related to the physiological activity of the root, and probably related to the metabolism of cytokinin

(Jewer and Incoll, 1980) and abscisic acid (Davies, 1986; Zhang and Davies, 1989).

These researchers postulate that cytokinin and abscisic acid affect the stomatal aperture.

Much progress in the understanding of the transpiration process and stomatal aperture responses to root temperature and soil water stresses has been made during the last 20 years. However, the mechanisms for root temperature and soil water stress actions on transpiration and stomatal conductance are not fully understood. The purpose of this chapter is to investigate the responses of transpiration rate and stomatal conductance to root temperature and soil water stress by studying their diurnal courses at different root temperature and soil water stress conditions.

Results

The Daily Trend of Rate of Transpiration

The transpiration rate was measured several times throughout the light period. The daily trends of the transpiration rate were similar to that of the photosynthesis rate. One example of the transpiration rates measured during the light period is shown in figure 4-1. When the lights were turned on, the rate of transpiration increased, reaching a maximum value at 8:00, after which the rate of transpiration decreased consistently during the full light period. After the first light was turned off, the rate of transpiration declined. The same trend was observed for all the treatments. Maximum transpiration rates and the rates at which the transpiration rate decreased with time depended on root temperature and soil water potential. The daily change of transpiration rate also can be characterized by the

rates at 8:00 and 20:00. These rates are referred to as the morning and the evening rate of transpiration, respectively.

Morning rate and evening rate of transpiration

The method used to calculate the morning and evening rates of photosynthesis (chapter 5) was used to calculate the morning and evening rates of transpiration. A linear decrease was assumed for the rate of transpiration during the full light period. It was assumed that the effect of soil water potential on the rate of transpiration can be approximated by a polynomial function over the range of soil water potentials studied in this research, namely:

$$E = a + bt + c_1\psi_{\text{soil}} + c_2\psi_{\text{soil}}^2 + c_3\psi_{\text{soil}}^3 + \dots, \quad [4-1]$$

where E is the rate of transpiration expressed in $\text{m}^3 \text{m}^{-2} \text{s}^{-1}$; ψ_{soil} is the soil water potential in MPa; t is the time of day in hours; and a , b , and c are constants. Equation [4-1] was fitted to the experimental data set for each root temperature using the least square technique. The function which best approximates the data set was chosen on the basis of estimated standard errors of the parameters and R^2 . The final function is

$$E = a + bt + c_1\psi_{\text{soil}}. \quad [4-2]$$

Results of this statistical analysis are shown table 4-1.

The morning and evening rates of transpiration calculated by equation [4-2] with the parameters listed in table 4-1 are shown in tables 4-2a and 4-3a. Two-way analyses of variance were conducted on these data, shown in tables 4-2b and 4-3b, respectively.

Results show that the evening rate of transpiration strongly depends on both soil water

potential and root temperature at the 0.01 significant level, while the morning rate of transpiration depends on the soil water potential only.

Table 4-1. The parameters of equation [4-2]. The numbers in parentheses are the estimated standard error.

Estimated parameters	Root temperature °C				
	14	17	22	27	32
$a * 10^8 (\text{m}^3 \text{m}^{-2} \text{s}^{-1})$	6.79 (0.34)	6.91 (0.43)	6.39 (0.36)	7.27 (0.47)	6.21 (0.59)
$b * 10^8 (\text{m}^3 \text{m}^{-2} \text{s}^{-1} \text{h}^{-1})$	-0.149 (0.015)	-0.074 (0.016)	-0.054 (0.013)	-0.086 (0.018)	-0.097 (0.019)
$c * 10^8 (\text{m}^3 \text{m}^{-2} \text{s}^{-1} \text{MPa}^{-1})$	-15.57 (0.68)	-16.13 (0.72)	-13.45 (0.62)	-18.58 (0.84)	-12.85 (0.91)
R^2	0.85	0.75	0.75	0.77	0.55

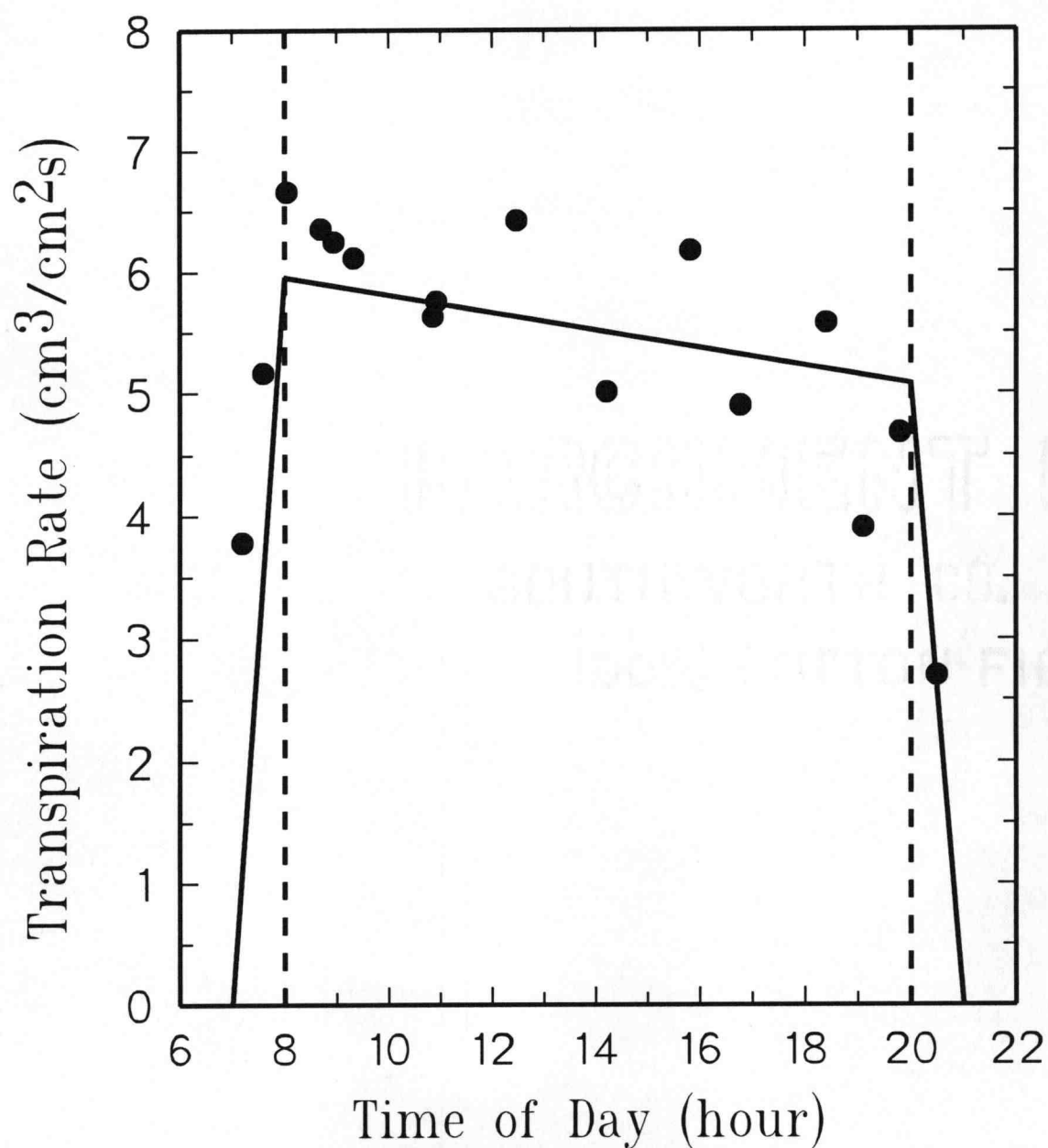


Figure 4-1. Transpiration rate plotted as a function of time of day at the soil water potential of -0.06 MPa and the root temperature of 17°C . Symbols are measurements made on the third. Solid line is derived from fitting equation [4-2] to these experimental data. All lights were on during the time between the dashed lines.

Table 4-2a. The morning rate of transpiration at the indicated combinations of soil water potential and root temperature.

Soil water potential	Root temperature °C					avg
	14	17	22	27	32	
---MPa---	----- $\text{m}^3 \text{m}^{-2} \text{s}^{-1} * 10^8$ -----					
-0.03	6.32	6.44	5.99	6.71	5.81	6.26
-0.06	5.87	5.96	5.58	6.16	5.44	5.80
-0.10	5.24	5.31	5.06	5.40	4.91	5.18
-0.17	4.14	4.18	4.10	4.10	4.01	4.11
-0.25	2.90	2.90	3.04	2.61	2.99	2.89
avg	4.89	4.96	4.76	5.00	4.63	4.85

Table 4-2b. ANOVA of data shown in table 4-2a.

Source of variation	SS	d.f	MSS	F
Soil temperature	0.45802	4	0.11451	2.7066
Soil water potential	36.9611	4	9.24001	218.408 **
Error	0.67689	16	0.04231	
Total	38.0949	24	1.58729	

Table 4-3a. The evening rate of transpiration at the indicated combinations of soil water potential and root temperature.

Soil water potential	Root temperature °C					
	14	17	22	27	32	avg
---MPa---	----- $\text{m}^3\text{m}^{-2}\text{s}^{-1} * 10^8$ -----					
-0.03	4.54	5.56	5.35	5.67	4.66	5.16
-0.06	4.07	5.08	4.95	5.11	4.27	4.69
-0.10	3.44	4.43	4.41	4.37	3.76	4.08
-0.17	2.36	3.29	3.47	3.08	2.86	3.01
-0.25	1.12	2.02	2.39	1.58	1.84	1.79
avg	3.10	4.08	4.11	3.96	3.48	3.75

Table 4-3b. ANOVA of data shown in table 4-3a.

Source of variation	SS	d.f	MSS	F
Soil temperature	3.86198	4	0.96549	23.3699 **
Soil water potential	36.8409	4	9.21001	222.935 **
Error	0.66101	16	0.04131	
Total	41.3639	24	1.72349	

The Daily Trend of Stomatal Conductance

The daily trends of the stomatal conductance were similar to that of the transpiration rate. One example of the stomatal conductance measured during the light period is shown in figure 4-2. When the lights were turned on, stomatal conductance increased, reaching a maximum value at 8:00, after which the stomatal conductance decreased consistently during the full light period. After the first light was turned off, the stomatal conductance decreased rapidly. The same trend was observed for all treatments. Maximum stomatal conductance and the rates at which the conductance decreased with time depended on root temperature and soil water potential. Similar to the rate of transpiration, the stomatal conductance in the morning (8:00) and evening (20:00) were used to characterize the daily change of stomatal conductance.

Stomatal conductance in the morning and evening

The method used to calculate the morning and evening rates of transpiration was used to calculate the values of stomatal conductance in the morning and evening. A linear decrease was assumed for the stomatal conductance during the full light period. It was assumed that the effect of soil water potential on the stomatal conductance can be approximated by a polynomial function over the range of soil water potentials studied in this research, namely:

$$G_s = a + bt + c_1\psi_{\text{soil}} + c_2\psi_{\text{soil}}^2 + c_3\psi_{\text{soil}}^3 + \dots, \quad [4-3]$$

where G_s is stomatal conductance expressed in $\text{mol m}^{-2} \text{s}^{-1}$; ψ_{soil} is the soil water potential in MPa; t is the time of day in hours; and a , b , and c are constants. Equation [4-3] was

fitted to the experimental data set for each root temperature using the least square technique. The function which best approximated the data set was chosen on the basis of estimated standard errors of the parameters and R^2 . The final function is

$$G_s = a + b * t + c_1 * \psi_{\text{soil}} + c_2 * \psi_{\text{soil}}^2, \quad [4-4]$$

Results of this statistical analysis are shown in table 4-4.

The values of stomatal conductance in the morning and evening were calculated by equation [4-4] with the parameters listed in table 4-4 and are shown in tables 4-5a and 4-6a. Two-way analyses of variance were conducted on these data shown in tables 4-5b and 4-6b, respectively. Results show that the stomatal conductance in the evening depends on soil water potential and root temperature at the 0.01 significant level, while the stomatal conductance in the morning depends on the soil water potential only.

Table 4-4. The parameters of equation [4-4]. The numbers in parentheses are the estimated standard errors.

Estimated parameters	Root temperature °C				
	14	17	22	27	32
a (mol m ⁻² s ⁻¹)	0.398 (0.042)	0.385 (0.049)	0.347 (0.048)	0.411 (0.056)	0.437 (0.052)
b (mol m ⁻² s ⁻¹ h ⁻¹)	-0.007 (0.001)	-0.005 (0.001)	-0.003 (0.001)	-0.004 (0.001)	-0.009 (0.001)
c1 (mol m ⁻² s ⁻¹ MPa ⁻¹)	-0.172 (0.22)	-0.092 (0.022)	-0.142 (0.021)	-0.248 (0.025)	(0.024)
c2 (mol m ⁻² s ⁻¹ MPa ⁻²)	0.031 (0.008)	-0.001 (0.008)	0.024 (0.007)	0.054 (0.009)	0.059 (0.008)
R ²	0.745	0.719	0.618	0.689	0.692

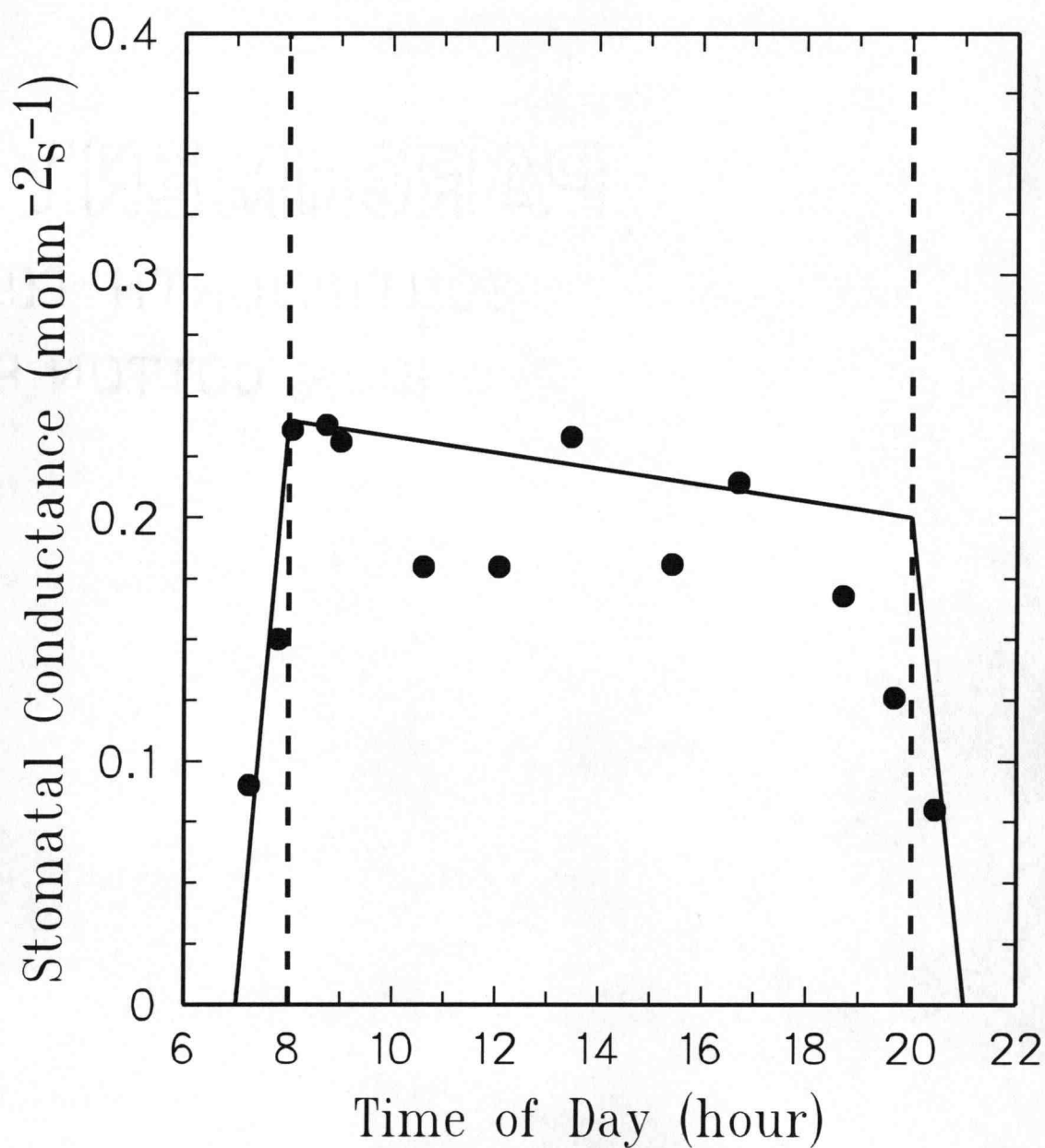


Figure 4-2. Stomatal conductance plotted as a function of time of day at the soil water potential of -0.06 MPa and the root temperature of 17°C. Symbols are measurements made on the third. Solid line is derived from fitting equation [4-4] to these experimental data. All lights were on during the time between the dashed lines.

Table 4-5a. Stomatal conductance in the morning at the indicated combinations of soil water potential and root temperature.

Soil water potential	Root temperature °C					
	14	17	22	27	32	avg
---MPa---	----- mol m ⁻² s ⁻¹ -----					
-0.03	0.293	0.312	0.280	0.307	0.296	0.298
-0.06	0.250	0.252	0.244	0.247	0.240	0.246
-0.10	0.201	0.232	0.203	0.183	0.182	0.200
-0.17	0.140	0.177	0.149	0.112	0.126	0.141
-0.25	0.108	0.106	0.116	0.096	0.133	0.112
avg	0.198	0.212	0.198	0.189	0.195	0.199

Table 4-5b. ANOVA of data shown in table 4-5a.

Source of variation	SS	d.f	MSS	F
Soil temperature	0.00240	4	0.00060	2.2242
Soil water potential	0.13803	4	0.03451	128.016 **
Error	0.00431	16	0.00027	
Total	0.14474	24	0.00603	

Table 4-6a. Stomatal conductance in the evening at the indicated combinations of soil water potential and root temperature.

Soil water potential	Root temperature °C					avg
	14	17	22	27	32	
---MPa---	mol m ⁻² s ⁻¹					
-0.03	0.208	0.256	0.241	0.254	0.186	0.229
-0.06	0.165	0.216	0.205	0.195	0.129	0.182
-0.10	0.116	0.177	0.163	0.130	0.071	0.132
-0.17	0.055	0.121	0.109	0.059	0.015	0.072
-0.25	0.023	0.051	0.077	0.043	0.022	0.043
avg	0.114	0.164	0.159	0.136	0.085	0.132

Table 4-6b. ANOVA of data shown in table 4-6a.

Source of variation	SS	d.f	MSS	F
Soil temperature	0.02633	4	0.00658	25.8504 **
Soil water potential	0.14039	4	0.03510	137.818 **
Error	0.00407	16	0.00025	
Total	0.17081	24	0.00712	

Rate of Transpiration

Water movement is from regions of high water potential toward regions of low water potential. In the soil-plant system, water movement is driven by the difference between soil water potential and leaf water potential. The transpiration rate is assumed to be proportional to the quantity of $\psi_l - \psi_{soil}$. The proportionality factor represents the permeability to water flow through the soil-plant system and is expressed as a water conductance of the plant as follows:

$$E = L * (\psi_l - \psi_{soil}) , \quad [4-5]$$

where E is transpiration rate expressed in $\text{cm}^3 \text{ cm}^{-2} \text{ s}^{-1}$; ψ_l and ψ_{soil} are leaf water potential and soil water potential in MPa; and L is the water conductance expressed in $\text{cm s}^{-1} \text{ MPa}^{-1}$, indicating the permeability of the soil-plant system to water flow. L includes the conductance of the soil and the plant.

Thus, the rate of transpiration depends on the difference between the soil water potential and leaf water potential, $\Delta\psi$, and the water conductance of the plant, which depends on the plant characteristics and water viscosity. Consequently, the rate of transpiration is controlled by a combination of physiological and physical factors. Water viscosity, which decreases with increasing temperature, is considered as a major physical factor controlling the rate of transpiration, although the temperature treatment was imposed only on the roots. This consideration was based on the assumption that the major control of water movement in the plant was in the root (Blizzard and Boyer, 1980; Boyer, 1985). Therefore, as a first step in this analysis, it seemed reasonable to adjust for changes

in the water viscosity to understand the response of transpiration process to root temperature.

Adjusted transpiration rates were obtained by multiplying the measured results (tables 4-2a and 4-3a) with the ratio of water viscosity at the experimental temperatures to that at 14°C. Results of the adjustment are reported in tables 4-7 and 4-8. The morning and evening rates of transpiration with and without adjustment for changes in water viscosity are plotted as functions of root temperature in figures 4-3 and 4-4.

Table 4-7. Adjusted morning rate of transpiration at the indicated combinations of soil water potential and root temperature.

Soil water potential	Root temperature °C					
	14	17	22	27	32	avg
---MPa---	----- $\text{m}^3 \text{m}^{-2} \text{s}^{-1} * 10^8$ -----					
-0.03	6.33	5.95	4.89	4.89	3.81	5.17
-0.06	5.86	5.50	4.56	4.48	3.56	4.79
-0.10	5.24	4.91	4.12	3.94	3.22	4.29
-0.17	4.15	3.87	3.36	2.99	2.63	3.40
-0.25	2.90	2.67	2.48	1.91	1.96	2.38
avg	4.90	4.58	3.88	3.64	3.03	4.01

Although statistical analysis suggested that the morning rate of transpiration was independent of the root temperature, the morning rate of transpiration decreased with increasing root temperature for all soil water potential treatments after adjusting for the water viscosity as shown in figure 4-3B.

According to the equation [4-5], a decrease in leaf water potential causes an increase in transpiration rate, as long as the water conductance of the plant remains constant. The driving force for water movement, $\Delta\psi$, in the morning increased with increasing root temperature, as was shown in figure 3-4 (Chapter 3). Thus, the decrease in the transpiration rate shown in figure 4-3B could only have occurred as the result of a decrease in the water conductance of the plant.

Table 4-8. Adjusted evening rate of transpiration at the indicated combinations of soil water potential and root temperature.

Soil water potential	Root temperature °C					avg
	14	17	22	27	32	
---MPa---	----- $\text{m}^3 \text{m}^{-2} \text{s}^{-1} * 10^8$ -----					
-0.03	4.53	5.14	4.37	4.13	3.05	4.24
-0.06	4.06	4.69	4.04	3.73	2.80	3.86
-0.10	3.44	4.10	3.60	3.18	2.46	3.36
-0.17	2.35	3.05	2.83	2.24	1.87	2.47
-0.25	1.11	1.86	1.95	1.16	1.20	1.46
avg	3.10	3.77	3.36	2.89	2.27	3.08

The measured evening rate of transpiration increased with increasing root temperature from the temperature of 14°C to approximately 22°C, and decreased with further increasing root temperature. The response of the evening rate of transpiration to root temperature was the same for all soil water potential treatments. The temperature at which the transpiration rate was highest was somewhere between 17°C and 27°C (Figure

4-4A). The number of observations was not sufficient to establish the temperature at which the highest rate occurred. After adjustment for water viscosity, the results indicated an increase of transpiration rate from 14° to approximately 17°C, followed by a decrease (Figure 4-4B). The increase from 14°C to 17°C occurred at all soil water potential treatments and is probably a true response to temperature rather than an experimental error. The driving force for water movement, $\Delta\psi$, in the evening increased with increasing root temperature. This indicates that the water conductance of the plants must decrease with increasing root temperature from 17°C to 32°C.

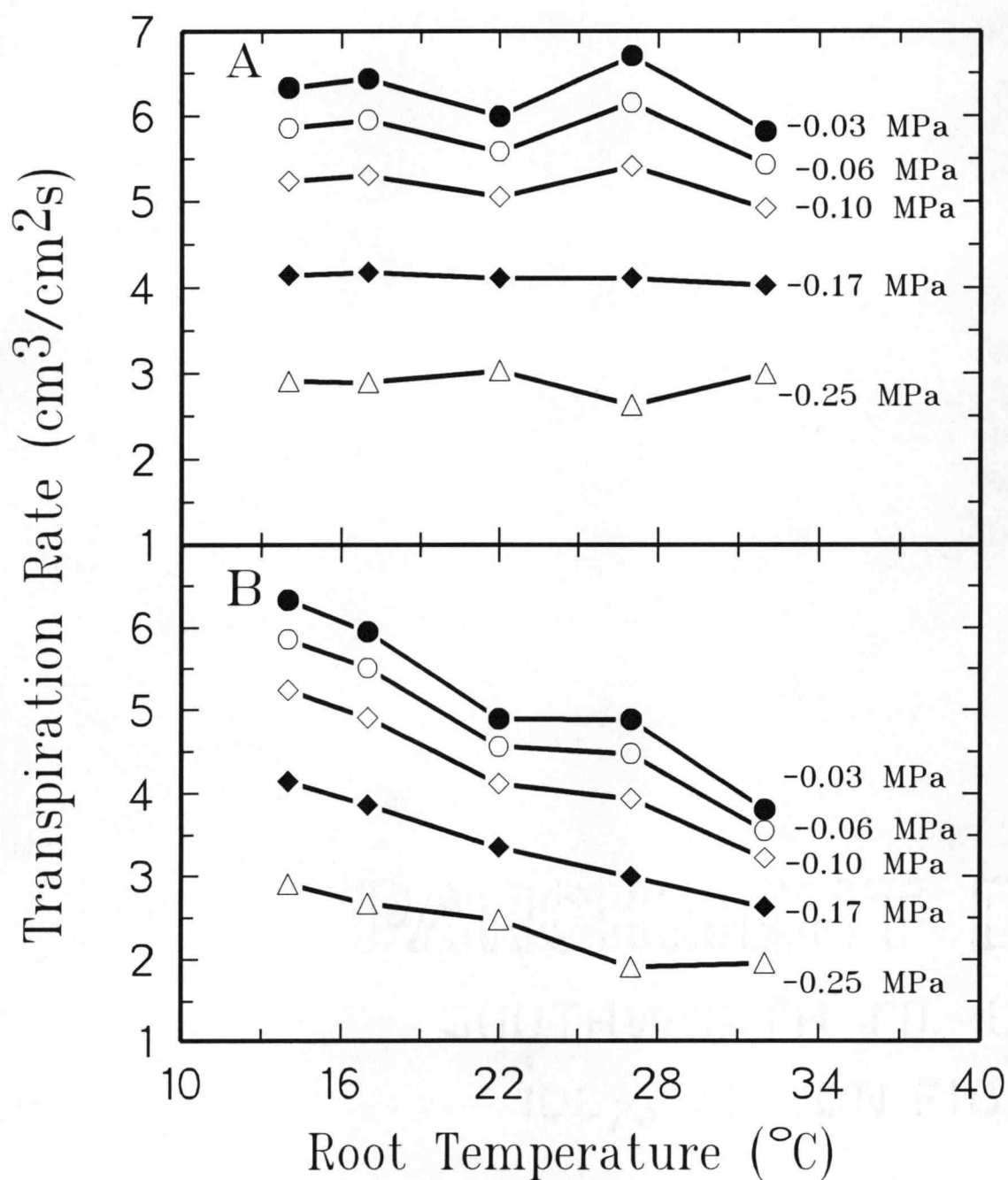


Figure 4-3. Morning rate of transpiration plotted as a function of root temperature for all soil water potential treatments. A. Transpiration rate before adjustment for water viscosity; B. Transpiration rate after adjustment for water viscosity.

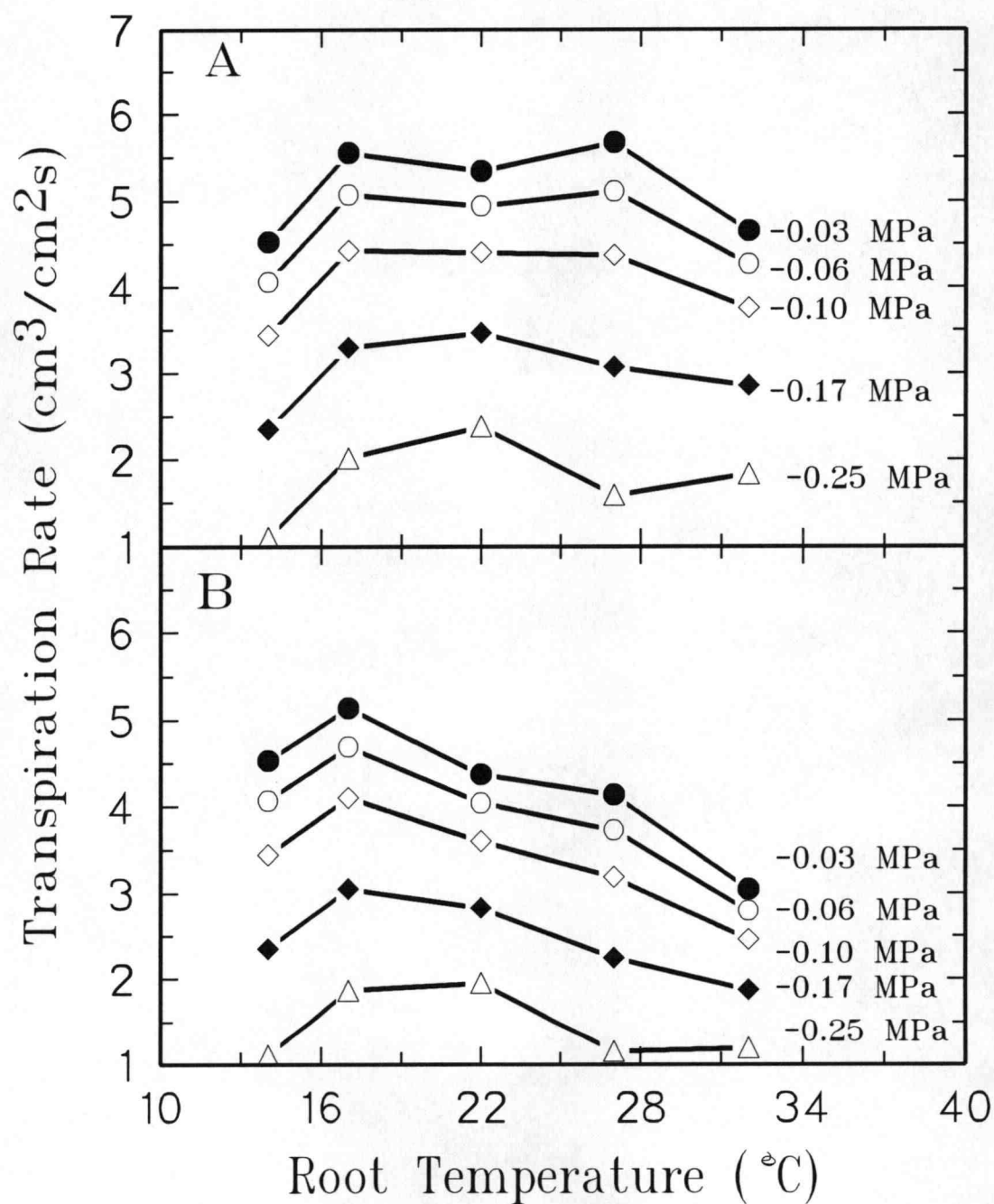


Figure 4-4. Evening rate of transpiration plotted as a function of root temperature for all soil water potential treatments. A. Transpiration rate before adjustment for water viscosity; B. Transpiration rate after adjustment for water viscosity.

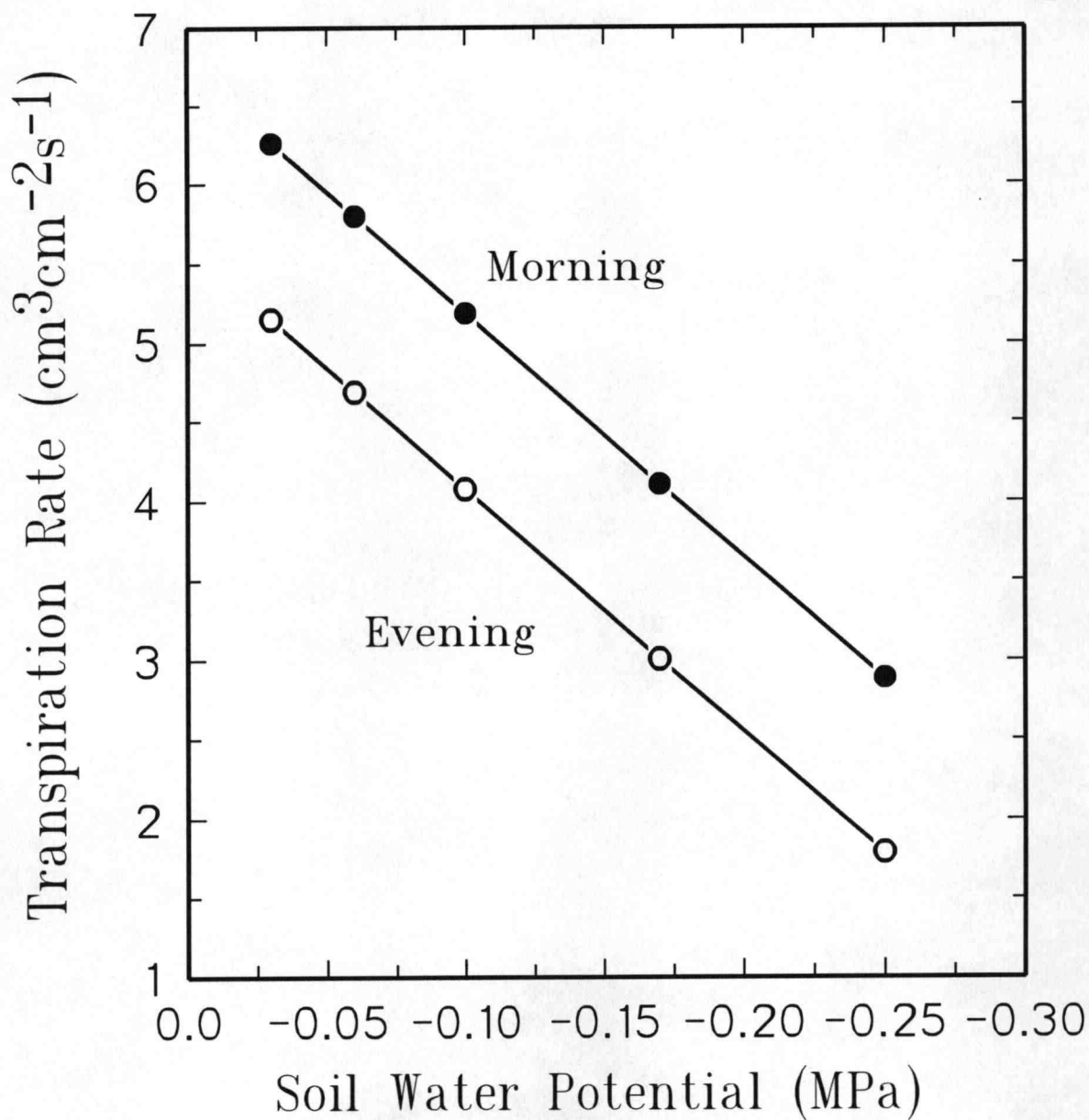


Figure 4-5. The rates of transpiration averaged over five root temperatures plotted as functions of soil water potential.

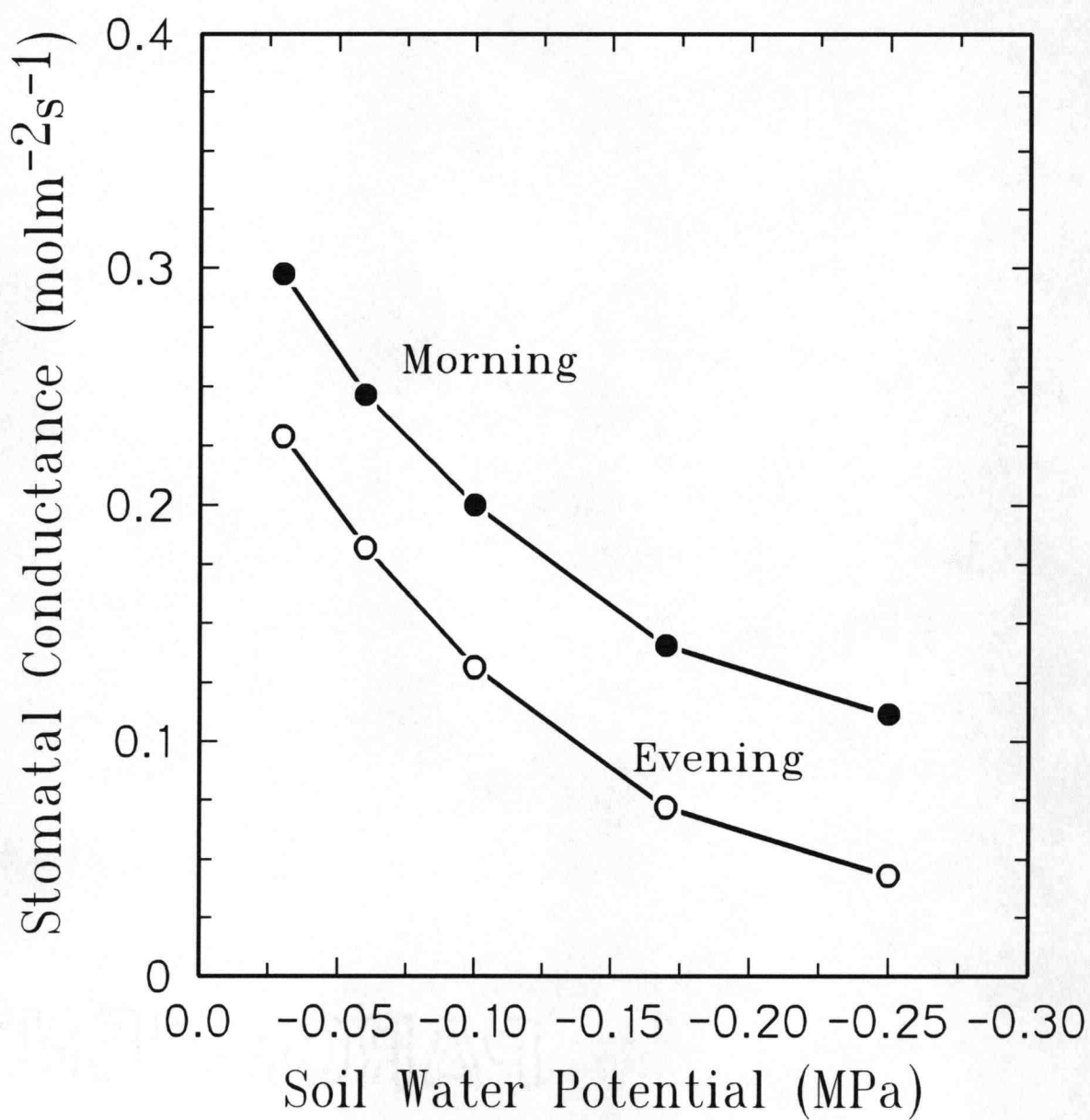


Figure 4-6. Stomatal conductance averaged over five root temperatures plotted as functions of soil water potential.

The differences between the morning and evening rates of transpiration in response to root temperature was because that the transpiration rate in the evening was mainly controlled by the plant response to developing leaf water stress. Plant water stress developed progressively during the day. During the night period, stomata closed and the rate of transpiration was near zero. During this time, the plant recovered from water stress.

A decrease in the transpiration rate with increasing soil water stress (Figure 4-5) results from effects of soil water stress on leaf water potential and on the water permeability of the roots (Munns and King, 1988). The results discussed in Chapter 3 demonstrated that the leaf water potential decreased with decreasing soil water potential. However, the differences between leaf water potential and soil water potential, $\Delta\psi$, remained constant at each root temperature for both in the morning and evening (Figure 3-4). The decrease in the transpiration rate must be due to a decrease in the water conductance of plant. In the meantime, the decrease in leaf water potential results in the stomatal closure and consequently in the decrease of the transpiration rate (Jenson, Hensan, and Turner, 1989). The rate of transpiration in the morning was always higher than in the evening. This indicated that the plants were more stressed in the evening than in the morning, causing stomatal closure in the evening.

Stomatal Conductance

The stomatal opening is affected by water stress. As soil water stress increased, the leaf water potential decreased (Chapter 3), causing stomatal closure, thus, a decrease in

stomatal conductance occurs. The stomatal conductance averaged over five root temperatures in the morning and evening were plotted as a function of soil water potential in figure 4-6. The stomatal conductance in the morning decreased from 0.30 to 0.12 mol m⁻² s⁻¹ as soil water potential decreased from -0.03 to -0.25 MPa and decreased from 0.23 to 0.04 mol m⁻² s⁻¹ in the evening over the same soil water stress range. Similar to the rate of transpiration and leaf water potential, the stomatal conductance in the morning was always higher than in the evening. This indicates that stomata approached closure in the evening for all soil water potentials.

Analysis of the response of stomatal conductance to root temperature revealed that the stomatal conductance only in the evening depended on the root temperature (Tables 4-5b and 4-6b). This agreed with the response of morning transpiration rate to root temperature. The stomatal conductance in the evening were plotted as functions of the root temperature for five soil water potential treatments in figure 4-7. It shows that the stomatal conductance increased with increasing root temperature from the temperature of 14°C to approximately 20°C and decreased with further increasing root temperature. The response of the stomatal conductance in the evening to root temperature was similar for all soil water potential treatments. The temperature at which the stomatal conductance was highest was between 17°C and 27°C. The number of observations was not sufficient to establish the temperature at which the highest conductance occurred. But the optimum root temperature range for stomatal conductance in the evening included the optimum temperature for the photosynthetic rate. This suggests that the stomatal opening is also controlled by the plant physiological processes, besides leaf water potential.

Relation Between Stomatal Conductance and Turgor Potential

Stomatal conductance was plotted against leaf turgor potential for in the morning and evening in figure 4-8. The values used in the graph were the averages of five root temperature treatments. The stomatal conductance decreased with decreasing leaf turgor potential, ranging from 0.3 to 0.7 MPa. Over the soil water stress range, the stomatal conductance decreased by 60% in the morning and 80% in the evening, while the leaf turgor potential decreased by 25% and 45% in the same time. The constant reduction of the morning and evening between stomatal conductance and turgor potential suggests that the loss of turgor in leaf cells is the principal cause of closure of stomata (Kramer and Boyer, 1995).

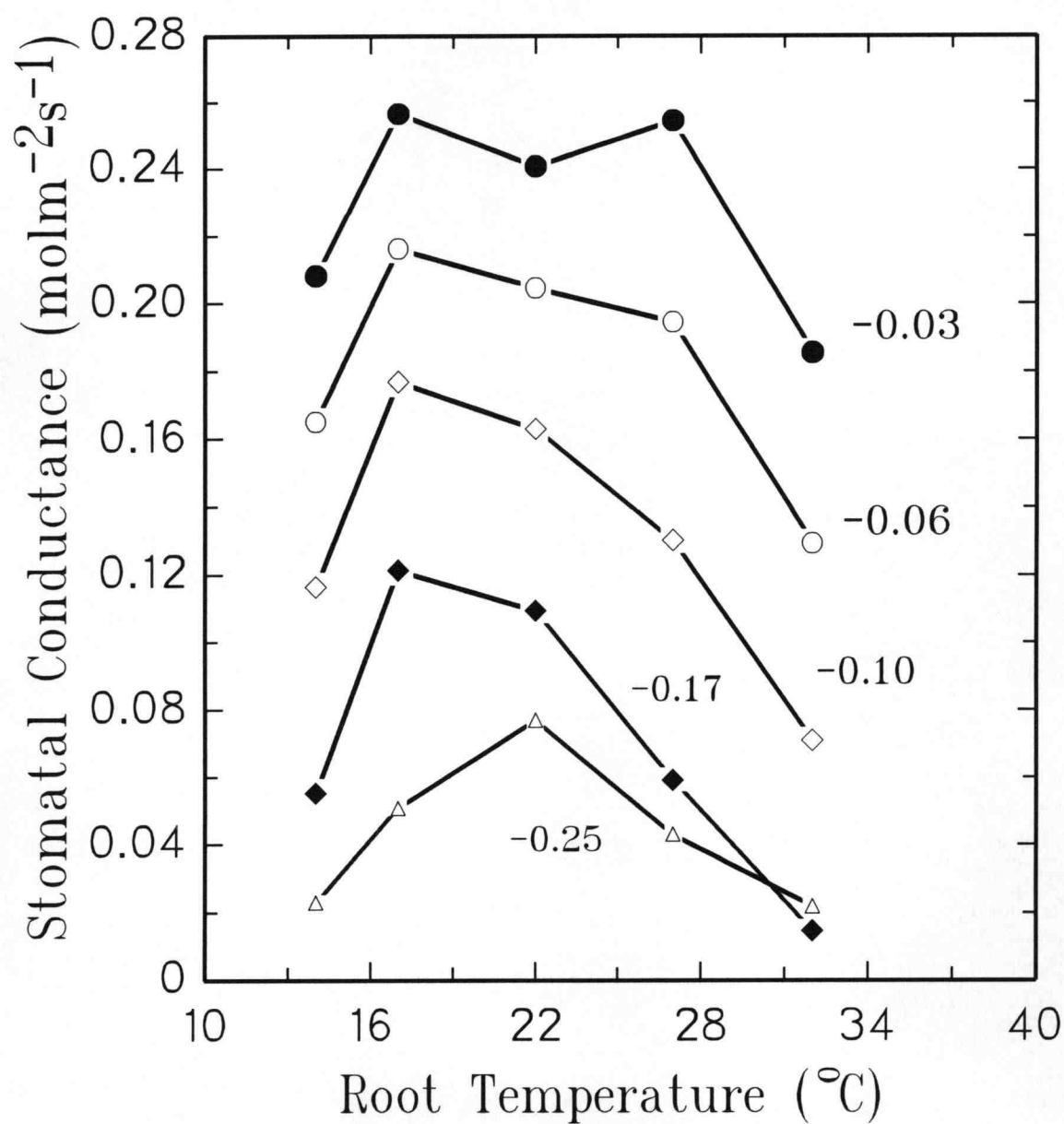


Figure 4-7. Stomatal conductance in the evening plotted as a function of root temperature for all soil water potential treatments

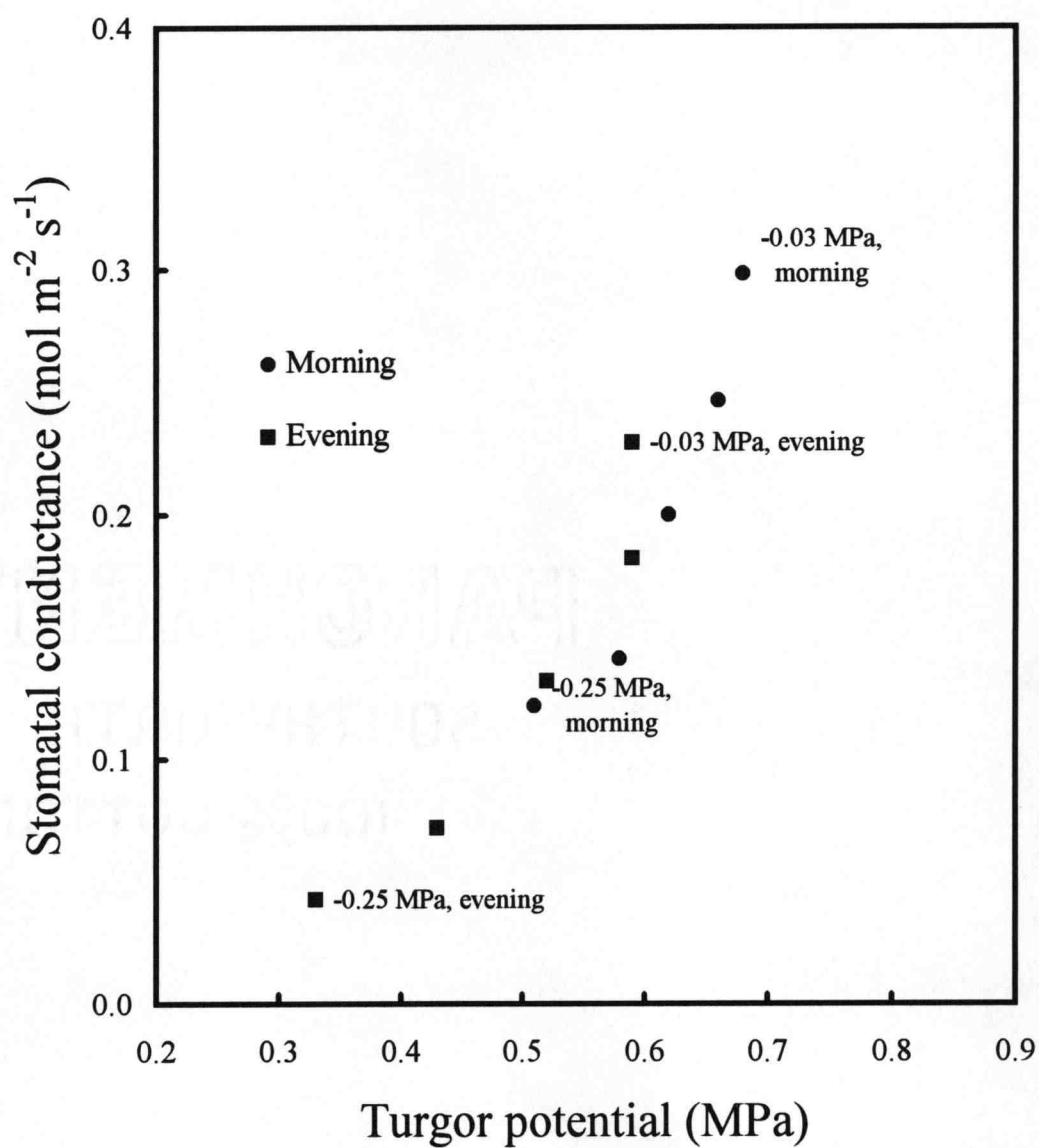


Figure 4-8. Stomatal conductances plotted against turgor potential. The data were averaged over five root temperature treatments.

Summary

Morning rate of transpiration remained almost constant with increasing root temperature. While evening rate of transpiration increased with increasing root temperature from the temperature 14°C to approximately 22°C and decreased with further increasing root temperature.

Water viscosity was considered a major physical factor controlling the rate of transpiration. After adjusted for water viscosity, the morning rate of transpiration decreased with increasing root temperature over the experiment range. The evening rate of transpiration increased with increasing root temperature from 14°C to 17°C, followed by a decrease with further increasing root temperature. Transpiration rates both in the morning and evening decreased with decreasing soil water potential. Similar responses were observed for the stomatal conductance.

Since difference between the soil water potential and leaf water potential increased with increasing root temperature and remained constant as decreasing soil water potential (Chapter 3), the decrease in transpiration rate resulted from a decrease in the water conductance of the plant and in the stomatal conductance under soil water and root temperature stressed conditions.

The stomatal conductance decreased with decreasing leaf turgor potential. The constant reduction between stomatal conductance and turgor potential from the morning to evening over the soil water potential ranges suggested that the loss of leaf turgor may be the primary cause of the stomata closure.

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5. PHOTOSYNTHESIS

Introduction

The process of photosynthesis is affected by temperature. There are numerous reports in the literature on the response of photosynthesis to temperature, determined on different species in diverse environments (Ingraham, 1958; Ludlow and Wilson, 1971; Björkman, Mooney, and Eleringer, 1975; Pearcy, 1977; Mooney and Björkman, 1978). Generally, the rate of photosynthesis increases to an optimum with an increase in temperature and then decreases as the temperature further increases (Ludlow, 1983).

Cooper (1973) published an extensive review of the literature on root temperature. He reported contradictory results and concluded that the shape of the response curve of net photosynthetic rate to root temperature differed between species, but in all the species examined there was a broad optimal root temperature band suggesting that, in general, net photosynthetic rate may be independent of root temperature over a range of 15°C to 35°C, except at the extremes of root temperature. Similar results were reported by Barlow et al. (1977) for corn seedling, by Gosselin and Trudel (1984) for tomatoes, by Johnson and Ingram (1984) for *Pittosporum tobira*, and by Delucia (1986) for Engelmann spruce seedlings. The physiological mechanisms underlying the response of the photosynthetic process to root temperature is not well understood.

It is well known that the rate of photosynthesis of higher plants is inhibited by water stress and may cease completely under severe water stress. The reduction in photosynthetic rate under water stress is caused by both stomatal closure and non-

stomatal factors and/or chloroplast activity (Jones, 1973a,b; Farquhar and Sharkey 1982;; Prioul, Conic, and Jones, 1984). The effects of water stress on photosynthetic processes often interact with temperature (Barlow et al., 1977; Harrison, Walton, and Rothery, 1986). Little quantitative research has been reported where both soil water stress and root temperature are involved (Barlow et al., 1977). In this case the usual statistical analysis of variance yields limited information about the nature of these responses. A more theoretically based approach is preferred.

The rate of photosynthesis is also moderated by other plant physiological processes, such as translocation and utilization of carbohydrates (Bagnall, King, and Farquhar, 1988). These processes are functions of root temperature and water stress. A theoretical analysis which could quantify the response of the rate of photosynthesis to root temperature and soil water stress and the relations between the photosynthetic process and other physiological processes does not exist. Such an analysis is needed, especially with respect to the combined effects of temperature and water stress.

The objective of this chapter is to investigate the manner in which root temperature and water stress affect the photosynthetic process of spring wheat seedlings, and to use mathematical analysis as a tool for quantifying the combined effects of root temperature and soil water stress on the process of photosynthesis.

Theoretical Consideration

The Arrhenius equation for the rate of a chemical reaction as a function of temperature states that

$$K' = K_a e^{-E_a/RT}, \quad [5-1]$$

where K' represent the rate of reaction. For photosynthesis, the rate units are $\mu\text{mol m}^{-2} \text{s}^{-1}$.

E_a (J Mol^{-1}) is the activation energy. K_a is a constant, which can be viewed as the maximum rate of reaction when there is no energy barrier (activation energy) between reactant and product. R is the universal gas constant expressed in $\text{J Mol}^{-1} \text{ } ^\circ\text{K}^{-1}$ and T is temperature in unit of $^\circ\text{K}$.

Johnson and Thornley (1985) considered that the rate of an enzyme-catalyzed reaction depends on the fraction of the enzymes in the active state. Assuming that an enzyme exists in either an active or an inactive state and that the Boltzman distribution is used to describe the distribution of enzymes between the two states,

$$f_a = 1/(1+e^{-dG/RT}), \quad [5-2]$$

where f_a is the fraction of enzymes in the active state and dG (J Mol^{-1}) is the free energy difference between active and inactive states of the enzyme. The total rate of reaction is written as

$$K = f_a * K'. \quad [5-3]$$

Combining equations [5-1] through [5-3] with the relation

$$dG = -TdS + dH \quad [5-4]$$

results in

$$K = \frac{K_a e^{-E_a/RT}}{1 + e^{dS/R - dH/RT}} \quad [5-5]$$

where dS ($\text{J Mol}^{-1} \text{K}^{-1}$) and dH (J Mol^{-1}) are, respectively, the entropy and enthalpy differences between the active and inactive enzyme states.

Equation [5-5] is the form of the Arrhenius equation described by Johnson and Thornley (1985). They referred to K as the "rate constant". The term "constant" is misleading because, as equation [5-5] indicates, K varies with temperature. K may also vary with water stress, a possibility which is investigated in this study.

Feng et al. (1990) simplified equation [5-5] by defining the constants

$$B = E_a/R, \quad (^\circ\text{K}) \quad [5-6a]$$

$$C = dS/R, \quad (\text{dimensionless}) \quad [5-6b]$$

$$\text{and } D = dH/R, \quad (^\circ\text{K}) \quad [5-6c]$$

and substituting these into [5-5], yielding:

$$K = \frac{K_a e^{-B/T}}{1 + e^{C-D/T}} \quad [5-7]$$

At the optimum temperature $T=T_0$, $dK/dT=0$, so that

$$T_0 = \frac{D}{C + \ln(D/B-1)}, \quad [5-8]$$

or

$$C = D/T_0 - \ln(D/B-1). \quad [5-9]$$

The existence of an optimum temperature requires that $D > B$, or $dH > E_a$, i.e., the enthalpy of the photosynthetic process must be greater than its activation energy. From a practical perspective, the optimum temperature, T_0 , is a more meaningful parameter than the entropy change between active and inactive states of enzymes. The rate of

photosynthesis is the result of a combination of several complex processes where the active and inactive states of the enzyme system are not easily defined. Substituting equation [5-9] into equation [5-7] produces

$$K = \frac{K_a e^{-B/T}}{1 + m^* e^{D(1/T_0 - 1/T)}}, \quad [5-10]$$

where

$$m = B/(D-B). \quad [5-10a]$$

The parameters in equation [5-5] which was developed by Johnson and Thornley (1985) include activation energy, the maximum rate of reaction, and entropy and enthalpy changes between the active and the inactive states of the enzyme. These parameters are defined when applied to enzyme reactions, but strict physical meanings of the parameters are not clearly defined for complex processes.

The flexibility of the Arrhenius equation, however, allows it to represent the temperature response of the photosynthetic process. When the Arrhenius equation derived for a single enzymatic reaction is used to describe this complex process, the parameters represent the combined responses of multiple enzyme systems. The equation is used in this way as a semi-empirical relation.

The temperature is the only variable in equation [5-10]. However, equation [5-10] can be considered as a basis for comparison of the sensitivity of different plant processes to water stress. In the case where temperature and soil water potential are involved, K can be expressed:

$$K = f(T, \psi) , \quad [5-11]$$

where ψ is soil water potential (MPa). For any fixed soil water potential,

$$K = f(T_{\psi=\text{constant}}) . \quad [5-12]$$

The assumption that soil water potential affects K in equation [5-10] by affecting its parameters leads to the following relationships:

$$K_a = K_a(\psi) , \quad [5-13a]$$

$$B = B(\psi) , \quad [5-13b]$$

$$D = D(\psi) , \quad [5-13c]$$

$$\text{and } T_0 = T_0(\psi) . \quad [5-13d]$$

Equations [5-10] and [5-13] are then specific expressions of equations [5-11] and [5-12]. Equations [5-10] and [5-13] are applied to the rates of net photosynthesis of spring wheat seedlings measured at combinations of all soil temperatures and soil water potentials.

Results

Diurnal Course of The Net Photosynthesis

The rate of net photosynthesis was measured several times throughout the light period. One of example is shown in figure 5-1. The photosynthesis rate increased sharply from 7:00 when the first light was turned on, to 8:00 when the full light intensity was reached. The rate reached its peak value after all the lights were on at 8:00. The rates rose

initially to relative high values which then decreased to lower values. This initial rise or "overshoot" often occurs in similar treatments. The photosynthetic rate declined to the lower value after about half hour and thereafter decreased continuously with a constant slope during the rest of the full illumination period. Then, as lights were turned off the photosynthesis rate quickly decreased and reached zero at 9:00 when the last light was extinguished.

The "over shoot" phenomenon may be explained as following. When the lights were turned on, the photosynthesis apparatus was initially free from the inhibiting effects of its products (Bagnall et al, 1988) as well as from the effects of lower leaf water potential. The main limiting factor for the rate of photosynthesis was the light intensity. Consequently, the rate of net photosynthesis increased with increasing light intensity during the first hour of the light period.

Because of the low photosynthetic product concentration initially in leaf, the initial rates of utilization and translocation, which depends on the concentration of photosynthetic products, were low. The combined effects of low initial rates of utilization and translocation and fast increasing rate of photosynthesis when the lights were turned on lead to an accumulation of photosynthesis products in the leaf. This is shown by the initial fast decline of the leaf osmotic potential over this time (chapter 3). Also the leaf water potential quickly decreased with time after the light period started. The increasing photosynthetic product concentration and the lowering leaf water potential tended to decrease the rate of net photosynthesis.

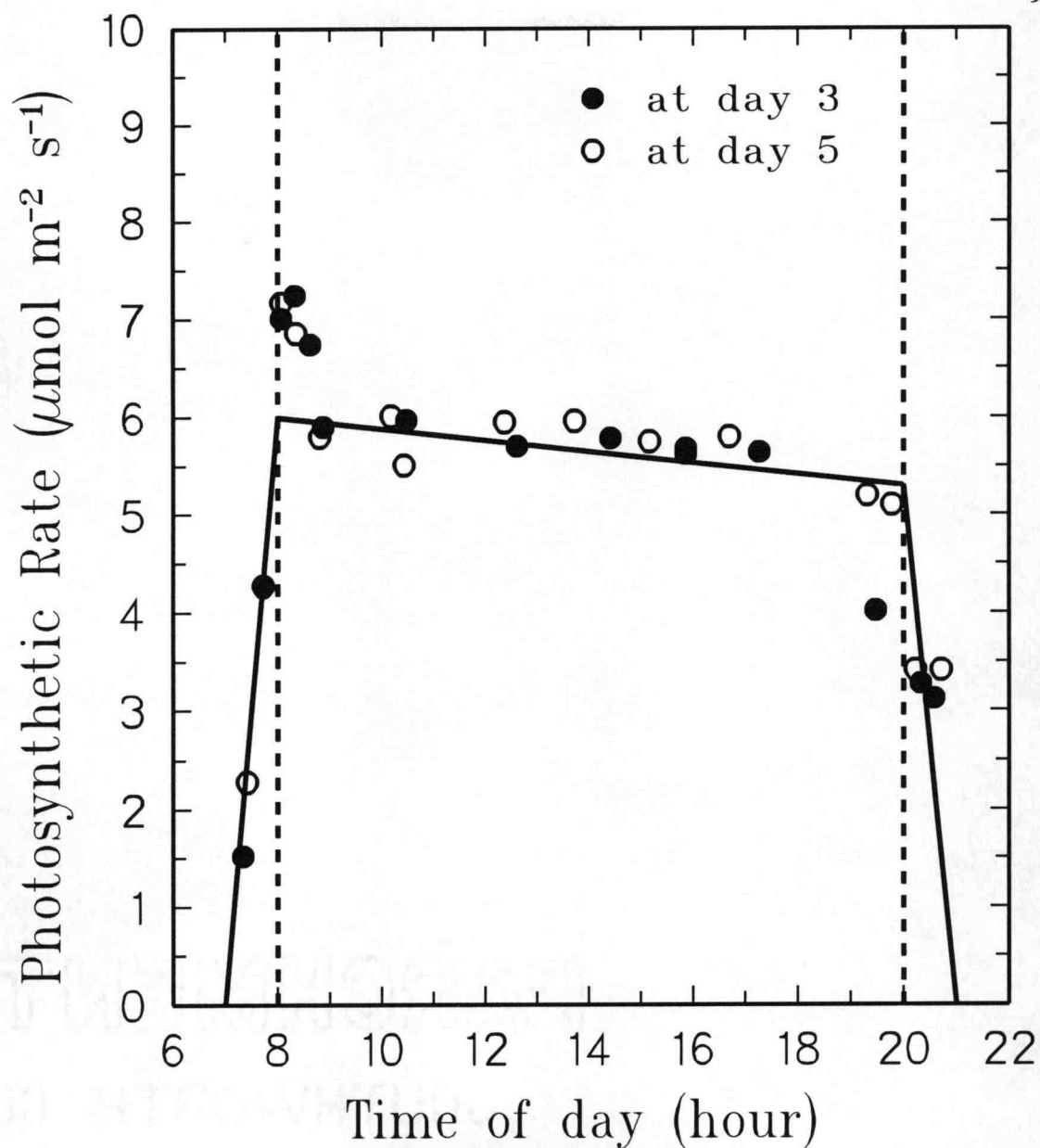


Figure 5-1. Diurnal cycle of net photosynthetic rate at a root temperature of 27°C and soil water potential of -0.25 MPa. Symbols represent experimental data; the solid line represents fitted results. The time between the two vertical dashed lines is the full light period.

When the lights were turned on, the increasing light intensity had the dominant effect, resulting in a quick increase in the rate of net photosynthesis. After reaching full light intensity, the increases photosynthetic product concentration and the lower leaf water potential results in a fast decline of the net photosynthesis rate until a new point of balance was reached. The rate of net photosynthesis then slowly decreases with time as water stress developed during the light period.

The rate of photosynthesis decreased linearly with time during the full light period (Figure 5-1). The slope at which the photosynthesis rate decreased during the day was expected to differ between treatments. Thus the diurnal course of net photosynthetic rates can be characterized by the rates of net photosynthesis at 8 a.m. and at 8 p.m. These two rates are referred to as the morning and evening rates of net photosynthesis, respectively. The following discussion will based on the morning and evening rates of net photosynthesis.

There were no significant differences between measurements made on day 3 and on day 5 (Figure 5-1). The low rate of net photosynthesis measured in this experiment, in comparison to literature values (Gordon et al, 1987; Manhas and Sukumaran, 1988), is due to the low light intensity used in the growth room.

Morning and Evening Rates of Photosynthesis

The rate of photosynthesis decreased linearly with time between 8:00 and 20:00. For this analysis, the initial overshoot was not considered. A linear regression between the rate of net photosynthesis and the time of the day during the full light period was

conducted for each treatment using the least square technique. Morning and evening rates of net photosynthesis were calculated using the results of linear regressions. The calculated results are shown in tables 5-1a and 5-1b. Two-way analyses of variance were conducted on these data and the results are shown in tables 5-1b and 5-2b.

The results show that the morning and evening rates of net photosynthesis depend on soil water potential and root temperature at the 0.01 significance level.

Fitting the Modified Johnson and Thornley Equation

A modified Johnson and Thornley equation was fitted to the experimental data (Tables 5-1a and 5-2a) using a least square technique. At first, equation [5-10] was fitted to morning and evening rates of net photosynthesis to obtain parameter estimates for each soil water potential treatment (Table 5-3).

The results indicated that the optimum temperature, T_o , and the parameter, D , which reflects enthalpy differences between active and inactive states of enzymes, were independent of soil water potential. However, K_a and B were functions of soil water potential. $\ln K_a$ was linearly related to B with a slope equal to κ/T_o , which expressed by

$$\ln K_a = \ln K_0 + \kappa B(\psi)/T_o, \quad [5-14]$$

where K_0 was a constant independent of soil water potential, κ is a constant. For spring wheat κ equals to 1.

Substituting equation [5-14] into equation [5-10] resulted in

$$K = \frac{K_0 e^{-B(\psi)/(1/T_0 - 1/T)}}{1 + m e^{D(1/T_0 - 1/T)}}, \quad [5-15]$$

In equation [5-15], B is the only parameter which depends on water stress. The equation defines the photosynthetic rate as a joint function of root temperature and soil water potential. The function of B(ψ) is unknown. It was assumed that B(ψ) can be approximated by a polynomial expansion,

$$B = B_0 + B_1 \psi + B_2 \psi^2 + \dots \quad [5-16]$$

Equation [5-15] combined with [5-16] was fitted to the experimental data set of all treatments for both morning and evening rates of photosynthesis. The function, which best approximates the data set, was chosen on the basis of estimated standard errors of parameters and R^2 . The final function is

$$B = B_0 + B_1 \psi + B_2 * \psi^2. \quad [5-17]$$

Results are shown in table 5-4.

Typically, for enzyme-substrate reactions, B and D take values on the order of 5,000-15,000°K and 5,000-25,000°K, respectively (Dixon and Webb, 1964). The values of B and D from this fitting were 6,000-11,000°K and 12,000- 16,000°K and are considered valid. The morning and evening rates of photosynthesis from the experimental data and fitted results are plotted against root temperature in figures 5-2 and 5-3.

Table 5-1a. The morning rate of net photosynthesis at the indicated combinations of soil water potential and root temperature.

Soil water potential	Root temperature °C					
	12	14	17	22	27	32
--MPa--	----- $\mu\text{mol m}^{-2} \text{s}^{-1}$ -----					
-0.03	7.80	7.85	9.00	9.25	8.75	7.10
-0.06	7.45	7.49	8.70	9.00	8.25	7.00
-0.10	6.90	6.82	7.90	8.00	7.25	6.70
-0.17	6.05	6.42	7.20	7.50	6.50	6.12
-0.25	5.30	5.87	6.40	6.80	6.00	5.44

Table 5-1b. ANOVA of data shown in table 5-1a.

Source of variation	SS	d.f	MSS	F
Soil temperature	10.6596	5	2.1319	47.99077 **
Soil water potential	21.8574	4	5.4644	123.0063 **
Error	0.8885	20	0.0444	
Total	33.4054	29	1.1519	

Table 5-2a. The evening rate of net photosynthesis at the indicated combinations of soil water potential and root temperature.

Soil water potential	Root temperature °C					
	12	14	17	22	27	32
--MPa--	----- $\mu\text{mol m}^{-2} \text{s}^{-1}$ -----					
-0.03	6.35	7.12	8.20	9.00	8.00	6.04
-0.06	6.40	6.78	7.80	8.40	7.25	5.61
-0.10	5.00	5.87	7.00	7.00	6.50	4.76
-0.17	4.70	4.66	5.50	6.25	5.70	4.49
-0.25	3.50	4.50	5.00	5.10	5.30	3.97

Table 5-2b. ANOVA of data shown in table 5-2a.

Source of variation	SS	d.f	MSS	F
Soil temperature	19.2458	5	3.8492	36.3401 **
Soil water potential	35.1288	4	8.7822	82.9133 **
Error	2.1184	20	0.1059	
Total	56.4930	29	1.9480	

Table 5-3. Parameter values of equation [5-10] for the morning and evening rates of net photosynthesis.

Ψ_{soil}	K_a	T_o	D	B	R^2
(MPa)	($\mu\text{mol}/\text{m}^2/\text{s}$)	K°	K°	K°	
<u>Morning</u>					
-0.03	30.9	293.4	12849.9	8137.8	0.97
-0.06	31.6	293.7	12859.1	8223.8	0.89
-0.10	33.0	294.0	12840.9	8761.7	0.95
-0.17	34.4	293.0	12830.1	9123.6	0.95
-0.25	35.6	293.2	12829.5	9515.8	0.89
<u>Evening</u>					
-0.03	24.6	294.4	15594.0	6436.6	0.98
-0.06	26.2	295.1	15596.1	6903.1	0.92
-0.10	30.2	295.5	15593.5	8124.5	0.94
-0.17	33.9	293.9	15584.8	9169.9	0.91
-0.25	36.6	294.6	15579.9	9983.6	0.93

Table 5-4. Parameter values of equations [5-15] and [5-17] for the morning and evening rates of net photosynthesis.

Parameter	Morning rate		Evening rate	
	value	ese	value	ese
K_0 (mmol m ⁻² s ⁻¹)	19.12	4.86	15.25	2.07
$b_0 \times 10^{-3}$ (°K)	5.837	1.750	5.606	1.260
$b_1 \times 10^{-3}$ (°K MPa ⁻¹)	-11.911	2.749	-29.311	3.951
$b_2 \times 10^{-3}$ (°K MPa ⁻²)	-15.281	6.489	-46.119	11.119
$D \times 10^{-4}$ (°K)	1.201	0.061	1.558	0.049
T_0 (°K)	294.0	0.4	294.4	0.3
R^2	0.96		0.98	

Discussions

Response To Root Temperature

Figures 5-2 and 5-3 show that both morning and evening rates of photosynthesis increased as root temperatures increased and reached optimum temperature at $21 \pm 0.4^\circ\text{C}$ for all soil water potential treatments. Both rates decreased with further increase of root temperature. Cooper (1973) reported that low root temperature (12°C) reduced CO_2

assimilation of beans and corn, whereas high root temperature, 28°C had similar effects on peas. The studies of Duke et al (1979) with soybeans have shown that higher rates of photosynthesis of soybean leaves grown at the root temperature of 20°C compared to those grown at the root temperature of 13°C were related to lower stomatal resistance and higher concentration of ribulose-1,5-biphosphate carboxylase. Under root temperature stress, the source-sink balance may play a controlling factor in the photosynthetic process. The source-sink balance refers to the phenomenon that the rate of photosynthesis of mature leaves (source) increases with the increase in the utilization rate of photosynthetic products, which are used by the rest of plant (sink) (Neales and Incoll, 1968). The sink demand in plant parts and the translocation to those parts increase with an increase of root temperature. The ability of the root system to supply water and nutrient requirements of the plant increases as root temperature increases. This results in an increase in the rate of photosynthesis. There is, however, a biological optimum root temperature for plant growth processes (Cooper, 1973). All biological processes are directly or indirectly disturbed if the root temperature exceeds this optimum value. Under high root temperature stress, stomatal resistance may also play a role in determining the rate of photosynthetic processes. High root temperature causes the leaf water potential to decrease during the full light period (Chapter 3) with a concurrent stomatal resistance increase. The increase of stomatal resistance resulted in a decrease in the rate of photosynthesis, especially the evening rate of photosynthesis.

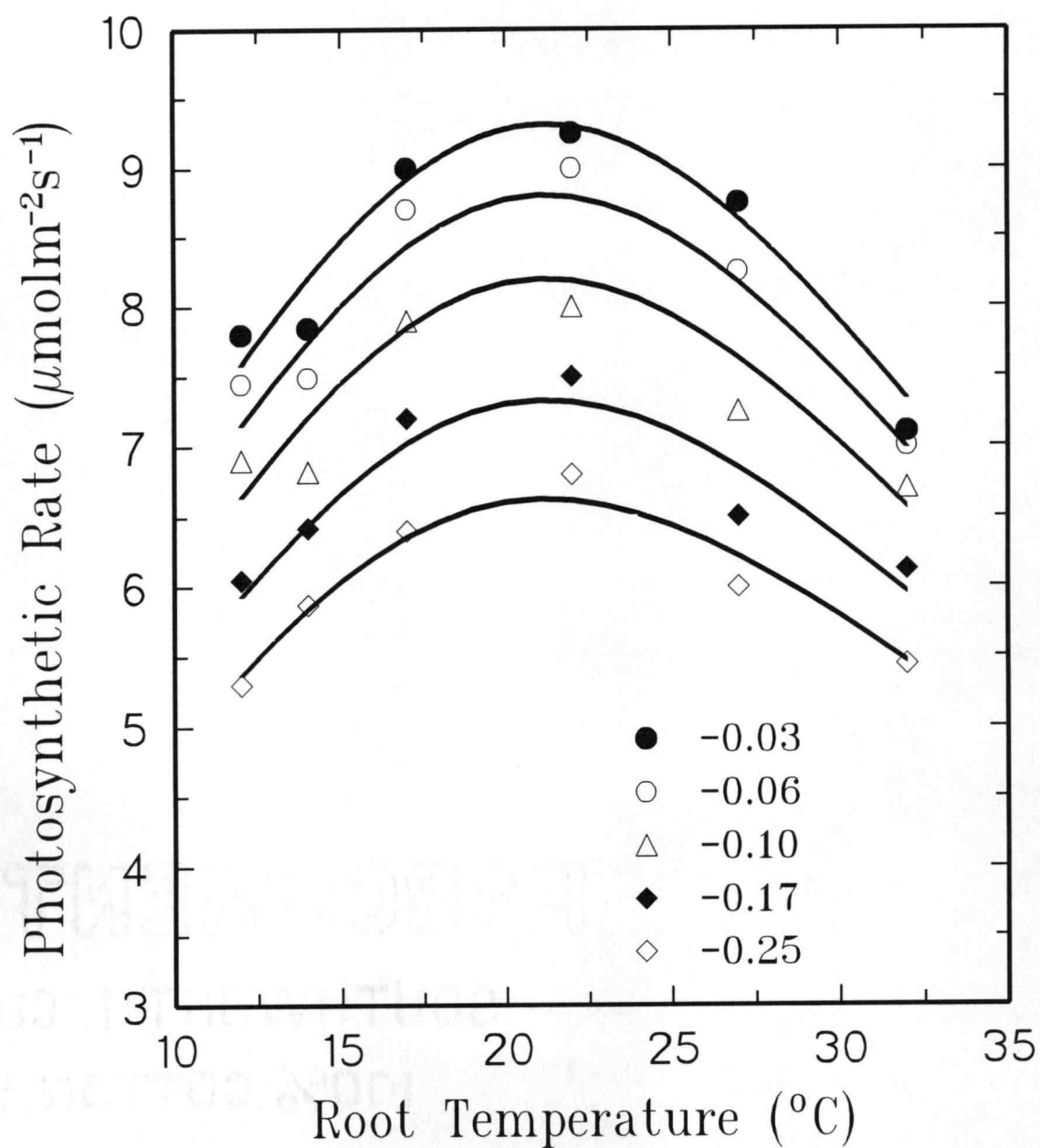


Figure 5-2. Morning rate of net photosynthesis plotted as a function of root temperature. The symbols represent experimental data and the solid lines represent the modified Johnson and Thornley equation.

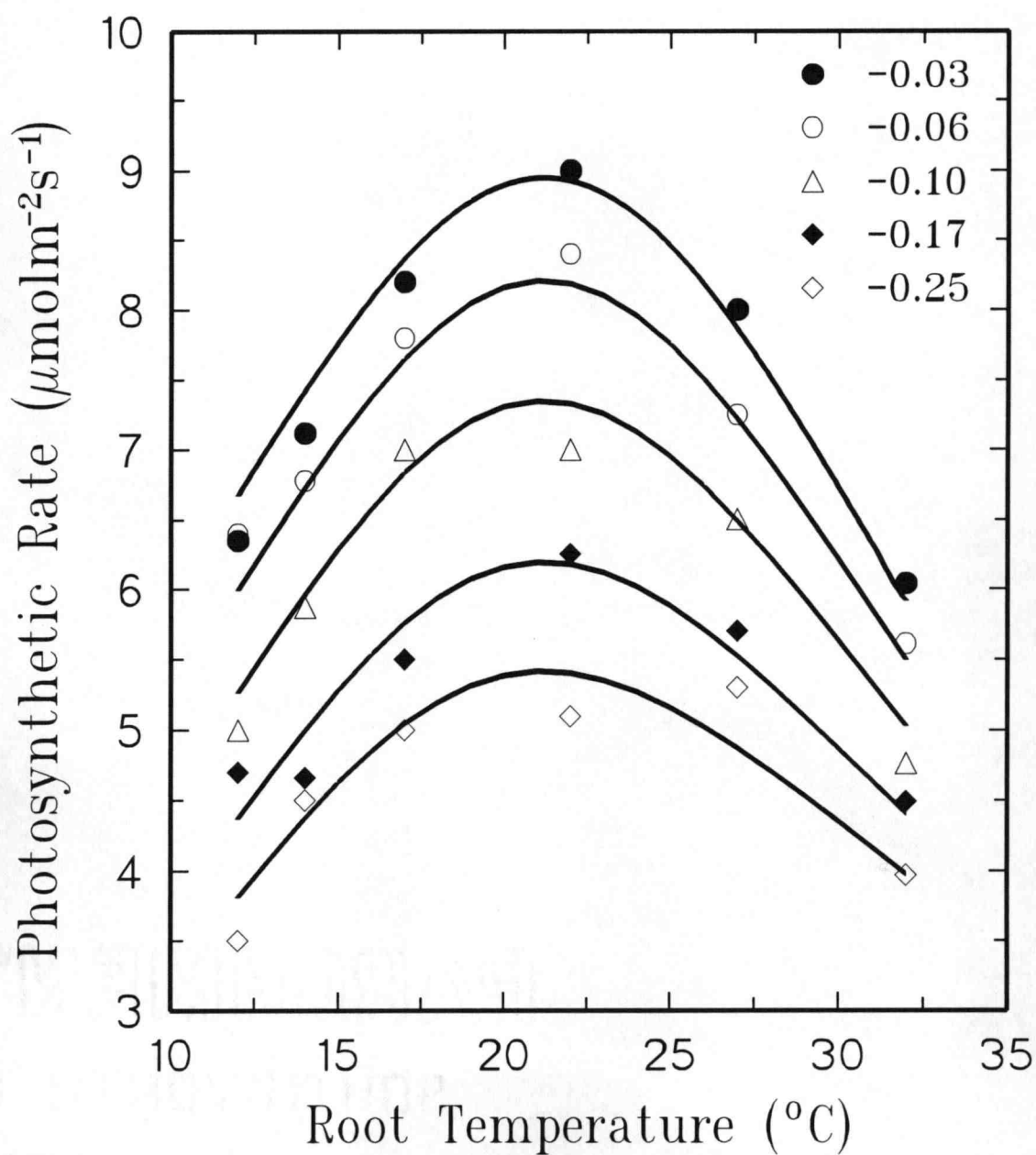


Figure 5-3. Evening rate of net photosynthesis plotted as a function of root temperature. The symbols represent from experimental data and the solid lines represent the modified Johnson and Thornley equation.

The morning rate of photosynthesis decreased 18.5% as the root temperature decreased from 21°C to 12°C at the soil water potential of -0.03 MPa. The evening rate decreased 25% under the same conditions (Figure 5-4). A decrease of 58% for the rate of photosynthesis of soybeans as root temperature decreased from 20°C to 13°C was reported by Duke et al. (1979).

When the root temperature increased from 21°C to 30°C, the morning rate of photosynthesis rate decreased 19%, about the same percentage as resulted from cooling the roots at the same soil water potential treatment. The evening rate decreased 33% at the same conditions, i.e., increasing the root temperature from 21 °C to 30 °C at the soil water potential of -0.03 MPa. This indicates that the evening rate is more sensitive to root temperature stress than the morning rate. The conditions were slowly changed during the day. During the light period, the stress in the plant develops progressively. Plants recovered more or less from stress during the dark period. Plants were stressed the least in the early morning and stressed the most in the evening. Larger K_0 values of the morning rates confirmed this occurrence. The larger value for the parameter, D , (Table 5-4), which is related to the enthalpy of photosynthetic processes, indicated that the evening rate of photosynthesis decreased more than the morning rates at higher root temperature stress.

Results that the morning and evening rates declined more under high root temperature stress than under low root temperature stress agreed with the fact that spring wheat seedlings are adapted to low root temperatures. The seedlings are more tolerant of low root temperatures than of high root temperatures.

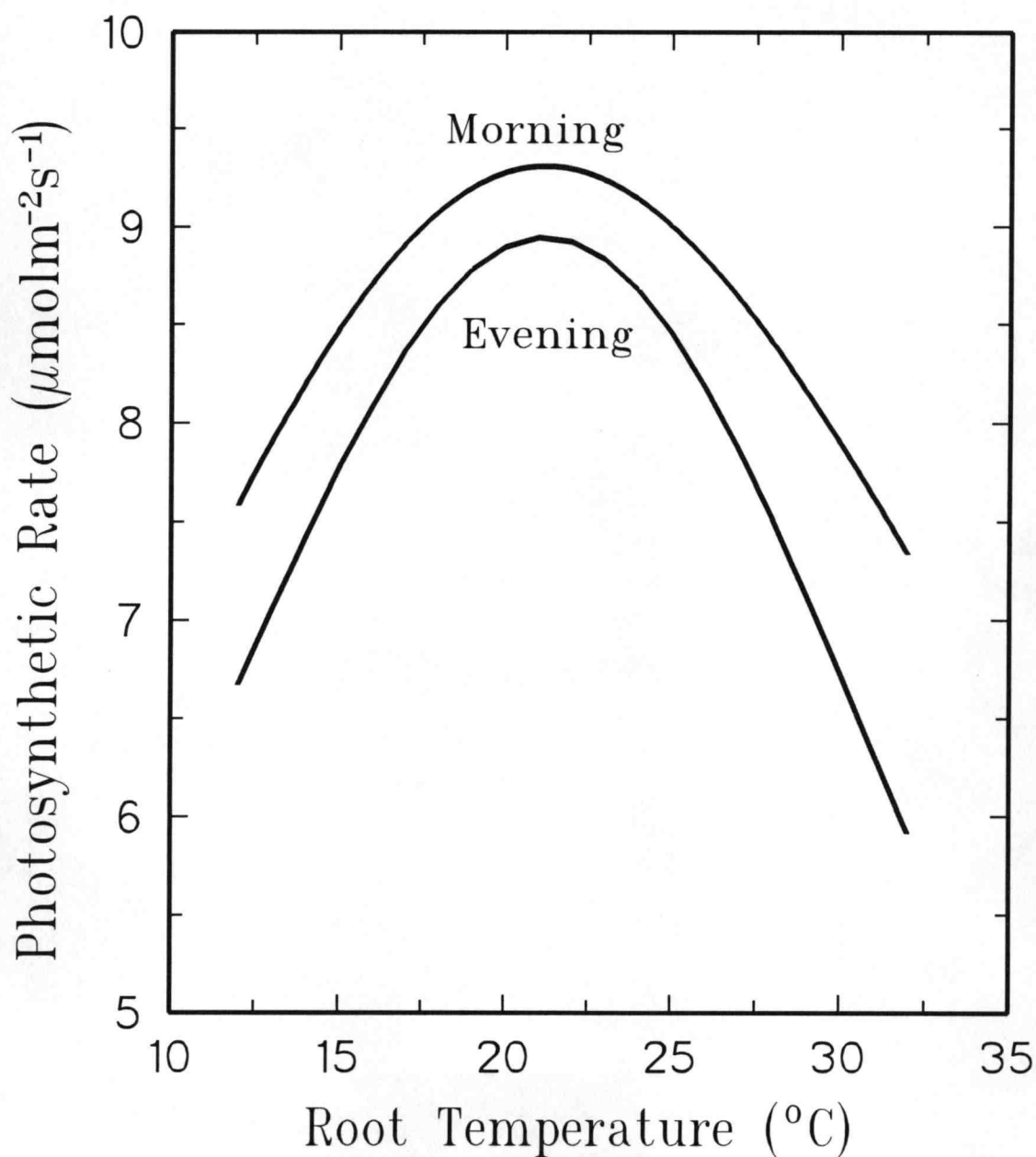


Figure 5-4. The morning and evening rates of photosynthesis of the -0.03 MPa treatment plotted as a function of root temperature. The data are from the modified Johnson and Thornley equation.

Response To Soil Water Stress

The morning and evening rates of photosynthesis decreased with decreasing soil water potential at all root temperatures (Figures 5-2 and 5-3). The morning rates of photosynthesis of the -0.25 MPa soil water potential treatment were 75% of the values of the -0.03 MPa soil water potential at 21°C. At the same temperature, the evening rate at -0.25 MPa was 59% of the rate at -0.03 MPa. A similar, but smaller decrease was reported by Babalola et al. (1968) for Monterey pine seedlings under similar water stress conditions.

The reduction in photosynthetic rate caused by water stress is attributable to stomatal closure, decrease of chloroplast activity, and decrease of transportation rate. According to diffusion theory, an increase in stomatal resistance due to leaf water potential decreases the rate of photosynthesis. However, the mechanisms of non-stomatal factors remain unclear. Water stress-induced inhibition of the dark reactions of photosynthesis has been reported in earlier research. Reduction of the activity of chloroplast enzymes has been observed during water stress (Jones, 1973a; O'Toole et al., 1976). The reduction in the rates of net photosynthesis (65%, the value at -0.25 MPa over at -0.03 MPa) due to water stress measured in this study revealed a correlation with the reduction in the activity of ribulose 1,5-biphosphate carboxylase (76%) of bean under the similar water stress condition by O'Toole et al.(1976).

There are also several reports of water stress-induced inhibition of the light reactions of photosynthesis. Chloroplast isolated from moderately stressed leaves displayed a reduced oxygen evolution capacity (Boyer and Bowen, 1970). Loss of

chloroplast capacity for photoreduction was observed in severely desiccated chloroplast (Boyer, 1976a,b). However, Keck and Boyer (1974) reported that the activity of photosystem in chloroplast from moderately stressed leaves remained the same until leaf water potentials were lower than 1.0 MPa. Their results do not correlate with the results of this study. Measurements of leaf water potential revealed that the lowest leaf water potential measured was -1.05 MPa under the most stressed condition (-0.25 soil water potential and 32°C root temperature, Chapter 3). But the rates of net photosynthesis decreased with the water stress increase.

The photosynthetic process is carried out by a series of enzyme systems. It is difficult to describe the response of the photosynthetic process to root temperature and water stress by the activity of a specific enzyme and to distinguish between the stomatal and non-stomatal factors which affecting the photosynthetic process. The parameter activation energy in the modified Johnson and Thornley equation reflects the total effects of these two factors at the whole plant level.

The activation energy, B , of spring wheat seedlings is a quadratic function of water stress. The activation energy increased by increasing water stress from -0.03 MPa to -0.25 MPa for both morning and evening rates (figure 5-5). These results suggest that as the plants were increasingly water stressed, the activation energy of the photosynthetic processes increased and the rate of photosynthesis decreased. The values of B_0 , which represent the activation energy of the photosynthetic process under conditions without water stress, were the same for morning and evening rates. This occurred because the same enzyme system is involved in this process. The increase of B for the evening rates

was faster than for morning rates. These responses of two rates of photosynthesis to water stress illustrated that the evening rate of photosynthesis was more sensitive to water stress than the morning rates.

To summary of the responses of morning and evening rates photosynthesis to root temperature and soil water stress, the morning rates were plotted as a function of the evening rates in figure 5-6. Plants with a high morning rate have a high evening rate. At the least stressed condition, the evening rate approaches the morning rate. In other words, there was only a small difference between the morning and evening rates for unstressed plants. As the morning rate decreased with stress, the difference between morning and evening rates increased on an absolute basis and the ratio of the morning rate divided by evening rate increased from 1.06 to 1.3 indicating that the evening rates were more suppressed by stress than the morning rates.

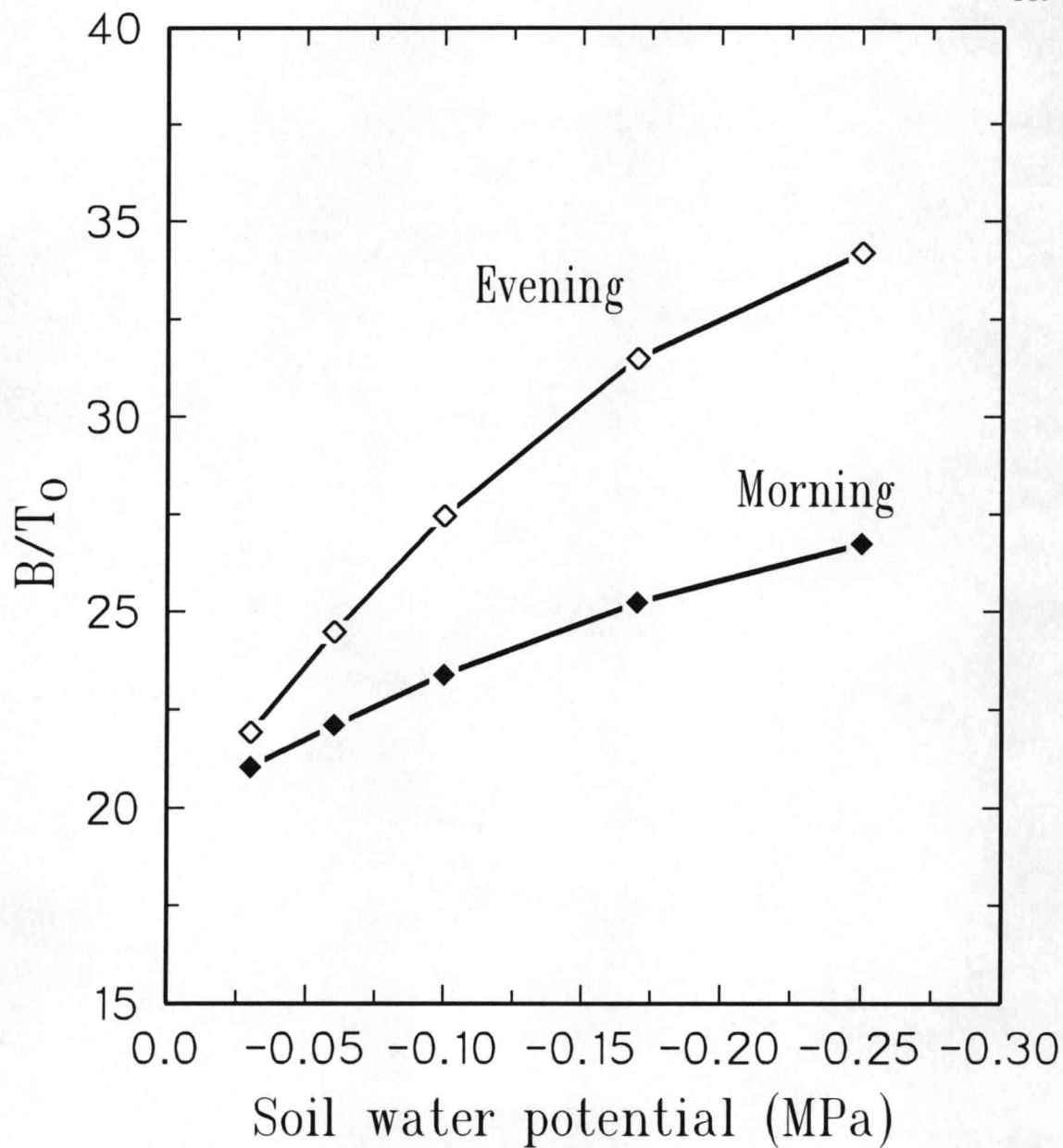


Figure 5-5. The activation energy of morning and evening photosynthetic rates as a function of soil water potential.

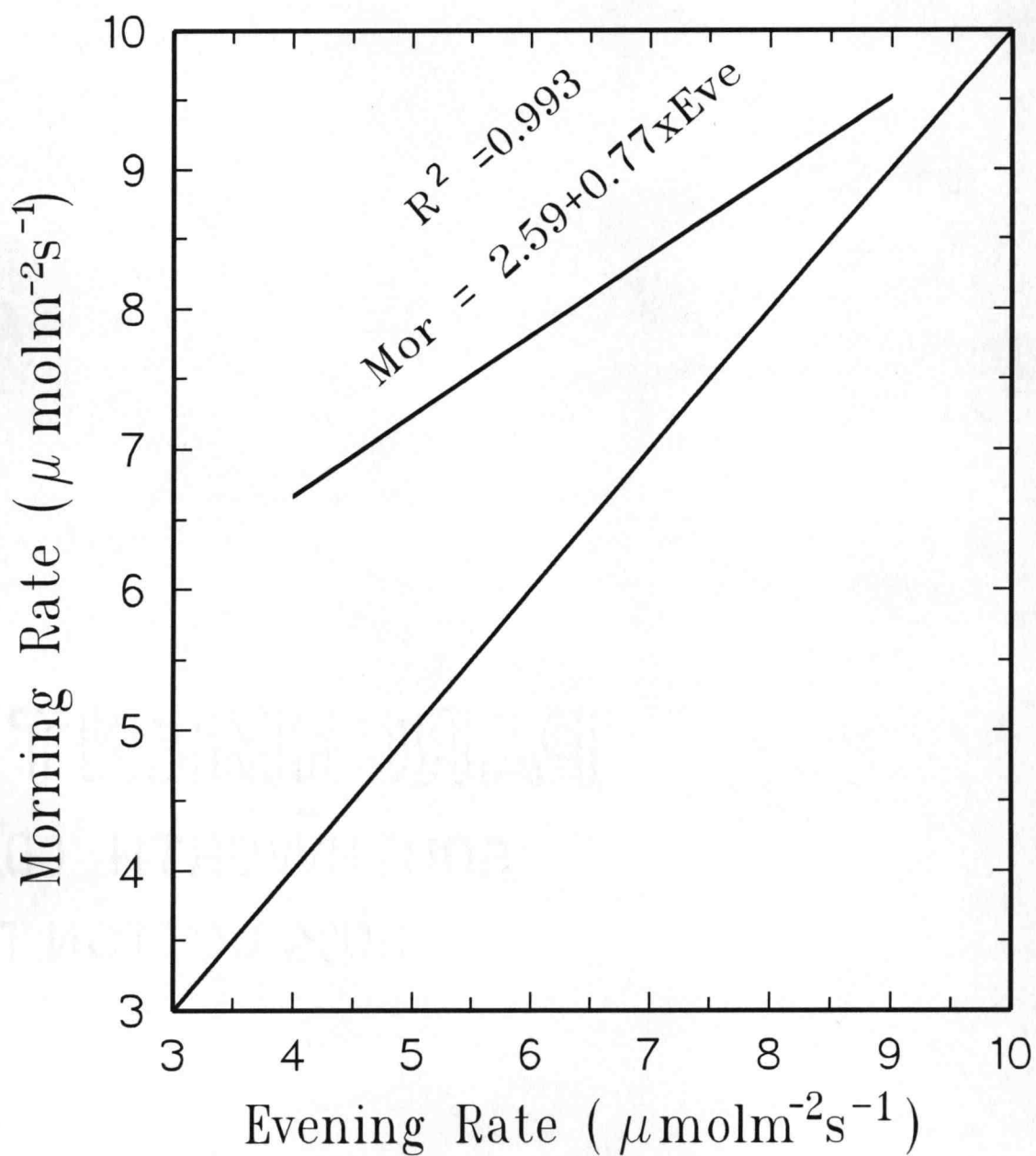


Figure 5-6. The morning rate of photosynthesis plotted as a function of the evening rate.

Comparison of the Responses of Photosynthesis and Transpiration to Stresses

The rate of transpiration is described by

$$T_r = \frac{\rho_{v,i} - \rho_{v,a}}{r_{s,v}} \quad [5-18]$$

where T_r is the rate of transpiration, $\rho_{v,a}$ is water vapor density in the air, $\rho_{v,i}$ is water vapor density in the stomata cavity, and $r_{s,v}$ is the resistance for water vapor diffusion, including both stomata resistance and the boundary layer resistance. The $\rho_{v,a}$ is constant in all experiments, since both room temperature (22°C) and relative humidity (50%) were kept constant. The $\rho_{v,i}$ is a function of leaf temperature. The combined stomata and boundary layer resistance for water vapor, $r_{s,v}$ is thus calculated by

$$r_{s,v} = \frac{\rho_{v,i} - \rho_{v,a}}{T_r} \quad [5-19]$$

Movement of CO_2 from the atmosphere to intercellular space of the leaves is similarly described by

$$P_n = \frac{\rho_{c,a} - \rho_{c,i}}{r_{s,c}} \quad [5-20]$$

where P_n is the rate of net photosynthesis, $\rho_{c,a}$ is CO_2 concentration in the air, $\rho_{c,i}$ is CO_2 concentration at intercellular, $r_{s,c}$ is the combined stomata and boundary layer resistance to CO_2 .

The stomata resistance to CO_2 , $r_{s,c}$ is related to the stomata resistance to water vapor by

$$r_{s,c} = \alpha r_{s,v} = \frac{\alpha(\rho_{v,i} - \rho_{v,a})}{T_r} \quad [5-21]$$

where $\alpha=1.6$ (Harley et. al. 1992; Nobel, 1991; Campbell 1977) is a constant. Substituting equation [5-20] into [5-21] results in

$$\frac{\rho_{c,i}}{P_n} = \frac{\rho_{c,a}}{P_n} - \frac{\alpha(\rho_{i,v} - \rho_{a,v})}{T_r} \quad [5-22]$$

The $P_n/\rho_{c,i}$ is defined as the carboxylation efficiency by Kanechi et al. (1996). It relates to the activity of photosynthesis system. Kanechi et al.(1996) observed that the carboxylation efficiency decreases with increasing water stress. They also suggested that the inhibition of photosynthesis in water-stressed coffee leaves was mainly caused by non-stomatal limitation, which can be expressed by carboxylation efficiency.

If we let $m = P_n/\rho_{c,i}$,

$$\frac{1}{m} = \frac{\rho_{c,a}}{P_n} - \frac{\alpha(\rho_{i,v} - \rho_{a,v})}{T_r} \quad [5-23]$$

The $1/m$ can be calculated using the rates of transpiration and photosynthesis, leaf temperature at a given room temperature, relative humidity, and CO_2 concentration in the air. The m for both the morning and the evening are plotted as a function of P_n in figure 5-7. The rate of photosynthesis increased nearly linearly with increasing carboxylation efficiency. There is no significant difference between morning and evening. Daily average net photosynthesis rate of sudangrass, obtained in a earlier study in the same laboratory, follows the same trend (Figure 5-7). Thus, the change of the rate of photosynthesis in response to root temperature and soil water potential results from changes in both stomata

conductance and carboxylation efficiency. However, the transpiration process is a physical process. It is mainly controlled by the stoma conductance (equation [5-18]) if leaf temperature remains constant.

The rate of transpiration was more sensitive to water stress than the rate of photosynthesis, especially in the morning. Both stoma conductance and carboxylation efficiency decreased with increasing water stress (Figure 5-8). In the morning, the stoma conductance decreased from 100% to 50% as the soil water potential decreased from -0.03 MPa to -0.25 MPa, while the carboxylation efficiency decreased from 100% to 82% under the same condition. As a consequence, the rate of transpiration decreased with increasing soil water stress more than rate of photosynthesis did. However, in the evening, the stomata conductance decreased from 100% to 44% while the carboxylation efficiency declined from 100% to 61% as the soil water potential decreased from -0.03 MPa to -0.25 MPa. The reduction difference was 17% compared with 32% in the morning. As a result, the reduction difference between photosynthesis rate and transpiration rate was also small in the evening.

The photosynthesis rate increased with increasing root temperature, reached a maximum rate at 22°C root temperature, and then decreased with further increasing root temperature. However, the rate of transpiration remained relatively constant or has a small change between 17 to 27°C root temperature. The response of stomata conductance to the root temperature stress was similar to that photosynthesis rate (chapters 4). The leaf temperature increased with increasing root temperature. The increase of leaf temperature

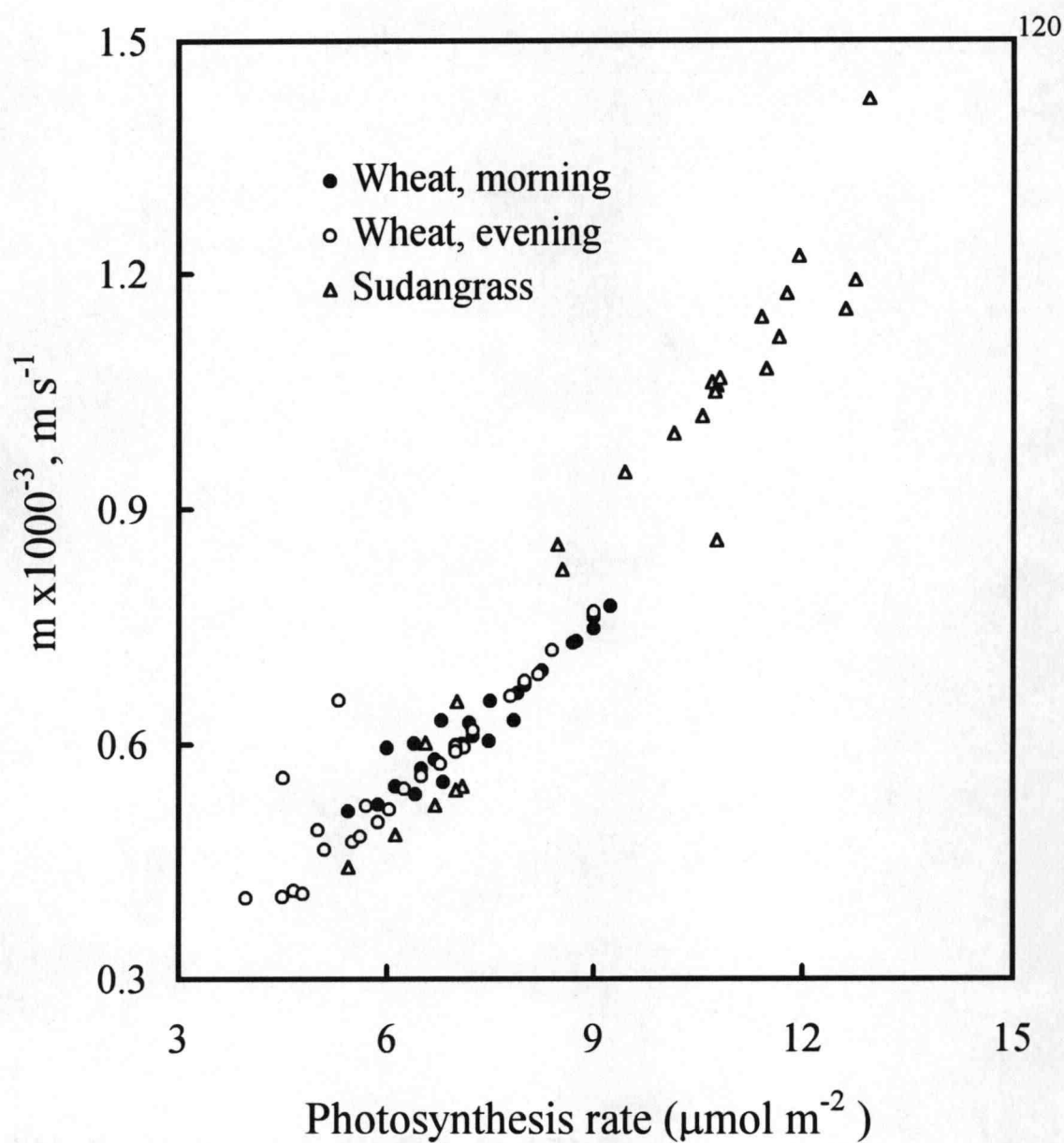


Figure 5-7. The carboxylation efficiency a function of the rate of photosynthesis. The data includes the five soil water potential and five root temperature treatments.

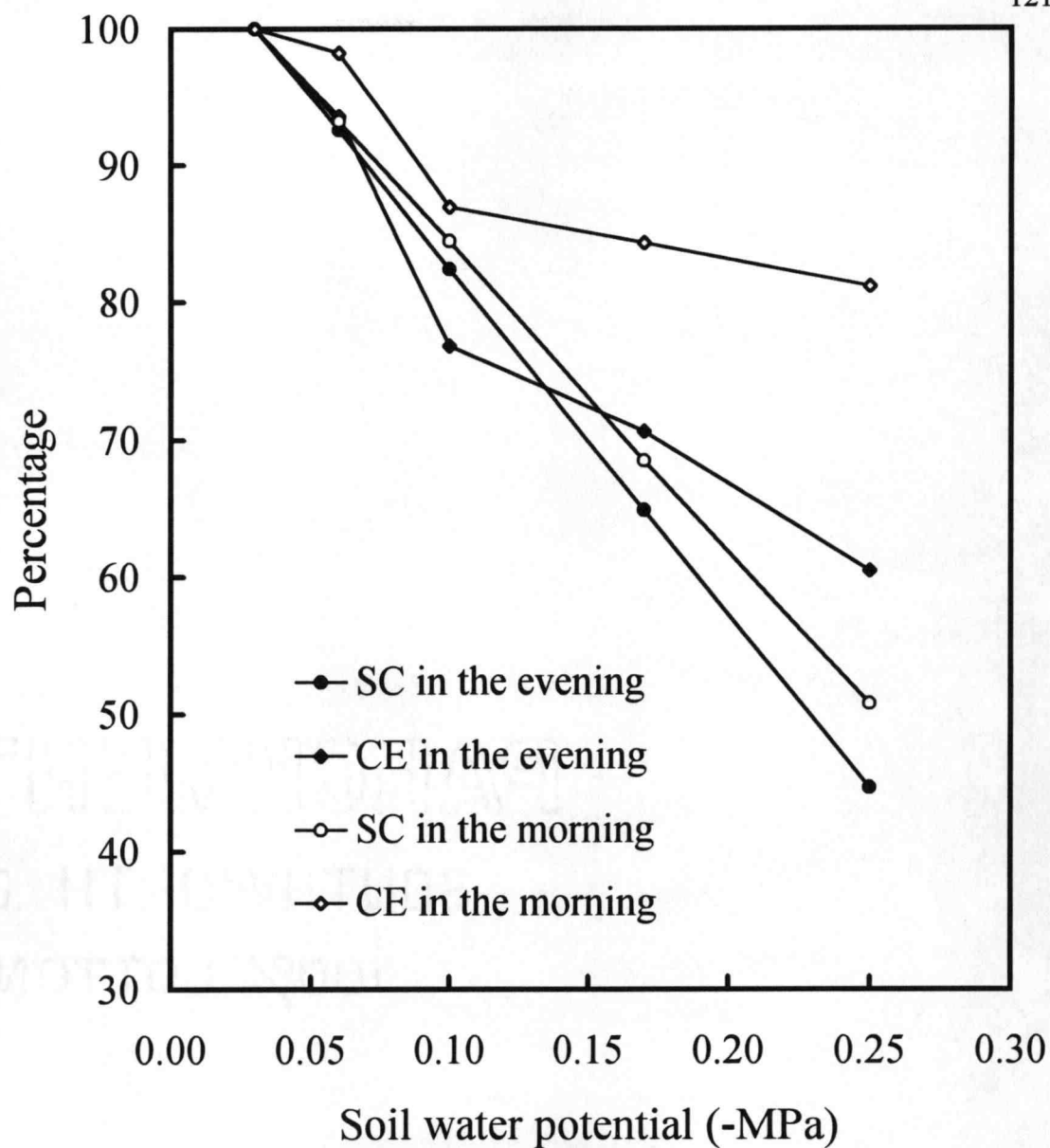


Figure 5-8. Comparison of reduction in stomata conductance and carboxylation efficiency in response to soil water stress at the root temperature of 22°C. SC=stomata conductance; CE=carboxylation efficiency.

results in an increase in the rate of transpiration. The balance between reduced stomata conductance and increased leaf temperature with increasing root temperature would result in a relatively constant rate of transpiration in response to the change of root temperature. There may be other causes to these different behaviors need to be identified.

Summary

The modified Johnson and Thornley equation describes the response of net photosynthesis rates to the root temperature and soil water stress. It provided a tool for studying the combined effects of temperature and water stresses on photosynthetic process in terms of physiologically meaningful parameters based on well founded theoretical considerations.

The water stress inhibited the rate of photosynthesis by increasing the activation energy of photosynthetic processes. The evening rate of photosynthesis is more sensitive to root temperature and soil water stress than the morning rate of photosynthesis. This suggests that the conditions describing energy relations changed during the day. This change is reflected by an increase in activation energy. The optimum temperature for photosynthesis of spring wheat seedlings is 21 ± 0.4 °C. The parameters D and K_0 were constants.

The change of the photosynthesis rate in response to root temperature and soil water stresses resulted from changes in both stomata conductance and carboxylation efficiency. However, the transpiration process is a physical process, which mainly

controlled by the stomata conductance. This resulted in the different behaviors in response to root temperature and water stresses.

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6. PLANT GROWTH

Introduction

The rate of plant growth usually increases with root temperature to an optimum, followed by a decrease in rate of growth with further increasing root temperature (Cooper, 1973). Although this general trend of plant growth response to root temperature has been long recognized, at least qualitatively, a general procedure which can be used to characterize such a response with physically meaningful parameters has been lacking. Typically the analysis of experimental observations consists of a plot of observed rates vs. temperature and regression of observations against some empirical relationships (Washitani and Saeki, 1986; Woledge and Parsons, 1986; Douglas, 1987). These procedures often encounter difficulties in quantitative extrapolation of observations from one study to another, as well as difficulties in comparing the temperature response of one plant process to another

The ratio of root/shoot mass provides information about the interrelation of the root and shoot, although it provides no information about the actual magnitudes involved (Cooper, 1973). Cooper (1973) reviewed the effect of root temperature on partitioning between root and shoot for several plant species and concluded that the most common response is that a high root/shoot ratio occurs at both low and high root temperatures, whereas at intermediate root temperatures, a greater proportion of the total dry mass is found in the shoot.

Soil water stress also affects plant growth processes and often interacts with root temperature (Barlow, Boersma, and Young, 1977). Little quantitative research has been reported where both soil water potential and root temperature are involved (Barlow et al., 1977). In this case the usual statistical analysis of variance yields limited information about the nature of these responses. A more theoretically based approach which could accurately quantify the response of the growth rate of a plant to root temperature and soil water potential is preferred.

Johnson and Thornley (1985) considered theoretical aspects of temperature effects on the rate of plant processes. They derived an equation which describes the temperature response of plant processes by combining the Arrhenius equation for chemical reactions and the Boltzman distribution of enzymes between the active and inactive states. In Chapter 5, the Johnson and Thornley equation was modified. The modified equation was used to describe the responses of photosynthesis processes of plants to both soil water and root temperature stresses. The modified equation is,

$$K = \frac{K_0 e^{-B/(1/T_0 - 1/T)}}{1 + (B/(D-B)) e^{D(1/T_0 - 1/T)}}, \quad [6-1]$$

where K is the rate of a plant process; B is the activation energy divided by the universal gas constant with unit $^{\circ}\text{K}$; D is the enthalpy difference between active and inactive states of the enzyme divided by the universal gas constant with unit $^{\circ}\text{K}$; T_0 is the optimum temperature with unit $^{\circ}\text{K}$, and K_0 is a constant representing the process rate for conditions where the quantity multiplying K_0 is equal to one. The units of K and K_0 are determined

by the process being described. The parameters, B , D , T_o , and K_o , may be functions of water potential. This equation provides a tool for studying the combined effects of temperature and water stresses based on well-founded theoretical considerations.

This chapter was initiated to investigate the manner in which root temperature and soil water potential affect the plant growth processes and to explore the applicability of equation [6-1] to provide an explanation for observed responses of plant growth to soil water stress and root temperature, in terms of the mechanistically meaningful parameters.

Results

Leaf area and dry masses of shoots and roots were measured on days 0, 2, 3, 4, 5, and 6 or 7 after the plants were exposed to the experimental treatments. The results are shown in tables A1 through A3 in Appendix.

Relative Growth Rates of Leaf Area and Shoot Dry Mass

Relative growth rates of leaf area and shoot dry mass were calculated according to

$$Y = Y_0 e^{bt}, \quad [6-2]$$

where Y is leaf area, cm^2/slab , or shoot dry mass, g/slab ; t is time day; Y_0 is the initial value of Y ; and b is referred to as the relative growth rate, day^{-1} . The least square regressions of the natural logarithm of leaf area and shoot dry mass measured against to time were conducted for each treatment using the data from tables A1 and A2 in Appendix I. The slopes of these regressions were taken as the relative growth rates of leaf area and shoot dry mass. Results are shown in tables 6-1a and 6-2a. Two-way analyses of variance

were conducted on these data, illustrated in tables 6-1b and 6-2b, respectively. Results reveals that the relative growth rates of leaf area and shoot dry mass depend on both root temperature and soil water potential at the significant level.

Procedures similar to those used for analyzing the response of the rate of net photosynthesis to root temperature and soil water potential was used to analyze the responses of relative growth rates of leaf area and shoot dry mass to root temperature and soil water potential. Equation [6-1] was fitted to the experimental data for both relative growth rates of leaf area and shoot dry mass (Tables 6-1a and 6-2a) using a least square technique. The numerical procedure described in Chapter 5 was followed. It was discovered that only parameter B was a function of soil water potential. The function was

$$B(\psi) = B_0 + b\psi, \quad [6-3]$$

where B_0 and b are constants.

The results of the least square fitting are shown in table 6-3. The standard errors of estimated parameters for leaf area and shoot dry mass were small except for B_0 . For parameter B_0 , the standard errors are more than half of its value or larger. This indicates that there is no significant difference between the B_0 value and zero for both leaf area and shoot dry mass. R^2 values were 0.91 and 0.82 for leaf area and shoot dry mass, respectively.

The relative growth rates of leaf area and shoot dry mass from both the experimental data and fitted results are plotted as functions of root temperature for each soil water potential treatment in figures 6-1 and 6-2, respectively.

Table 6-1a. Relative growth rate of leaf area at the indicated combinations of root temperature and soil water potential.

Soil water potential	Root temperature °C							avg
	12	14	17	22	27	29	32	
---MPa---	-----day ⁻¹ -----							
-0.03	0.101	0.108	0.119	0.126	0.138	0.111	0.095	0.114
-0.06	0.086	0.107	0.104	0.117	0.132	0.106	0.083	0.105
-0.10	0.080	0.103	0.110	0.110	0.131	0.096	0.067	0.100
-0.17	0.062	0.079	0.086	0.096	0.100	0.086	0.064	0.082
-0.25	0.039	0.058	0.075	0.089	0.092	0.064	0.051	0.067
avg	0.074	0.091	0.099	0.108	0.119	0.093	0.072	0.093

Table 6-1b. ANOVA of data shown in table 6-1a.

Source of variation	SS	d.f	MSS	F
Soil temperature	0.00738	6	0.00123	49.607**
Soil water potential	0.00861	4	0.00215	86.786**
Error	0.00060	24	0.00002	
Total	0.01658	34	0.00049	

Table 6-2a. Relative growth rate of shoot dry mass at the indicated combinations of root temperature and soil water potential.

Soil water potential	Root temperature °C							avg
	12	14	17	22	27	29	32	
---MPa---	-----day ⁻¹ -----							
-0.03	0.098	0.125	0.113	0.135	0.139	0.108	0.085	0.115
-0.06	0.081	0.112	0.110	0.116	0.132	0.084	0.062	0.100
-0.10	0.083	0.094	0.092	0.110	0.127	0.072	0.044	0.089
-0.17	0.079	0.089	0.087	0.094	0.111	0.059	0.046	0.081
-0.25	0.048	0.073	0.070	0.083	0.078	0.045	0.036	0.062
avg	0.078	0.099	0.094	0.108	0.117	0.074	0.055	0.089

Table 6-2b. ANOVA of data shown in table 6-2a

Source of variation	SS	d.f	MSS	F
Soil temperature	0.01208	6	0.00201	56.620**
Soil water potential	0.00947	4	0.00237	66.554**
Error	0.00085	24	0.00004	
Total	0.02241	34	0.00066	

Table 6-3. Values of the parameters of equation [6-1] and [6-3] for relative growth rates of leaf area and shoot dry mass.

Parameter	Leaf area		Shoot dry mass	
	value	ese	value	ese
k_0 (day ⁻¹)	0.143	0.009	0.128	0.008
$b_0 \times 10^{-3}$ (°K)	1.29	0.66	0.10	0.58
$b_1 \times 10^{-3}$ (°KMPa ⁻¹)	-27.18	2.38	-28.09	4.48
$D \times 10^{-4}$ (°K)	2.48	0.32	3.43	0.76
T_o (°C)	23.8	0.4	23.4	0.8
R^2	0.91		0.82	

Ratio Between Root and Shoot Dry Masses

In order to calculate the ratio between root and shoot mass, the measured dry masses of shoots and roots at days 3, 4, and 5 were averaged for each treatment using the data from tables A2 and A3 in Appendix I. Results are shown in tables 6-4a. Two-way analyses of variance were conducted on the data in table 6-4a and reported in Table 6-4b. Result shows that the ratio between root and shoot dry masses depended on both root temperature and soil water potential at a 0.01 significant level.

Table 6-4a. Ratio between root and shoot dry mass at the indicated combinations of root temperature and soil water potential.

Soil water potential	Root temperature °C							avg
	12	14	17	22	27	29	32	
---MPa---	-----day ⁻¹ -----							
-0.03	0.38	0.50	0.56	0.51	0.40	0.38	0.40	0.44
-0.06	0.36	0.48	0.52	0.53	0.41	0.40	0.43	0.45
-0.10	0.39	0.52	0.59	0.54	0.42	0.41	0.43	0.47
-0.17	0.46	0.57	0.63	0.56	0.47	0.43	0.43	0.51
-0.25	0.48	0.63	0.70	0.62	0.52	0.47	0.44	0.56
avg	0.41	0.54	0.60	0.55	0.45	0.42	0.43	0.49

Table 6-4b. ANOVA of data shown in table 6-4a.

Source of variation	SS	d.f	MSS	F
Soil temperature	0.17027	6	0.02838	35.184**
Soil water potential	0.06033	4	0.01508	18.702**
Error	0.01936	24	0.00081	
Total	0.24997	34	0.00735	

Discussion

Relative Growth Rates of Leaf Area and Shoot Dry Mass Responses to Root Temperature

Figures 6-1 and demonstrate that relative growth rates of leaf area and shoot dry mass increased with increasing root temperature and reached the optimum temperature at $23.4 \pm 0.8^{\circ}\text{C}$ for all soil water potential treatments. As root temperature further increased, relative growth rates of leaf area and shoot dry mass decreased. The response of the plant growth to root temperature was similar to that of the rate of net photosynthesis (Chapter 5). This occurred because the growth of each plant part is a function of available carbohydrate supply to that part. The carbohydrate production rate is equal to the rate of net photosynthesis. In the meantime, the rate of translocation is a controlling factor in plant growth. The available carbohydrates for the growing point of the plant are determined by both rates of photosynthesis and translocation. Therefore, all factors which control the rate of net photosynthesis and translocation rate under stressed conditions affect the growth rates of leaf area and shoot dry mass.

There exists a physiological optimum root temperature for plant growth processes (Cooper, 1973). Physiological processes are directly or indirectly disturbed if the root temperature is higher or lower than this optimum value. This research reveals that the optimum root temperature for both growth rates of leaf area and shoot dry mass was 2°C higher than the optimum temperature for the rate of net photosynthesis. This may occur because photosynthesis is mainly a physiological process carried out by a series of enzyme systems, while growth is a result of cell division and expansion which involve both

physiological processes of cell wall synthesis and wall loosening and physical processes of deformation in the cell walls (Kramer and Boyer, 1995).

The growth rate of leaf area at the 14°C root temperature was 85% of the value at the optimum root temperature of 23°C at the soil water potential of -0.03 MPa. For the same soil water potential treatment, the growth rate at 32°C was 70% of the value at the 23°C root temperature. The growth rate decreased more under high root temperature stress than under low root temperature stress. This agreed with the fact that spring wheat is adapted to low root temperatures. Similar responses in the growth rate of shoot dry mass were observed. The decrease in growth rate with increasing root temperature stress, due to either lower or higher root temperature, increased with increasing soil water stress. The growth rate of leaf area of the -0.25 MPa treatment at 32°C was 50% of the value at 23°C, while the growth rate at 14°C was 57% of the value at 23°C temperature for the same soil water potential treatment.

Relative Growth Rates of Leaf Area and Shoot Dry Mass Responses to Soil Water Potential

The growth rates of leaf area and shoot dry mass decreased with decreasing soil water potential at all root temperatures (figures 6-1 and 6-2). The growth rate of leaf area at the -0.25 MPa was 73% of the value of the -0.03 MPa soil water potential treatment at 23°C. The growth rate of shoot dry mass of the -0.25 MPa was 80% of that of the -0.03 MPa at the same root temperature.

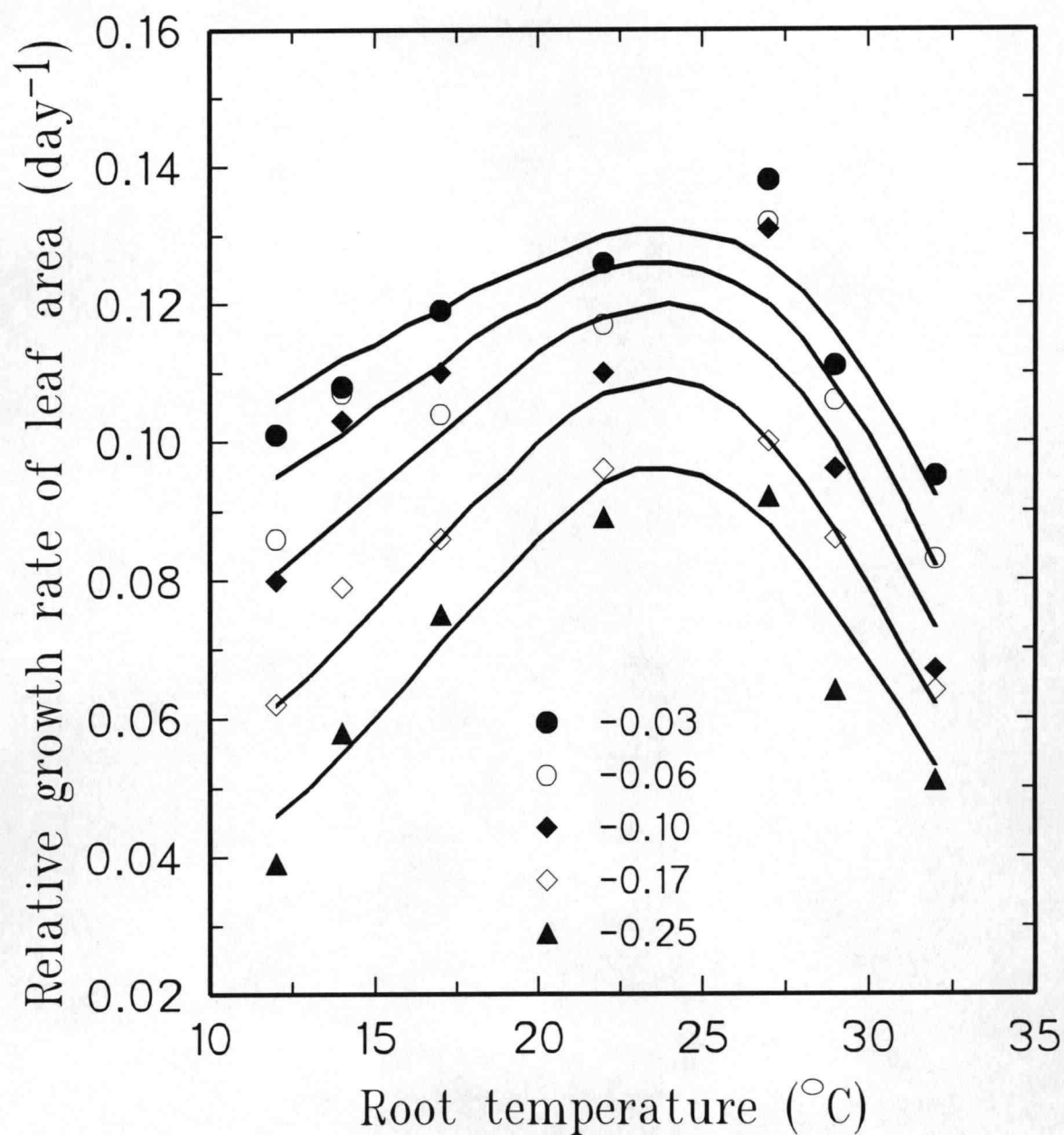


Figure 6-1. The relative growth rate of leaf area plotted as a function of root temperature for all soil water potentials. Symbols represent experimental data. Solid lines were calculated using equations [6-1] and [6-3] with the parameters shown in table 6-3.

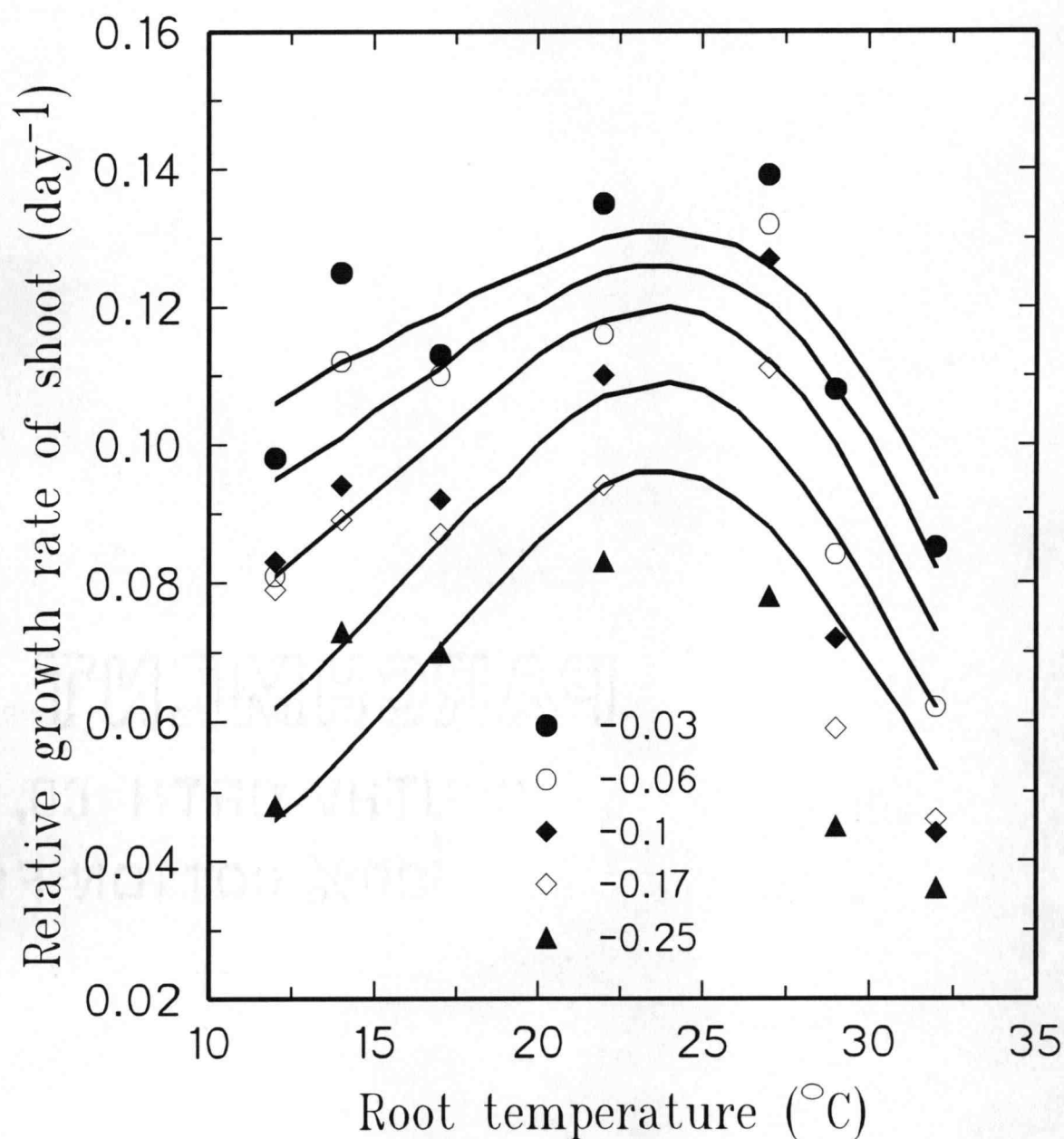


Figure 6-2. The relative growth rate of shoot dry mass plotted as a function of root temperature for all soil water potentials. Symbols represent experimental data. Solid lines were calculated using equations [6-1] and [6-3] with the parameters shown in table 6-3.

Although several physiological mechanisms, including reduced water absorption, nutrient uptake, and photosynthetic rate have been proposed to be responsible for the deleterious effects of soil water stress on the plant growth, a quantitative measure of the effect of soil water potential remains inadequately documented. The activation energy in equation [6-1] reflects the total effects of soil water stress on these physiological factors at the whole plant level.

The activation energies of both growth rates of leaf area and shoot dry mass linearly decreased as water stress increased, as indicated by equation [6-3] (figure 6-3). These results suggest that as the plants were increasingly stressed, the activation energy increased, therefore, the rate of reaction must decrease. Since the Arrhenius equation (equation [5-1] in Chapter 5) was originally derived for a single enzymatic reaction, the absolute value of B may not be mechanistically meaningful considering the complexity of plant processes. However, the rate of change of B with environmental stress may be significant. The sensitivity of a process to water stress can be judged by the rate (b) at which B increases with decreasing soil water potential. As soil water potential decreased from -0.03 MPa to -0.25 MPa, the activation energies for growth rates of leaf area and shoot dry mass increased four to five times, while the activation energies of rates of net photosynthesis increased 27% in the morning and 55% in the evening. This indicates that the growth rates of leaf area and shoot dry mass were more sensitive to water stress than the photosynthetic rate. This result agrees with the general theory that the leaf expansion is more sensitive to water stress than photosynthetic process (Boyer, 1970; Barlow, 1983).

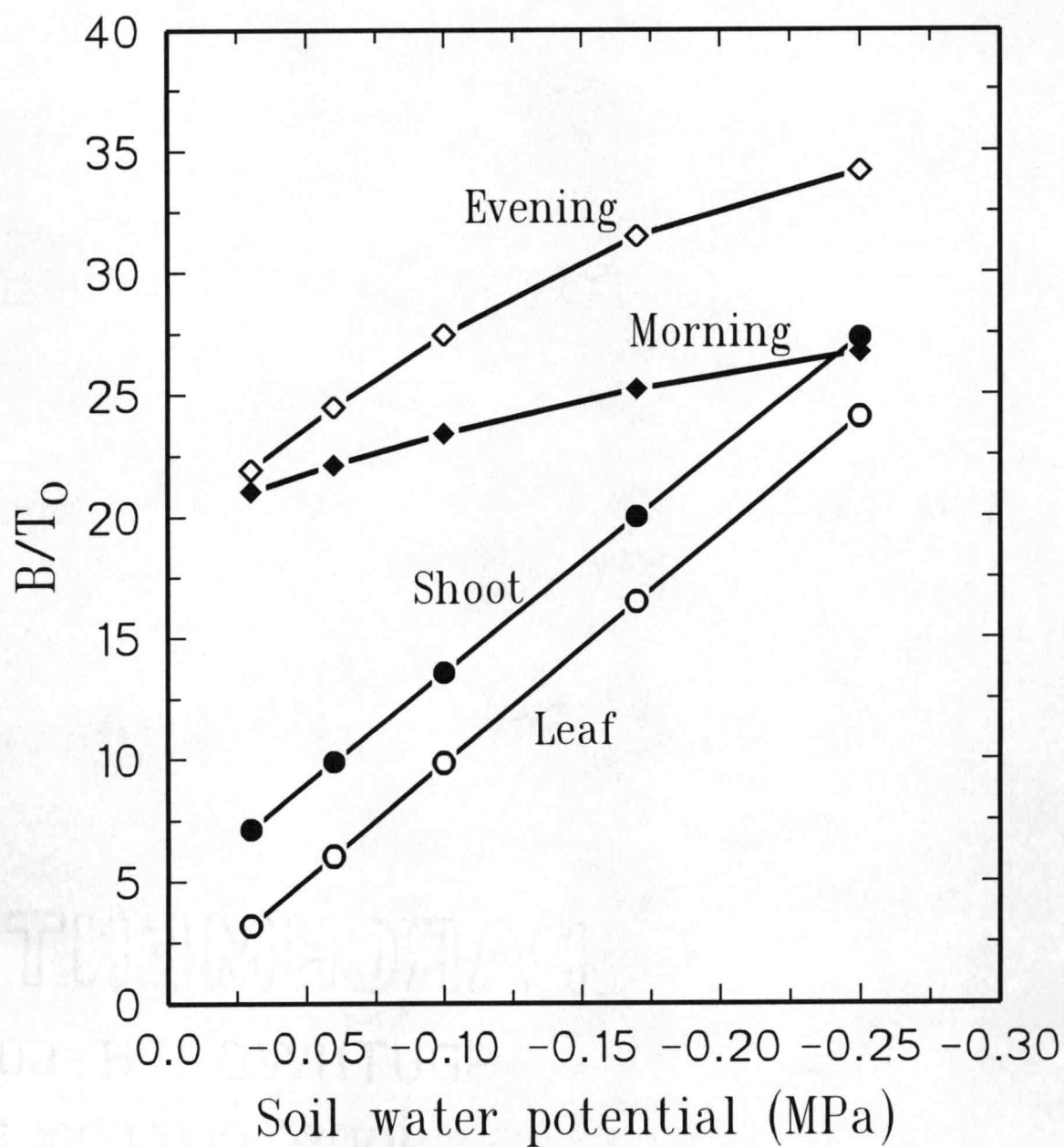


Figure 6-3. Activation energy plotted as a function of soil water potential.

Relationship between Growth Rates of Leaf Area and Shoot Dry Mass

It was noticed that similar rates of growth were observed for leaf area and shoot dry mass (tables 6-1a and 6-2a). Figure 6-4 shows that the growth rate of shoot dry mass increased as a function of the growth rate of leaf area with a 1:1 slope. This occurs because the shoot dry mass was contributed mainly by leaves. This close relationship was suggested by the fact that there was no difference between the values of constant, K_0 , of leaf area and shoot dry mass (table 6-3). Table 6-3 also shows that there was no difference between the b values for leaf area and shoot dry mass, which suggests that the two processes were equally susceptible to water stress in these experiments. T_0 values for the relative growth rate of leaf area and shoot dry mass were 23.8 and 23.4°C, respectively. It is evident by comparing the difference between these two values and their standard errors that there was no difference between T_0 values for leaf area and shoot dry mass. This result agrees with the observations that the reduction in the growth of maize leaf and stem was similar by Westage and Boyer (1985).

Ratio Between Root and Shoot Dry Masses

The ratio of root/shoot dry masses increased with increasing root temperature from 12°C to 17°C for all soil water potential treatments (figure 6-5). After achieving the optimum temperature of 17°C, the ratio decreased with further increasing root temperature. The responses of the ratio of root/shoot to root temperature was similar to the response of growth rate of shoot dry mass. This suggests that the growth rate of root dry mass may follow a similar trend in response to root temperature. However, the change

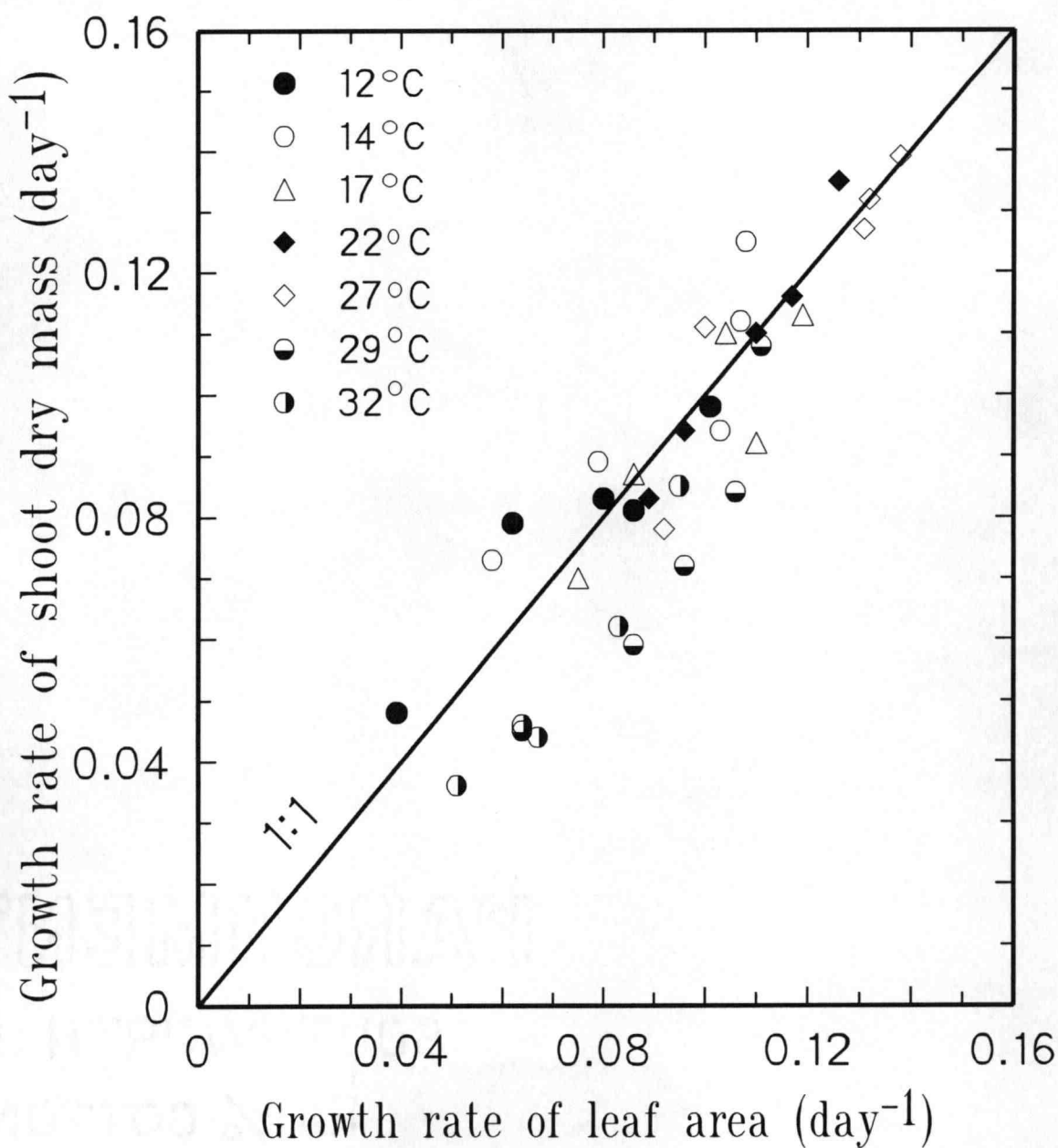


Figure 6-4. Relative growth rate of shoot dry mass plotted against relative growth rate of leaf area for 35 combined treatments of soil water potential and root temperature.

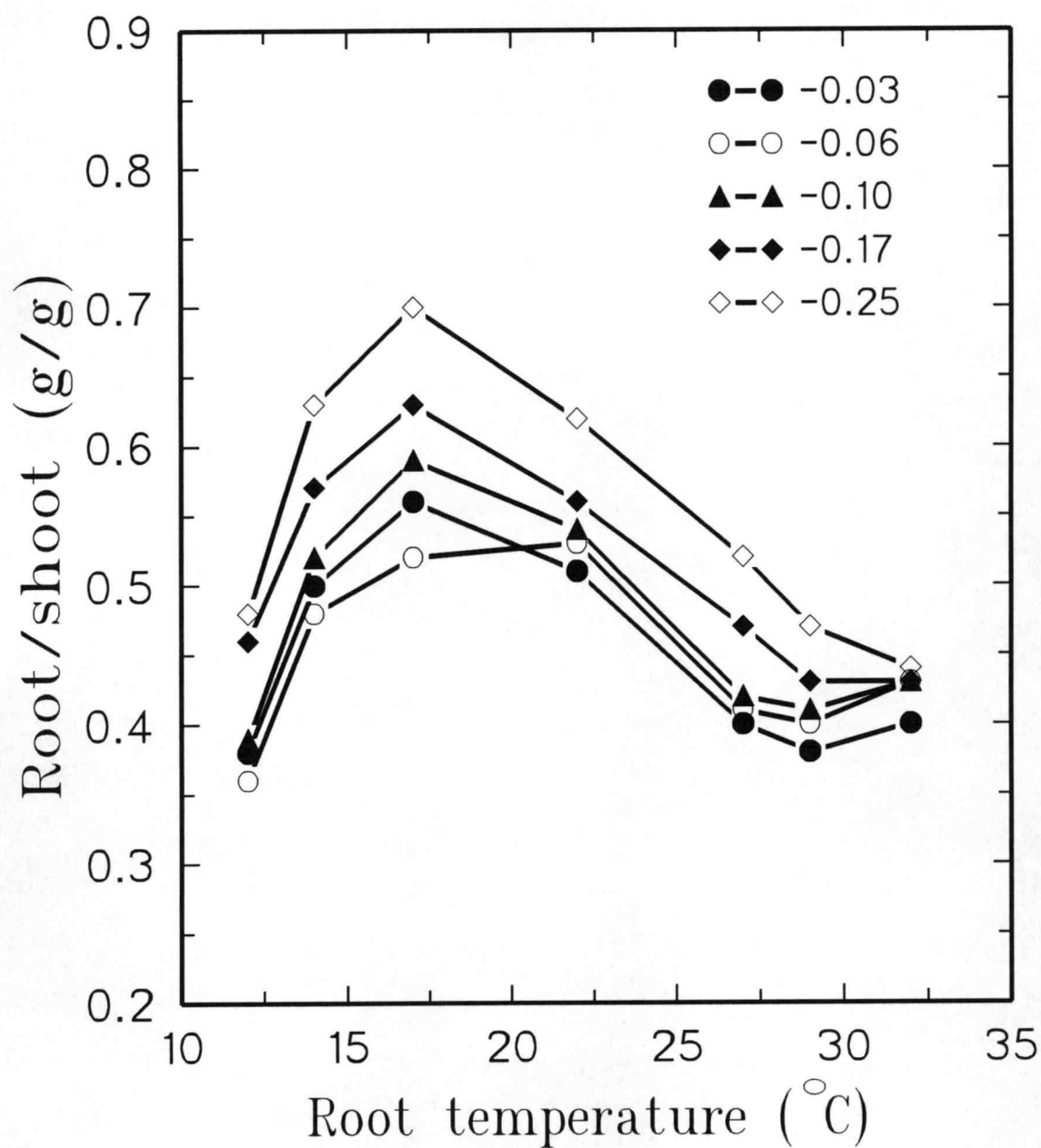


Figure 6-5. Ratio between root and shoot dry masses plotted as a function of root temperature for all soil water potentials.

in growth rate of root dry mass would be more than the change in growth rate of shoot dry mass with increasing root temperature. The root growth may be more sensitive to root temperature stress than the shoot. It is noticed that the optimal root temperature for the root/shoot ratio was 5-6 °C lower than that for shoot growth. This agrees with that the optimal root temperature for the rate of transpiration was lower than for other plant process (Chapters 4, 5).

The decrease of the ratio at both lower and higher root temperatures indicates that a smaller proportion of the total dry mass was found in the roots under root temperature stressed conditions. Similar results were reported by Cooper (1973) for maize. However, Cooper (1973) also reported the opposite responses by some plant species, such as strawberry, spring wheat, and *loium perenne*. These plants had the lowest ratio between root and shoot at intermediate root temperatures, whereas at low and high root temperatures, a larger proportion of the total dry mass was found in the roots. It was observed that the ratios remained consistent between the root temperature of 29°C and 32°C.

The ratio of root/shoot increased with decreasing soil water potential for each root temperature treatment (figure 6-5). But the ratios of root/shoot at the soil water potential of -0.03 MPa were not significant from those at the -0.06 MPa soil water potential. Under soil water stressed conditions, a larger proportion of dry mass was translocated to the roots. The root system was more developed at the low soil water potential (Kramer and Boyer, 1995). This enables the plant to adapt to water stress. However, the ratios at 32°C root temperature were almost the same for five soil water potential treatments. This

occurred because at the root temperature of 32°C, both growth of roots and shoots were inhibited by the root temperature.

Summary

The modified Johnson and Thornely equation describes the responses of plant growth processes to root temperature and soil water stresses. Relative growth rates of leaf area and shoot dry mass increased to an optimum at 23°C with increasing root temperature and followed by decreases with further increasing root temperature.

The activation energies of growth rates of leaf area and shoot dry mass increased with increasing soil water stress. Thus, as the plants were increasingly stressed, the activation energy increased and, therefore, the rate of reaction must decrease. The parameters of D and K_0 were constants for the growth rates of leaf area and shoot dry mass.

The ratio of root/shoot dry masses increased with increasing root temperature from 12°C to 17°C and then decreased with further increasing root temperature. This suggested that a smaller proportion of the total dry mass was found in the roots under root temperature stressed condition, due to either lower or higher temperatures. However, the ratio of root and shoot increased with increasing soil water stress. Under soil water stressed condition, a larger proportion of dry mass was translocated in the root.

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7. ACTIVATION ENERGY AS A MEASURE OF PLANT RESPONSE TO TEMPERATURE AND WATER STRESS

Introduction

Many studies of the effects of environmental stress on plant growth have focused on the response of plant processes to water and temperature stresses. Plant performance under water and temperature stresses have been studied at the molecular level (Davies et al., 1986; Singh et al., 1989), the cellular level (Green, Erickson and Buggy, 1971; Cleland, 1977; Boyer et al., 1985; Cosgrove et al., 1985), and the whole plant level (Berry and Björkman, 1980; Passioura, 1988; Kuang, Turner, and Henson, 1990). Unfortunately, large gaps of understanding remain between information drawn from studies at these three levels.

Although it is known that the rate of plant processes generally increases with temperature to an optimum and then decreases with further increase in temperature (Ingraham, 1958; Cooper, 1973; Ludlow, 1983; Feng, Li and Boersma, 1990), a general procedure which can be used to characterize such a response with physiologically meaningful parameters has been lacking (Johnson and Thornley, 1985; Feng et al., 1990).

Turgor has been considered a major factor influencing plant processes, including growth (Kuang et al., 1990), stomatal aperture and photosynthesis (Ludlow, 1983). The most widely used model describing the relationship between growth rate and turgor potential, originally proposed by Lockhart (1965) and later "popularized" by Ray et al. (1972), is

$$\text{Rate} = m(\sigma - Y), \quad [7-1]$$

where rate is usually a relative rate, with units of $\text{cm}^2 \text{ cm}^{-2} \text{ s}^{-1}$ for the rate of leaf area expansion; m ($\text{s}^{-1} \text{ MPa}^{-1}$) is commonly referred to as cell wall extensibility; Y (MPa) is the cell wall yielding stress; and σ (MPa) is the total mechanical stress in the cell wall, often equated with turgor potential. Green et al. (1971) explained that the three variables of equation [7-1] all have physical units, but that any or all could be under immediate metabolic control. However, little has been said about how these variables may be controlled by metabolic processes. There have been controversial conclusions regarding the role of turgor potential in plant growth (Passioura, 1988; Munns, 1988; Kuang et al., 1990). On the one hand, there are reports suggesting that growth is controlled by turgor, based on correlations between turgor potential and the growth rate. In cases where there is little such correlation, it is often argued that the lack of correlation is due to variations in either cell wall extensibility or yielding stress induced by experimental conditions and treatments (Turner, 1986). On the other hand, there are reports arguing that growth does not depend on turgor, a conclusion based on the observed lack of correlation between turgor and growth rate (Passioura, 1988; Munns, 1988).

Water stress often interacts with temperature (Barlow, Boersma, and Young, 1977; Feng et al., 1990). Few experiments have been done where both water potential and temperature were involved as controlled variables (Feng et al., 1990). Johnson and Thornley (1985) considered theoretical aspects of temperature effects on the rates of plant processes. They derived an equation which describes the temperature response of plant processes by combining the Arrhenius equation for chemical reactions with the Boltzman

distribution of enzymes between the active and inactive states. Feng et al. (1990)

modified the Johnson and Thornley equation and used the modified equation to describe the responses of whole plant processes to both water and temperature stresses. The modified equation is

$$K = K_0 \left(\frac{e^{-B(1/T_0 - \kappa/T)}}{1 + B(D - B)e^{D(1/T_0 - 1/T)}} \right), \quad [7-2]$$

where K is the rate of a plant process; B ($^{\circ}\text{K}$) is the activation energy divided by the universal gas constant; D ($^{\circ}\text{K}$) is the enthalpy difference between active and inactive states of the enzyme divided by the universal gas constant; T_0 ($^{\circ}\text{K}$) is the optimum temperature; κ is a constant, which was found to be equal to 1.0 for the rate of growth of leaf area and shoot dry mass of spring wheat; and K_0 is a constant representing the process rate for the condition where the quantity multiplying K_0 is equal to one in chapters 5 and 6. The units of K and K_0 are determined by the process being described. The parameters, B , D , T_0 , and K_0 , may be functions of water potential (Feng et al., 1990). This equation provides a tool for studying the combined effects of temperature and water stresses on plant growth processes based on well founded theoretical considerations.

This chapter was initiated to further explore the applicability of equation [7-2] to provide an explanation for observed responses of plant processes to water and temperature stresses, in terms of the mechanically meaningful parameters. The roles of turgor and metabolic control in plant growth will be addressed in terms of equation [7-1].

Results

Leaf Water Potential, ψ_l

The average of morning and evening leaf water potentials (tables 3-2, 3-3) was used to represent the daily average leaf water potential for use in the subsequent analysis (Table 7-1). These calculations were necessary since daily averages were needed in the following analysis. Similar calculation was made for osmotic potential using the morning and evening values (tables 3-5a and 3-7). The corresponding average turgor potential, ψ_p , was calculated using the relationship,

$$\psi_l = B + \psi_p, \quad [7-3]$$

and results are shown in Table 7-1.

Production of Photosynthates

The rate of net photosynthesis (P_n) increased rapidly as lights were turned on in four steps, reaching full light intensity at 8:00 (Figure 7-1). The rate of net photosynthesis rose initially to relative high values, which then decreased to lower values. This initial rise or "over shoot" has been observed in similar treatments and was not considered a measure of treatment response. The rate of net photosynthesis decreased to a lower value after about one-half hour and thereafter decreased continuously with a constant slope during the remains of the full illumination period. At the end of the light period, P_n decreased rapidly as lights were turned off in four steps, and reached zero at 21:00 when the last light was extinguished. The assumption was made that P_n decreased linearly with time between 8:00 and 20:00. For this analysis the initial overshoot was not considered. A

linear regression between P_n and the time of the day during the full light period was conducted for each treatment using the least square technique. Morning rates, at 8:00, and evening rates, at 20:00, were calculated using the results of this linear regression. Then, the mass of photosynthates produced during the light period, P_t ($\text{g m}^{-2} \text{ day}^{-1}$), was obtained, using the equation for the area of a trapezoid (Figure 7-1),

$$P_t = 0.108\left(\frac{1}{2}H + \frac{1}{2}L + \frac{12}{2}(H - L)\right), \quad [7-4]$$

where H is the morning rate of net photosynthesis ($\mu\text{mol m}^{-2} \text{ s}^{-1}$), and L is the evening rate of net photosynthesis ($\mu\text{mol m}^{-2} \text{ s}^{-1}$). The factor 0.108 converts the rate of net photosynthesis in $\mu\text{mol m}^{-2} \text{ s}^{-1}$ to the rate of dry mass production in $\text{g m}^{-2} \text{ hr}^{-1}$. The results are listed in Table 7-2.

Parameters of Equation [7-2]

Values of parameters, B , D , T_o , and K_o , of equation [7-2], which describes the response of plant processes to temperature and water stresses (Feng et al., 1990), were obtained by fitting the equation to P_t from table 7-2 and the relative growth rates of leaf area and shoot dry mass from table 3, using root temperature and ψ_1 as independent variables. In an earlier report (Feng et al., 1990) soil water potential rather than ψ_1 had been used as the independent variable. The numerical procedures described by Feng et al. (1990) were followed.

It was assumed that,

$$B = f(\psi_1), \quad [7-5a]$$

$$D = f(\psi_1) \quad [7-5b]$$

$$T_o = f(\psi_1), \quad [7-5c]$$

$$K_o = f(\psi_1). \quad [7-5d]$$

Polynomials were used to approximate these functions. Equation [7-2], with the parameters substituted by the functions described by equation [7-5], was fitted to the experimental data (tables 7-1, 7-2, 6-1a and 6-2a). Results were chosen based on the estimated variances of individual parameters and R^2 values (Table 7-3).

The relations between the activation energy and ψ_1 are,

$$B = b_1 * \psi_1, \quad [7-6a]$$

for growth rates of leaf area and shoot dry mass, and

$$B = b_1 * \psi_1 + b_2 * \psi_1^2, \quad [7-6b]$$

for Pt, where b_1 and b_2 are constants. The constant term was not included in either equation [7-6a] or equation [7-6b] since it was statistically not significant. The second order term and the higher order terms for equation [7-6a] were not statistically significant and hence were excluded in the final results. The second order term in equation [7-6b] was included in the final results based on its statistical significance.

The activation energy for growth rates of shoot dry mass and leaf area increased linearly as ψ_1 decreased (Figure 7-2). The activation energy for Pt was nonlinear function of ψ_1 . The activation energy equals zero at zero ψ_1 for all three plant processes considered here, according to equation [7-6]. The parameter D, which is the enthalpy difference between active and inactive states of the enzyme divided by the universal gas constant, was found to be independent of ψ_1 for all three plant processes.

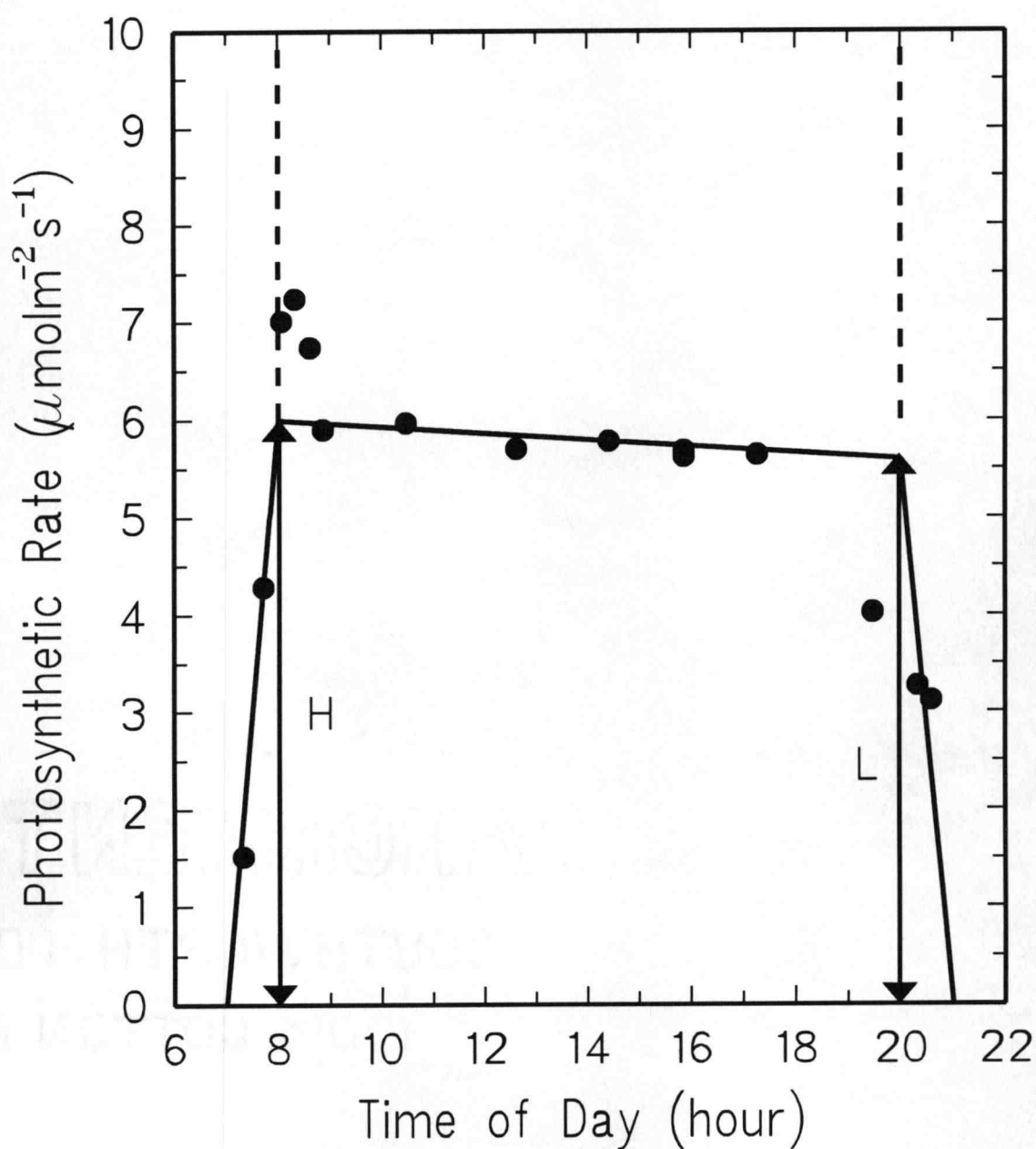


Figure 7-1. Net photosynthetic rate (P_n) at soil water potential of -0.25 MPa and root temperature of 27°C. Symbols are the experimental data, the solid lines are from fitting results. The full light period was between the dashed lines.

Table 7-1. Averaged values of leaf water potential and turgor potential at the indicated combinations of root temperature and soil water potential.

Indicated combinations of root temperature and soil water potential						
		Root temperature (°C)				
Soil water potential		14	17	22	27	32
-----MPa-----		-----MPa-----				
<u>Leaf water potential</u>						
-0.03	-0.47	-0.50	-0.53	-0.57	-0.61	
-0.06	-0.50	-0.52	-0.56	-0.60	-0.63	
-0.10	-0.53	-0.56	-0.59	-0.63	-0.67	
-0.17	-0.61	-0.63	-0.67	-0.70	-0.74	
-0.25	-0.70	-0.72	-0.76	-0.80	-0.84	
<u>Turgor potential</u>						
-0.03	0.70	0.73	0.73	0.66	0.53	
-0.06	0.67	0.74	0.74	0.62	0.51	
-0.10	0.64	0.65	0.74	0.55	0.48	
-0.17	0.59	0.58	0.59	0.50	0.41	
-0.25	0.48	0.44	0.55	0.46	0.42	

Table 7-2. Mass of photosynthates produced during one day at the indicated combination of root temperature and soil water potential.

Soil water potential	Root temperature (°C)				
	14	17	22	27	32
-----MPa-----	-----g m ⁻² day ⁻¹ -----				
-0.03	10.51	12.07	12.81	11.76	9.22
-0.06	10.02	11.58	12.21	10.88	8.85
-0.10	8.91	10.46	10.53	9.65	8.05
-0.17	7.78	8.92	9.65	8.56	7.45
-0.25	7.28	8.00	8.35	7.93	6.61

Table 7-3. Values of parameter of the equation [7-2] for relative growth rates of leaf area, and shoot dry mass, and P_t .

Parameter	Leaf area		Shoot dry mass		Rate of photosynthesis	
	value	ese	value	ese	value	ese*
k_0 (day ⁻¹)	0.29	0.020	0.29	0.028	-	-
k_0 (gm ⁻² day ⁻¹)	-	-	-	-	39.4	0.3
k_1 (d ⁻¹ MPa ⁻¹)	0.22	0.026	0.25	0.038	0.0	0.0
$b_1 \times 10^{-3}$ (°KMPa ⁻¹)	-8.9	0.20	-7.7	0.28	-26.5	3.3
$b_2 \times 10^{-3}$ (°KMPa ⁻²)	0.0	0.0	0.0	0.0	-14.9	1.8
$D \times 10^{-4}$ (°K)	2.7	0.39	3.4	0.55	1.5	0.15
T_0 (°K)	298.5	0.5	298.0	0.6	296.2	0.3
R^2	0.90		0.84		0.98	

* ese is estimated standard error.

The optimum root temperature was $23 \pm 0.3^\circ\text{C}$ for the rate of mass production of photosynthates, and $25 \pm 0.5^\circ\text{C}$ for growth rates of leaf area and shoot dry mass.

The parameter, K_0 , increased linearly with increasing ψ_1 for the both the growth rates of leaf area and shoot dry mass, according to

$$K_0 = k_0 + k_1 * \psi_1, \quad [7-7]$$

where k_0 and k_1 are constants. The K_0 for P_t , however, was constant. These calculations result in the constant κ being equal to 1.0 for the relative growth rates and P_t .

For enzyme-substrate reactions, typical values are of the order 1,000-15,000 °K for B, and 5,000-55,000 °K for D (Dixon and Webb, 1964). The values of B from 950-6100°K and D from 34000-64000°K found in this study are within these ranges and are believed to be generally valid.

Discussion

The parameter, B, of equation [7-2] represents the activation energy of the process being modeled. When it applied to growth as a function of water potential as done in this experiment, the relationship between B and water potential could be used as the basis for comparing the sensitivity of plant processes to water stress. As it was suggested by Feng et al., 1990, the absolute value of B may not be mechanistically meaningful considering the complexity of plant processes, but the rate of change of B with environmental stress can be significant. Figure 7-2 shows the activation energies for the growth rates of leaf area and shoot dry mass, and for P_t as functions of ψ_1 . As plants were increasingly stressed, the activation energies increased, resulting in lower reaction rates. Over the range of ψ_1

observed in this study, i.e. from -0.4 to -0.9 MPa, the activation energies for the growth rates of leaf area and shoot dry mass increased 120%, while the activation energy for photosynthesis as measured by mass of product produced in one day increased only about 45%. This result agrees with the general view that leaf expansion is more sensitive to water stress than the photosynthetic process does (Barlow, 1983). The close correspondence between the behaviour of activation energies for the growth rates of leaf area and shoot dry mass was expected because of the close relation between leaf area and shoot dry mass (Feng et al. 1990).

The parameter, K_0 , can be viewed as the maximum rate of the process when the activation energy is zero. This study showed that K_0 for growth increased linearly with ψ_1 (Equation [7-7]), while K_0 for photosynthesis was independent of ψ_1 . This difference in behaviour of K_0 for growth and photosynthesis is now further examined.

The Lockhart (1965) equation (equation [7-1]), describes the relationship between the steady state growth rate and turgor. It is generally believed that the wall extensibility and yield stress are both under metabolic control which may be exercised either directly or indirectly (Green et al., 1971). This means that the validity of the equation can only be examined under conditions of constant metabolic activity. In a study where both leaf water potential and temperature vary, the measured growth rates must be adjusted to a set of standard environmental conditions in order to assess the applicability of equation [7-1]. Since K_0 represents the rate of the process under the hypothetical condition of the zero activation energy, it may be used as the basis for examining the applicability of equation [7-1]. This will be illustrated in the following analysis.

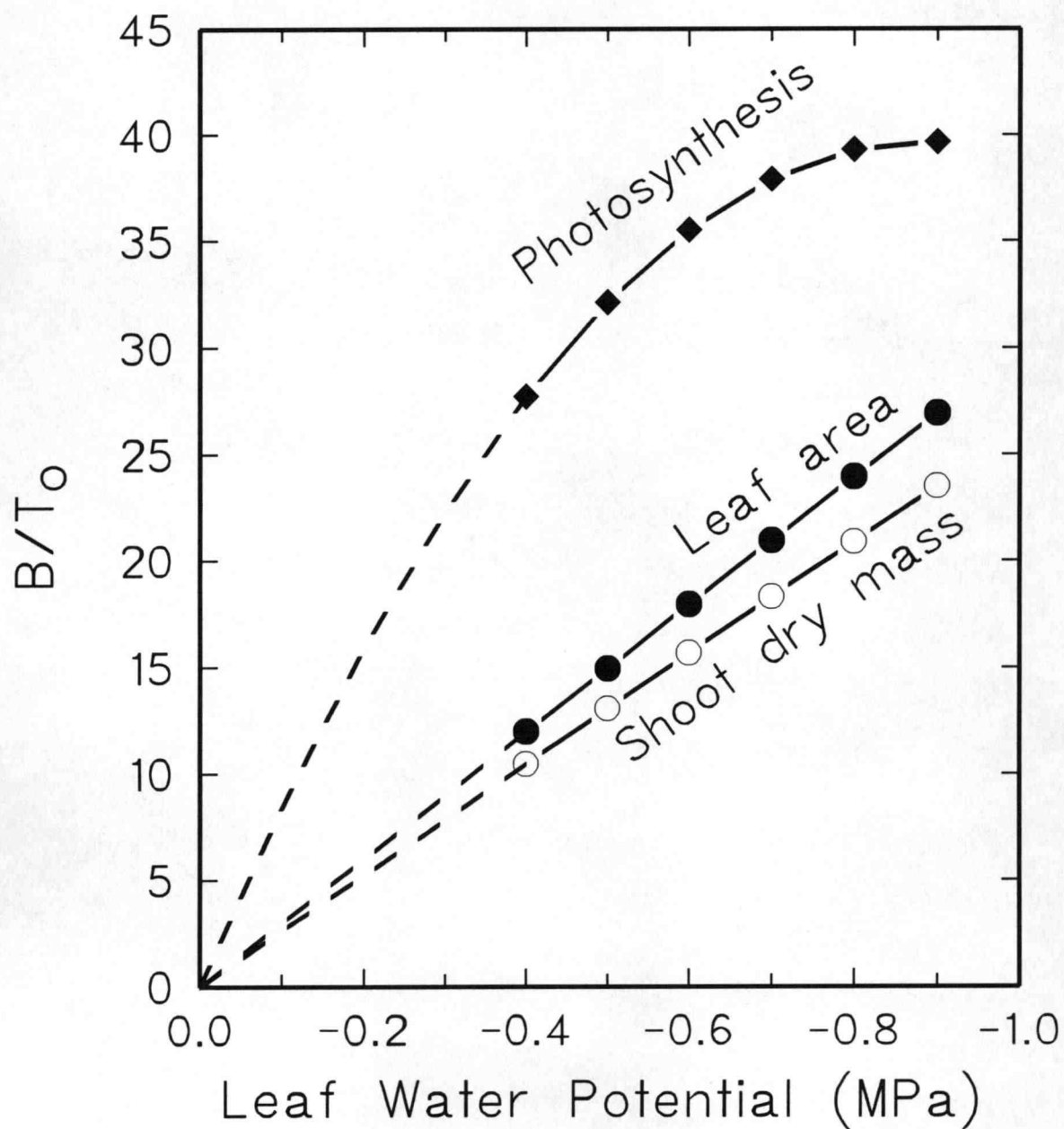


Figure 7-2. The activation energy, B , divided by T_0 plotted as a function of leaf water potential for Pt, and relative growth rates of leaf area and shoot dry mass.

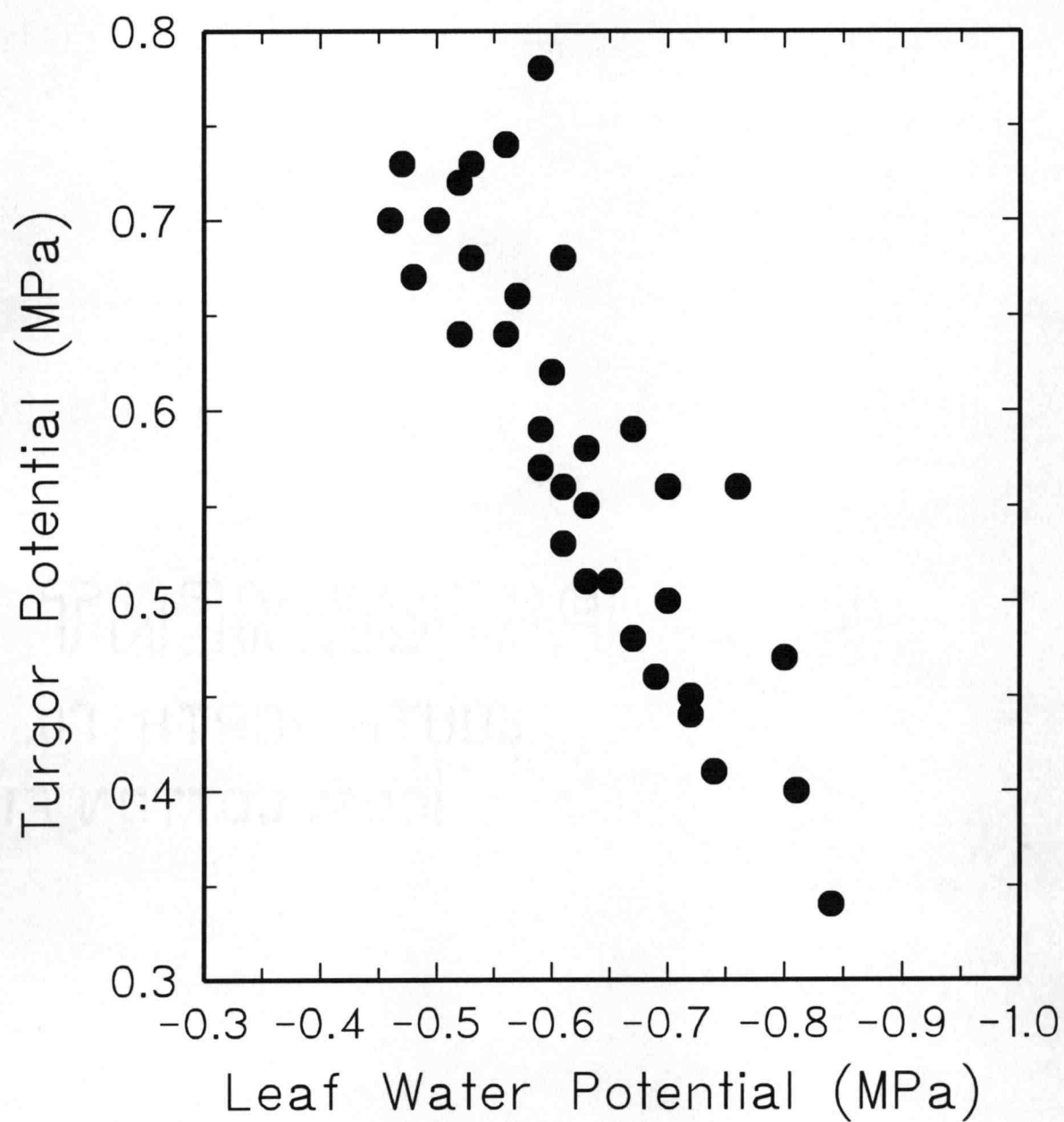


Figure 7-3. Turgor potential as a function of leaf water potential showing results for all 30 combinations of soil water potentials and root temperatures.

It can be started by examining the relationship between ψ_l and ψ_p . Turgor potential was plotted as a function of ψ_l (Figure 7-3). Results showed that ψ_p was linearly related to ψ_l . A linear regression between ψ_p and ψ_l results in

$$\psi_p = 1.17 \pm 0.05 + (0.94 \pm 0.10) \psi_l, \quad R^2 = 0.768. \quad [7-8]$$

The slope of the relationship between turgor and ψ_l is close to 1.0, indicating that ψ_p changes in parallel with total ψ_l . This shows that there was little osmotic adjustment.

Equation [7-1] states that growth is directly proportional to turgor potential. It is desirable to relate K_0 for the growth of leaf area and shoot dry mass to turgor potential. This can be done by substituting equation [7-7] into equation [7-14] using the data in table 4, yielding,

$$K_0 (\text{leaf}) = 0.02 \pm 0.05 + (0.23 \pm 0.04) \psi_p, \quad [7-9a]$$

$$K_0 (\text{shoot}) = -0.02 \pm 0.06 + (0.27 \pm 0.05) \psi_p. \quad [7-9b]$$

Equation [7-9] shows that K_0 is nearly zero for the growth of both leaf area and shoot dry mass when turgor is zero, suggesting that there is no growth when turgor is zero.

According to equation [7-2], this indicates that the yielding stress is zero.

Combining equations [7-1], [7-2], and [7-9] leads to the extensibility, m , for leaf area growth described by

$$m = m_0 \left(\frac{e^{-B(1/T_0 - \kappa/T)}}{1 + (B(D - B)e^{D(1/T_0 - 1/T)})} \right), \quad [7-10]$$

where $m_0 = 0.23$ and the rest of the parameters are in table 7-3. Comparing equation [7-10] and equation [7-2] shows that the extensibility of leaves was affected by temperature and

water stresses in a manner similar to a metabolic process. This strongly suggests that the extensibility may be under the direct control of metabolic processes.

The linear relation between K_0 and ψ_p (Figure 7-4) suggests that equation [7-1] is valid. However, it is important to notice that since the extensibility is under metabolic control, a lack of correlation between growth and turgor is not sufficient to disprove the role of turgor in growth. Figure 7-5 is a plot of growth rate of leaf area as a function of ψ_p , showing a lack of correlation. One may conclude, based on the lack of correlation between the two variable shown in figure 7-5, that there is no relation between leaf area growth and ψ_p . However, this analysis shows that this lack of correlation is the result of variations in cell extensibility, which is under metabolic control, caused by the range of environmental conditions represented in these data. A linear relation between growth and turgor emerges when the base rate, K_0 , is used for the analysis (Equation [7-9]).

The K_0 for the rate of growth of leaf area increased about 40% as ψ_p increased from 0.4 to 0.6 MPa. Barlow et al. (1977) observed that elongation rate of corn leaves increased by 34% over the same range of ψ_p . Additional evidence supporting the validity of this analysis is that the K_0 of the photosynthetic rate was found to be independent of turgor. This can be expected from the fact that a relation similar to equation [7-1] does not exist for photosynthesis.

By definition, the parameter, D , is the enthalpy difference between active and inactive states of the enzyme. In both these analyses and the analysis by Feng et al., 1990, D was not affected by water stress for any of the processes considered. It is noticed that this coincides with the fact that little change in osmotic potential occurred with any of the

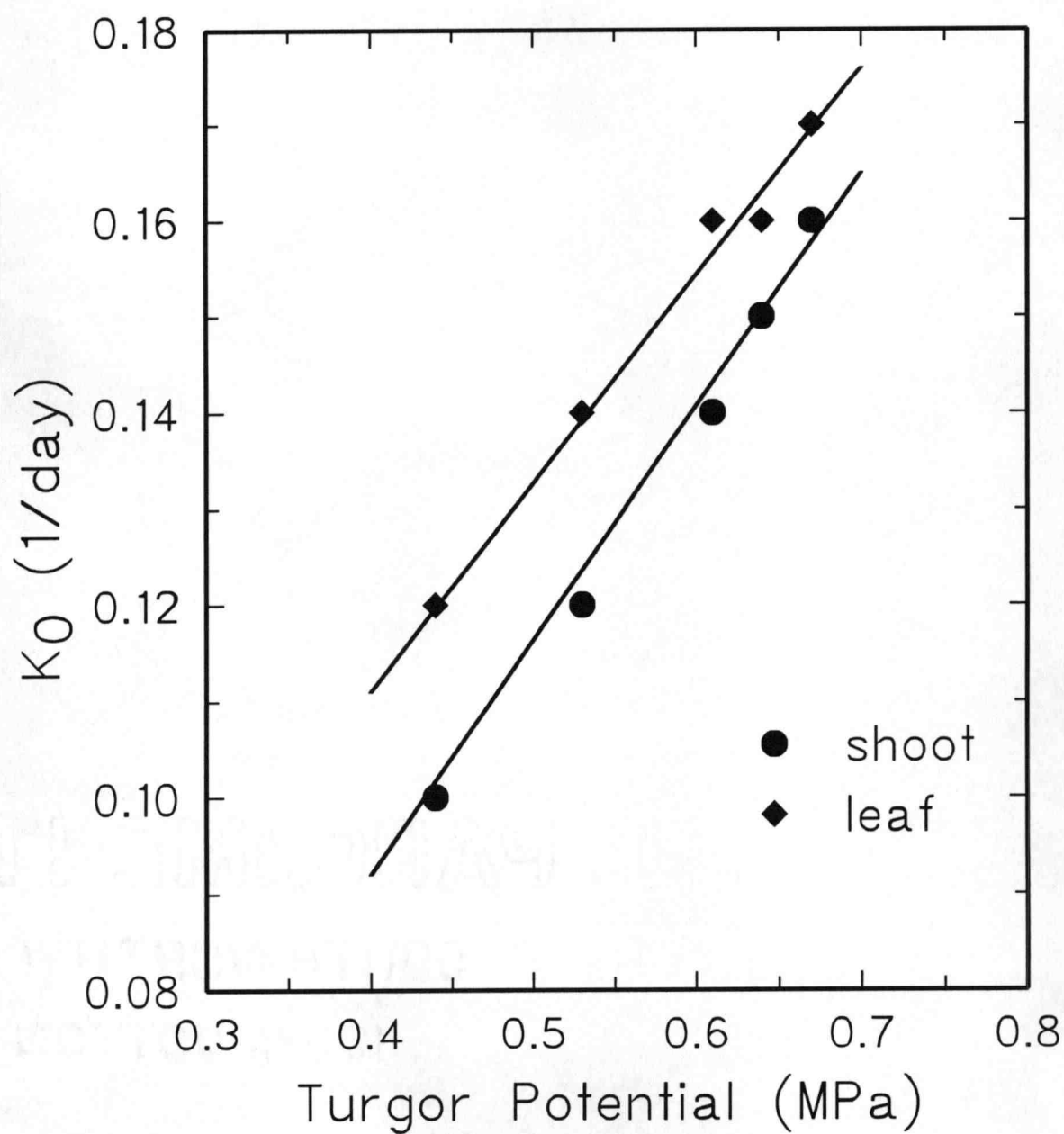


Figure 7-4. The base growth rate, K_0 , for leaf area and shoot dry mass growth rates plotted as a function of turgor potential.

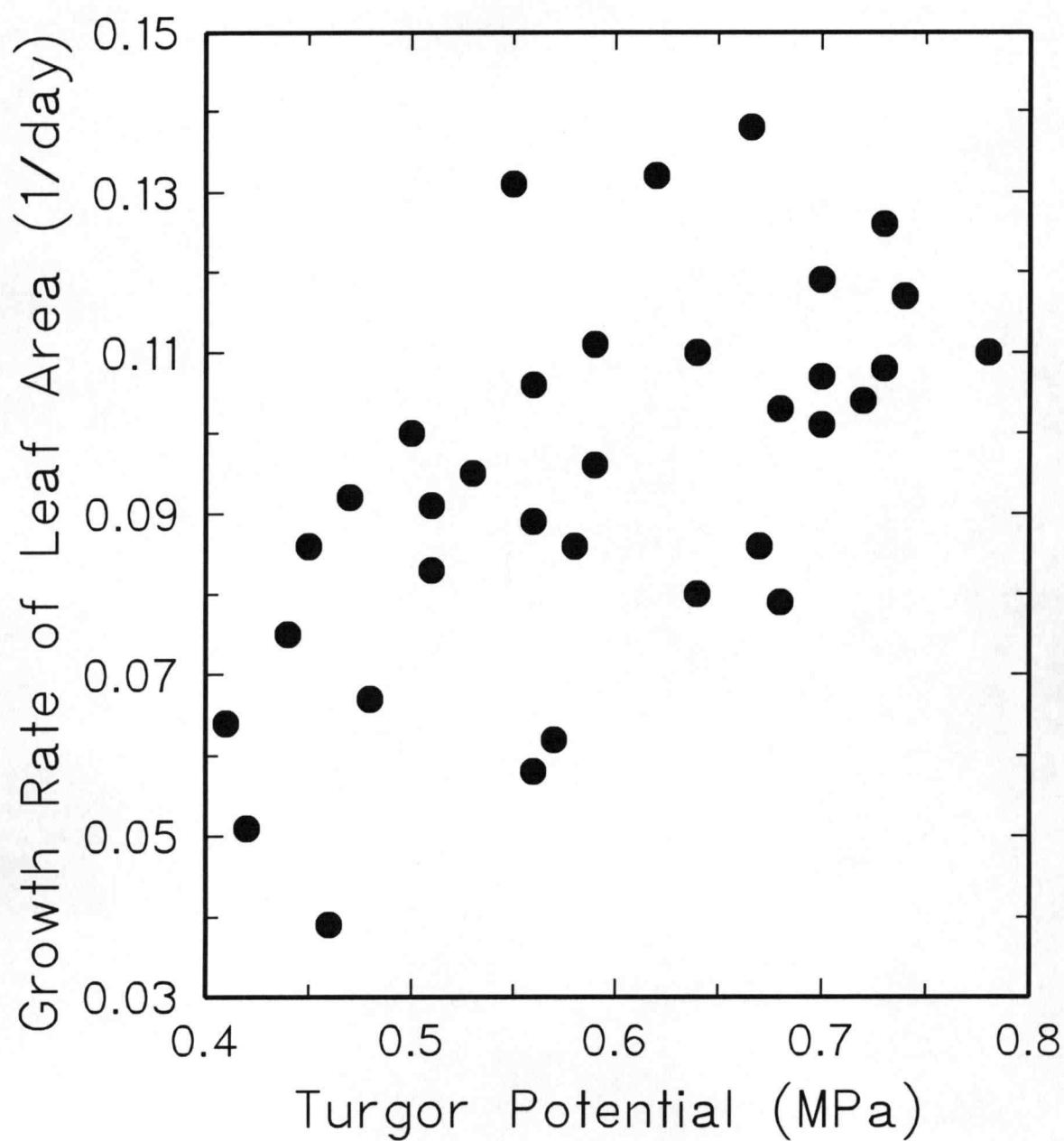


Figure 7-5. Growth rate of leaf area plotted as a function of turgor potential showing results for all combinations of soil water potential and root temperature treatments.

treatments. More study is needed regarding this observation. The possible connection between D and osmotic adjustment will be the subject of a future report.

Finally, attention is called to the observation that the optimum temperatures reported here and the values reported in chapter 5 are slightly different, namely, 23°C in this study and 21°C in chapter 5 for photosynthesis. The difference arises from the fact that leaf water potential was used in this chapter, while in the chapter 5 the soil water potential was used. The lower optimum temperatures reported in the chapter 5 resulted from the effect of root temperature on ψ_1 , as shown by equation [3-10]. Under constant soil water potentials and at temperatures lower than the optimum, an increase in temperature on the one hand causes the rate to increase, and on the other hand it also causes ψ_1 to decrease, which results in lower rates than if ψ_1 were maintained constant. The net result of the two opposing effects of root temperature is that the rates of growth start decreasing at a lower temperature under constant soil water potential than under constant ψ_1 .

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8. PARTITION OF PHOTOSYNTHATES BETWEEN SHOOT AND ROOT IN SPRING WHEAT SEEDLINGS (*Triticum aestivum* L.) AS A FUNCTION OF SOIL WATER POTENTIAL AND ROOT TEMPERATURE

Introduction

Partitioning of photosynthates plays a key role in determining the relative growth rates of competing plant parts. Unfavourable environmental conditions may cause shifts in the partitioning of photosynthates within plants so that growth of one organ may be affected less than that of another (Brouwer 1962). This shift in carbon allocation is important in plant adaptation to varying environmental conditions (Thornley 1990).

Roots are a major sink for assimilates, often requiring twice as much assimilate to produce a unit dry mass as required by the shoots due to higher respiratory energy costs and losses by exudation and senescence (van der Werf et al. 1988; Passioura 1983). Passioura (1993) suggested that the root system of many crop plants may be unnecessarily large, and that if it were smaller, more assimilate could be available for the shoot, to be used for higher grain production, with an increase in water use efficiency.

Growth of both shoots and roots is affected by water stress. However, under water stressed conditions the growth of leaves is usually reduced more than the growth of roots (Brouwer 1962; Setter 1990). Partitioning of photosynthates is altered, leading to an increase of the root/shoot ratio (Sharp and Davies 1979; Bradford and Hsiao 1982). Such a change is thought to improve the ability of plants to extract water and nutrients from the soil while limiting the potential for water loss by decreasing leaf area (Setter 1990). Hamblin et al. (1990) and Siddique et al. (1990) measured changes in partitioning

between roots and shoots resulting from water stress. Their results showed root length densities to be greater under stressed conditions, and based on theoretical considerations, much greater than required for extraction of available water. They noted that it remains unknown whether such an expenditure of photosynthates below ground is desirable, necessary or unavoidable in "stress" environments. Siddique et al. (1990) noted that their study confirmed the hypothesis that improved harvest index in modern varieties is associated with reduced investment of dry mass in the root system.

Few studies have focused on the effects of root temperature on carbon allocation in plants (Bowen 1991). The proposal has been made that low root temperature decreases the utilization of carbon in roots, resulting in carbon accumulation in the whole plant (Pollock et al. 1983) or in shoots (Walsh and Layzell 1986; Bowen 1991). Kuo and Boersma (1971) and Barlow et al. (1977) demonstrated that lowering root temperature decreased water potential throughout the plant and, as a result, decreased translocation.

Mathematical models have been commonly used to study partitioning of photosynthates (Moorby 1987; Amthor and McCree 1990; McCoy et al. 1989, 1990). Dry mass accumulation of plants is a function of the production of photosynthates and the respiratory activity. The works of Thornley (1972a,b) served to identify and quantify these processes and provided a conceptual framework for further experimental and theoretical works. Compartmental models (Kouchi et al. 1986; McCoy et al. 1989, 1990) usually divide plants into homogeneous compartments, such as the root, the stem, and the leaf compartments, and evaluate the carbon balance in each of the compartments under the

governance of rate constants which describe the utilization, the storage, and the translocation processes.

Besides providing a quantitative description of the complex interactions among carbon assimilation, translocation and utilization during plant growth, a properly designed mathematical model may also be used, in conjunction with experimental observations, to evaluate parameters that are not readily measurable for the particular experimental techniques (McCoy et al. 1989, 1990).

In this chapter I analyze the effects of soil water potential and root temperature on photosynthate partitioning of spring wheat (*Triticum aestivum* cv. Siete cerros) seedlings. Partitioning of photosynthates is evaluated by fitting a simple plant growth model, derived on the basis of mass balance considerations, to experimental observations of the rate of net photosynthesis, root and shoot dry mass accumulation and leaf area expansion.

Results

Mathematical Description

For the purpose of the study, each plant was considered to consist of a root and a shoot compartment. The rate of dry mass production by photosynthesis was calculated as the product of the rate of net photosynthesis ($\text{kg m}^{-2} \text{ day}^{-1}$) and total leaf area (m^2). The products of photosynthesis were partitioned between the shoot and the root compartments. In both the root and the shoot compartments, photosynthates are used for respiration, including growth and maintenance respiration, for dry mass accumulation, and for ion uptake respiration and exudation in the root compartment. The amount of

photosynthates used for respiration/exudation in the root and shoot compartments were assumed to be proportional to the dry mass of each compartment (Thornley 1990). Based on these assumptions, a mathematical model for partitioning of photosynthates between shoot and root compartments can be formulated in which the total dry mass produced by photosynthesis is given by

$$\frac{dM_p}{dt} = A(t)P_n \quad [8-1]$$

where dM_p/dt is the rate of total dry mass production (kg day^{-1}) by photosynthesis; $A(t)$ is leaf area (m^2); P_n is the average rate of dry mass production by photosynthesis during one day per unit leaf area ($\text{kg dry mass m}^{-2} \text{ day}^{-1}$). $M_p(t)$ and $A(t)$ are functions of time. The increase of dry mass in each compartment equals the amount of photosynthate allocated to that compartment minus the amount consumed by respiration. For the shoot compartment,

$$\frac{dM_s}{dt} = A(t)(\alpha P_n - R_s) \quad [8-2a]$$

where R_s is the rate of dark respiration of the shoot per unit leaf area ($\text{kg m}^{-2} \text{ day}^{-1}$) during the night, and α is the fraction of photosynthates partitioned to the shoot. Only the dark respiration during the night needs to be considered in equation [8-2a] since the net rate of photosynthesis, which is measured during the day, already accounts for the daytime respiration losses from the shoots. The shoots of the seedlings used in this study consist mainly of leaves, hence the total rate of respiration of shoots may be represented by the product of the respiration rate per unit leaf area and the total leaf area. R_s was

experimentally determined during the night. Following similar arguments, the increase of the root dry mass is

$$\frac{dM_r}{dt} = A(t)(1 - \alpha)Pn - R_r M_r \quad [8-2b]$$

where R_r is the root respiration/exudation coefficient ($\text{kg kg}^{-1} \text{ day}^{-1}$); M_r is the root dry mass (kg); and $R_r * M_r$ is the rate of respiration/exudation by roots (kg day^{-1}).

The rate of leaf area increase was assumed to be proportional to the rate of increase in shoot dry mass,

$$\frac{dA}{dt} = \beta \frac{dM_s}{dt} \quad [8-3]$$

where β ($\text{m}^2 \text{ kg}^{-1}$) is a proportionality constant. Although β has the same unit as the LAR (leaf area/plant dry mass), the two can not be equated. The parameter β is the ratio between the growth rate of leaf area and the growth rate of shoot dry mass after the experimental treatments were imposed, which will differ from the initial LAR of the plants.

Substituting equation [8-3] into [8-2a] yields

$$\frac{dA}{dt} = \beta A(t)(\alpha Pn - R_s) \quad [8-4]$$

Equations [8-2] and [8-4] are integrated to yield

$$M_s = M_{s0} + \frac{A_0}{\beta} (e^{bt} - 1) \quad [8-5a]$$

$$M_r = \frac{A_0 Pn(1 - \alpha)}{b + R_r} (e^{bt} - e^{-R_r t}) + M_{r0} e^{-R_r t} \quad [8-5b]$$

$$A = A_0 e^{bt} \quad [8-5c]$$

where $b = \beta(Pn\alpha - R_s)$ is the relative rate of increase of leaf area; A_0 , M_{s0} , and M_{r0} are the initial values for leaf area, shoot dry mass and root dry mass, respectively.

Equations [8-5a], [8-5b], and [8-5c] were fitted to the experimental observations of $A(t)$, $M_s(t)$, $M_r(t)$, R_s , and Pn , using a nonlinear least squares procedure to obtain the root respiration/exudation rate (R_r), the coefficient for partitioning of photosynthates between shoot and root compartments (α), and the proportionality constant (β). Thus the parameters to be evaluated were α , β , and R_r .

Data Preparation

The rates of net photosynthesis during the day and dark respiration of leaves (R_{ms}) during the night was measured in units of $\mu\text{mol-CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. They were converted to rates of dry mass production/ consumption by considering photosynthesis as the conversion of CO_2 and water into carbohydrate and oxygen and dark respiration as the complete oxidation of carbohydrates. The rate of dark respiration was found to be constant with time so that R_s ($\text{kg m}^{-2} \text{ day}^{-1}$), the total mass consumed by respiration during the night, is

$$R_s (\text{kg m}^{-2} \text{ day}^{-1}) = R_{ms} (\mu\text{mol m}^{-2} \text{ s}^{-1}) \times 10 \times 1.08 \times 10^{-4}, \quad [8-6]$$

where R_{ms} is the measured rate of respiration and 10 (hr) is the length of dark period. The factor 1.08×10^{-4} converts CO_2 uptake/evolution during photosynthesis/respiration in $\mu\text{mol-CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ to gain/loss of carbohydrate in $\text{kg m}^{-2} \text{ hr}^{-1}$ (Li, et al., 1991). Statistical analysis showed that R_s was affected by root temperature but not by soil water potential.

Average values of R_s for each root temperature are listed in Table 8-1.

Parameters of Equation [8-5]

Values of α , β , and R_r , of equation [8-5] were obtained by simultaneously fitting equations [8-5a], [8-5b], and [8-5c] to the experimental observations of leaf area, shoot dry mass, and root dry mass, along with P_n (table 7-2) and R_s determined as described above. A nonlinear, multivariable, maximum-likelihood procedure was used (Bard 1974). The statistical procedures are described in detail by Feng et al. (1990) and Li et al. (1991). An example of the fit between the model (equation 8-5) and the experimental observations of leaf area, shoot dry mass and root dry mass is shown in Figure 8-1. The effects of water stress were accounted for by allowing a , b , and R_r to be functions of soil water potential.

The results of these analyses showed that under constant root temperature, the relation between partitioning of photosynthates to the shoot and soil water potential can be described by a linear relation,

$$\alpha = A + A1\psi_s, \quad [8-7]$$

where A and $A1$ are functions of root temperature. The root respiration/exudation coefficient R_r was found to be affected only by root temperature. The proportionality constant, β , was found not significantly affected by either root temperature or soil water potential. The average value of this parameter was $24 \pm 1.8 \text{ m}^2 \text{ kg}^{-1}$. Values of these parameters are listed in Table 8-2.

Table 8-1. Total dry mass respired by shoots during darkness as a function of root temperature. The estimated standard error of these values is $0.03 \times 10^{-3} \text{ kg m}^{-2} \text{ day}^{-1}$.

Root temp.(°C)	14	17	22	27	32
$R_s \times 10^3 (\text{kg m}^{-2} \text{ day}^{-1})$	0.39	0.32	0.26	0.37	0.37

Table 8-2. Values of parameters of equation [8-5] with $\beta=24 \text{ m}^2 \text{ kg}^{-1}$. The numbers in the parentheses are the standard estimated errors.

Parameters	Root temperature °C					
	12	14	17	22	27	32
Photosynthate Partitioning						
$\alpha = A + A1\psi_s$						
A	0.435 (0.034)	0.505 (0.026)	0.444 (0.034)	0.560 (0.034)	0.596 (0.044)	0.403 (0.053)
A1	0.614 (0.276)	0.751 (0.183)	0.514 (0.147)	0.625 (0.170)	0.998 (0.200)	0.883 (0.229)
Root respiration						
R_r ($\text{kg kg}^{-1} \text{ day}^{-1}$)	0.229 (0.025)	0.208 (0.021)	0.236 (0.040)	0.178 (0.028)	0.181 (0.040)	0.280 (0.031)

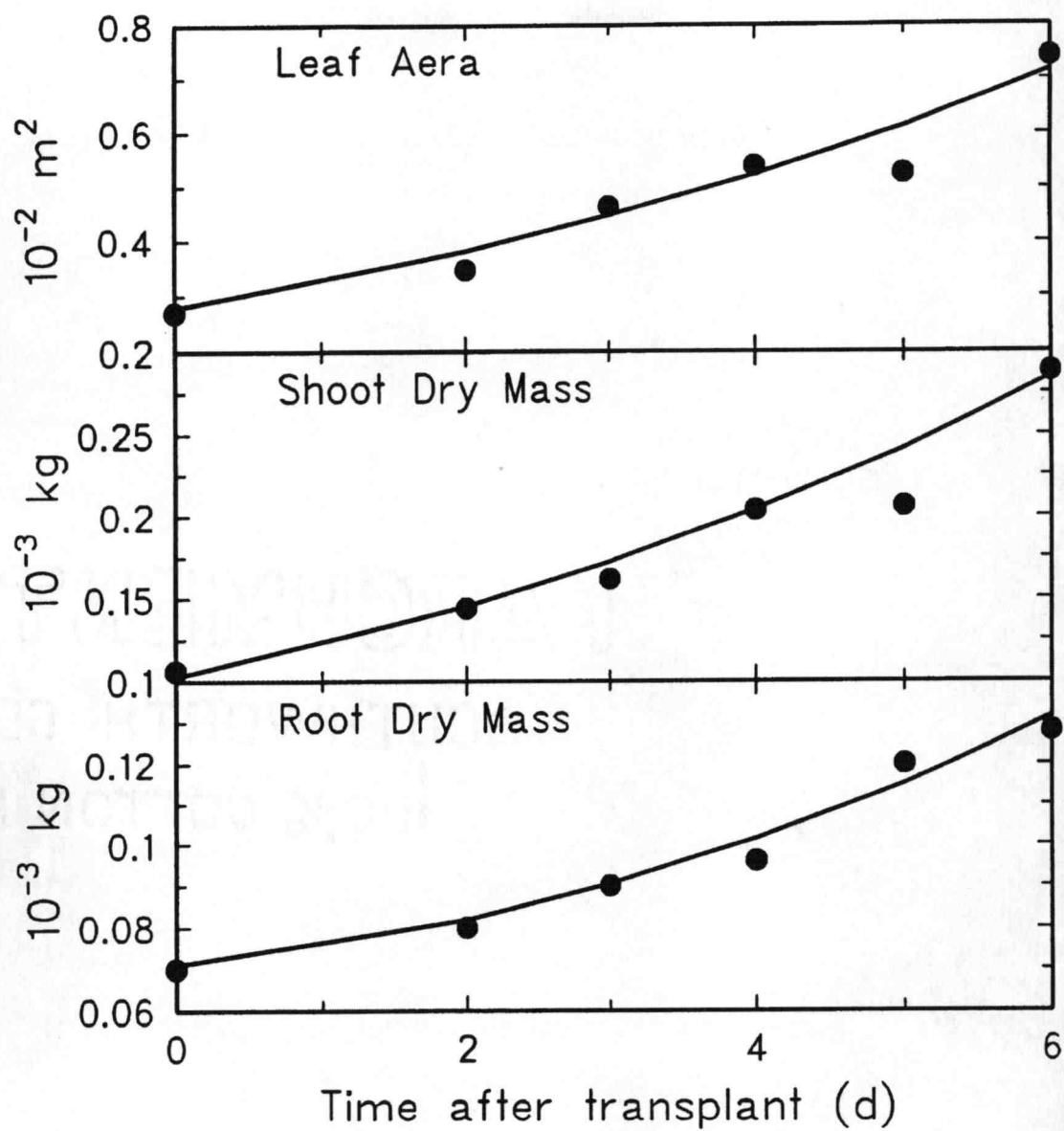


Figure 8-1. Least squares fit by equation [8-5] and measured (•) leaf area, shoot dry mass, and root dry mass as functions of time after treatment began at 22°C root temperature and -0.03 MPa soil water potential.

Discussion

Effects of Soil Water Potential and Root Temperature

Partitioning of photosynthates to the shoot compartment, expressed as a fraction of net dry mass production (Figure 8-2), decreased as the soil water potential decreased, at all root temperatures, or conversely, partitioning to the root compartment increased with decreasing soil water potential, at all root temperature treatments. The respiration/exudation coefficient of the roots was not significantly affected by soil water potential (Table 8-2). Consequently the root/shoot ratio increased as the soil water potential decreased. This result agrees with findings of other researchers (Bradford and Hsiao, 1982; Sharp and Davies, 1985; Hoogenboom, Huck, and Peterson, 1987). McCoy et al. (1990) reported that both the carbon partitioning and the sink size of roots increased under moderate water stress.

Partitioning of photosynthates to the shoot compartment increased with increasing root temperature for all soil water potential treatments (Figure 8-2), reaching a maximum at a root temperature between 22°C to 27°C, and then decreased as root temperature increased further. The optimum root temperature for the growth of the wheat seedlings used in this study was 25°C, as reported in chapter 7. This indicates that a larger fraction of photosynthates was directed toward the root compartment at root temperatures either lower than or higher than the optimum. This pattern is opposite to the responses of the rates of net photosynthesis and leaf area growth to root temperature, which were the

highest at the optimum root temperature and decreased at root temperatures either lower or higher than the optimum (chapter 7).

The increases in the partitioning of photosynthates to the root compartment at both low and high root temperatures were accompanied by increases in root respiration/exudation, expressed in $\text{kg kg}^{-1} \text{ day}^{-1}$ (Table 8-2). The parameter, R_r , calculated for this experiment represents the total carbon loss from the root compartment, including root respiration, exudation, and loss during root washing. The increased R_r at low root temperatures contradicts the expectation of lower root respiration at low temperatures (Lambers 1985). This could be the result of increases in other factors included in R_r . Evidence on the effects of temperature on root exudation is scarce and inconclusive (Bowen 1991). Root diameter generally decreases at both high and low temperatures (Bowen 1991). Thus it is possible that that increased loss of fine roots during root washing also contributed to the higher R_r values at low root temperatures. A definite conclusion is not possible because of the limited data. The results of my analysis are in agreement with those reported by McCoy et al. (1990). Using radioactive ^{14}C labelling technique and a more complicated compartmental analysis procedure, McCoy et al. (1990) concluded that carbon partitioning to the root increased under low root temperatures.

Soil water and root temperature stresses had compounding effects on the partitioning of photosynthates. At the root temperatures of 12, 22, and 32°C, the partitioning of photosynthates to the root compartment increased by 24%, 30%, and 32%, respectively, as soil water potential decreased from -0.03 to -0.25 MPa. At the 32°C root

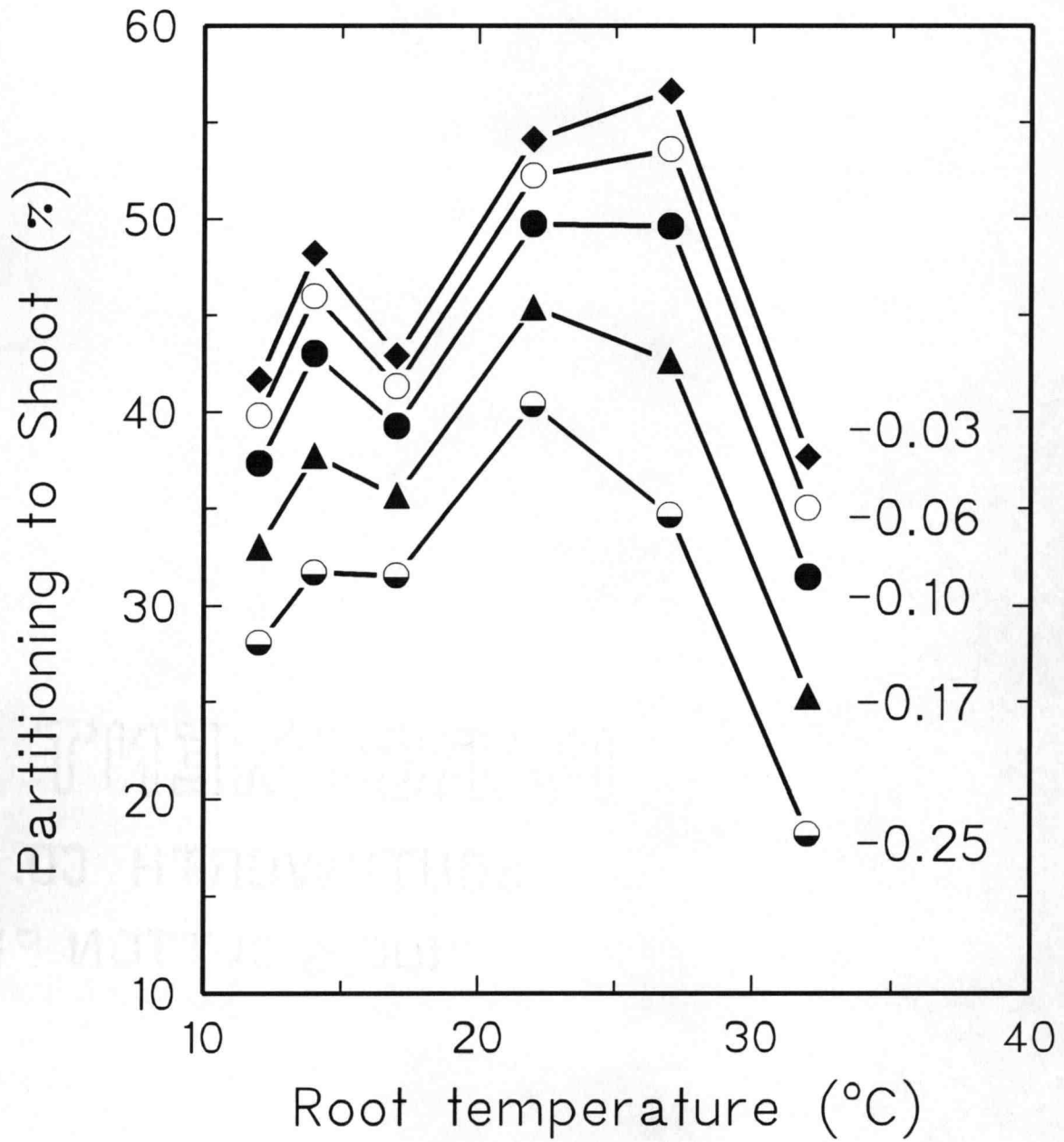


Figure 8-2. Fraction of photosynthates partitioned to the shoot compartments as functions of root temperature at indicated soil water potentials.

temperature and -0.25 MPa soil water potential treatment, more than 80% of the photosynthates was partitioned to the root compartment (Figure 8-2), as a result of the combined effects of root temperature and soil water stress. This is in agreement with the notion of McCoy et al. (1990) that the root temperature stress creates a pseudo water stress with regard to carbon partitioning and the pool sizes of all tissues.

Water stress had different effects on the rates of photosynthesis, carbon translocation, and utilization in the root and the shoot compartments. For example, as the soil water potential decreased from -0.03 to -0.25 MPa at 22°C root temperature, the net rate of photosynthesis was reduced by 35% (chapter 7). The partitioning of photosynthates to the root compartment increased from 46% to 60%, while the actual quantity of photosynthate exported to the root compartment decreased by only 15%. In contrast, the utilization of photosynthates in the shoots, indicative of the transport processes from the source to the sink regions within the shoot compartment, decreased by as much as 52%.

Partitioning as the Result of Competition between Roots and Shoots

The effect of stress on photosynthate partitioning can be further evaluated by considering the hypothesis that the increased partitioning to the root compartment with decreasing soil water potential was caused by decreased turgor potential gradient between the source and sink regions within the shoot compartment and a relatively smaller decrease in the turgor potential gradient between the shoot and the root compartments. The values

of total water potential, osmotic potential, and turgor potential of plant leaves obtained during the experiments have been published previously (Li et al. 1991, Feng et al. 1994).

It is generally accepted that translocation of photosynthates is driven by turgor potential gradient in the phloem system (Goeschl et al. 1976, Boersma et al. 1991, Minchin et al. 1993). The shift in the pattern of photosynthate partitioning under soil water stress has often been explained by considering the shift in the distribution of turgor potential gradients between the source and sink regions within the shoot compartment and between the shoot and the root compartments.

The turgor potential in the leaves decreased with decreasing soil water potential because spring wheat seedlings used in this study did not exhibit osmotic adjustment (Li et al. 1991, Feng et al. 1994), leading to reduced turgor potential gradient between source and sink leaves. As a result, the rate of transport, and utilization within the shoot compartment was reduced. At the same time, one may also expect a decrease in the water potential of the roots as soil water potential decreased. The net change in the turgor potential gradient between the shoot and the root compartments can thus be expected to be small. This change in turgor potential gradient distribution within the plant, according to the hypothesis, is reflected by a relatively small change in the rate of phloem transport between the shoot and the root compartments. The increased partitioning to the root compartment under water stress is thus a logical consequence of the shifted turgor potential gradient distribution in plants.

Similar results have also been reported by other studies (McCoy et al. 1989, 1990, Hamblin et al. 1990, Siddique et al. 1990). Cheeseman (1993) and Minchin et al. (1993)

recently modeled plant growth and carbon allocation based on the hypothesis that growth and resource allocation are results of local, internal resource concentrations and utilization kinetics, without involving root-shoot communication mechanisms.

These evidences, although do not constitute a concrete proof, provide strong circumstantial evidence in support of my hypothesis. Further studies with refined measurements of turgor potential distributions within plant systems are needed to provide a more rigorous validation of this hypothesis.

Validity of the Model and the Measurements

An alternative approach to the nonlinear least squares approach used in this study is to calculate the amount of photosynthates partitioned to the root by subtracting shoot dry mass accumulation and shoot respiration from total photosynthetic dry mass production. Root respiration/exudation may then be calculated by the difference between the amount of photosynthates partitioned to the root and root dry mass accumulation. However, the experimental errors compound in each step of these calculations. The values of root respiration/exudation so calculated become dominated by errors. The nonlinear least squares approach produces more reliable parameter estimates by avoiding this problem.

Constant values of P_n , α , and R_s were used in deriving equation [8-5]. This assumption is justified on the following grounds. Error resulting from using average, constant values of P_n , α , and R_s to represent plant growth over a short period, 7 days in this study. Preliminary measurements of P_n at day 3 and 5 after the treatment began did

not show significant difference. Leaf area expanded exponentially with constant relative rate $b = \beta(P_n \alpha - R_s)$ for all of treatments (Feng et al. 1990). In addition, from a statistical stand point, the fit of a more complex model, assuming P_n , α , and R_s to be functions of time, to experimental observations of leaf area, shoot dry mass and root dry mass is not significantly different from that of equation [8-5]. Although it may be arguable whether P_n , α , and R_s were truly constants during the experiment, I think partitioning of photosynthates estimated by using equation [8-5] is representative of the average values during the experiment.

Questions may also be raised as to the validity of using the rate of net photosynthesis and dark respiration measured on a single leaf to represent the average of a whole plant. Errors in R_s measurement will have little effect on these results because the shoot dark respiration rate is low compared to the net photosynthesis rate. Because the same measurement procedures were used for all treatments, the resulting errors in estimated photosynthate partitioning is expected to be consistent for all the treatments. Thus, although individual values may be in error, the comparison among treatments will still be valid. In addition, the respiration/exudation coefficient R_r obtained in this study fall well within the general range reported in the literature (Lambers 1985, Bowen 1991).

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9. CONCLUSIONS

A plant is a complex system. Growth and development of plants, and their response to environmental stresses, involve interactions among many physiological functions and processes on the one hand, and the environmental conditions on the other hand. A good understanding of the plant-environment interactions can only be achieved by studying multiple interactions among plant processes and environmental factors. In this study, I have attempted to follow this approach by investigating responses of several important plant processes with two common environmental stresses, i.e. soil water and soil temperature stresses. Major findings of the study are:

1. The modified Johnson and Thornley equation describes the responses of growth and the rate of net photosynthesis to root temperature and soil water stress. This equation provides a tool for studying the combined effects of temperature and water stresses on growth and photosynthesis in terms of physiologically meaningful parameters based on well founded theoretical considerations.
2. When applied to the complex processes such as plant growth and photosynthesis, the absolute value of the activation process may not be mechanistically meaningful. However, the rate of change of the activation energy with environmental stresses and the differences in the relative magnitude of activation energy between different processes can be used as

the basis for comparing the sensitivity of plant processes to water stress. For both shoot growth and photosynthesis, activation energy increased with decreasing water potential. The increase of activation energy was greater for growth rate than for photosynthesis, suggesting that growth was more sensitive to water stress than photosynthesis.

3. Analysis of the growth of leaf area suggested that leaf area expansion was proportional to turgor potential and the proportionality coefficient was affected by root temperature and soil water stress in a similar manner as photosynthesis.
4. Maximum partitioning of photosynthates to the shoot occurred under the optimum conditions for growth with respect to root temperature and water stress. Partitioning of photosynthates to shoot was the highest near the optimum root temperature, 22-27 °C, regardless soil water potential and decreased at both lower and higher root temperatures. At all root temperatures, water stress resulted in decreased partitioning of photosynthate to the shoot. Under the most stressed condition, -0.25 MPa soil water potential and 32 °C root temperature, more than 80% of photosynthates was allocated to roots. U
5. Root temperature and soil water stresses reduced shoot growth by the compounded effects of reduced net photosynthesis and reduced partitioning of photosynthates to the shoot. As a result, shoot growth is more sensitive to stress than photosynthesis.

6. Total leaf water potential and osmotic potential decreased during the light period. The daily decrease of total leaf water potential increased with decreasing soil water potential and increasing root temperature. There was little difference in daily change of osmotic potential between -0.03 MPa and -0.25 MPa soil water potential treatments despite the large difference in leaf water potential. Furthermore, there was little response in osmotic potential to soil water potential. This indicates that the cultivar of spring wheat used in these experiments lacks the ability for osmotic adjustment. As a result, the leaf turgor potential changed widely between -0.03 MPa and -0.25 MPa soil water potential treatments, almost in parallel with the change in total leaf water potential.
7. The osmotic potential during the light period decreased with increasing root temperature and reached the lowest values at the root temperature of 22°C, followed by an increase with further increase in root temperature. These phenomena lead to the highest turgor potential at the optimum root temperature of 22°C. Thus, the optimal growth near 22°C root temperature also corresponds to the highest turgor potential, a condition necessary for maximum leaf area expansion. Difference between leaf water potential and soil water potential increased with increasing root temperature, but remained the same as soil water potential decreased.
8. Viscosity of water is considered to be a major physical factor controlling the rate of transpiration. After adjusting for water viscosity, the morning rate of

transpiration decreased with increasing root temperature over the range of experimental conditions. The evening rate of transpiration increased with increasing root temperature from 14°C to 17°C, followed by a decrease with further increase in root temperature. Transpiration rates both in the morning and evening decreased with decreasing soil water potential. Similar responses were observed for stomatal conductance.

9. The stomatal conductance decreased with decreasing leaf turgor potential. The constant reduction between stomatal conductance and turgor potential from the morning to evening over the soil water potential ranges suggested that the loss of leaf turgor may be the primary cause of the stomata closure.
10. The decrease in transpiration rate resulted from reduced water conductance of the plant and decreased stomatal conductance under soil water and root temperature stresses. The change of the photosynthesis rate in response to root temperature and soil water stresses resulted from changes in both stomata conductance and carboxylation efficiency, with the latter being the dominant factor. This is consistent with the conclusions of the analysis based on modified Johnson and Thornley equation which indicated that water stress increased the activation energy for photosynthesis. The value of the activation energy for photosynthesis was consistent with the general ranges typical of enzymatic reactions, e.g. carboxylation.
11. Transpiration is controlled by the physical processes of vapor transfer from intercellular space to the atmosphere. Photosynthesis, on the other hand, is

controlled by both the physical process of CO₂ transfer from atmosphere to the site of fixation in the chloroplast and the subsequent carboxylation reaction. This difference resulted in the different responses of transpiration and photosynthesis to root temperature and water stresses.

Maximum plant growth under optimal environmental conditions require coordinated, optimal functioning of many plant processes, e.g. photosynthesis, partition and translocation of photosynthates, turgor potential in the leaves, among the factors investigated in this study. Reduced plant growth under environmental stresses is the result of the sub-optimal performance of all these processes and their complex interactions. Traditionally, responses of plants to adverse environmental conditions have often been studied in isolation, e.g. relationship between leaf expansion and water potential and the effects of stomatal conductance on photosynthesis. Although much insight has been gained by this approach, it can be said that a plant is much more than the simple addition of these individual responses and relationships. The complex interactions among many physiological processes and environmental factors can only be understood when they are studied together. The study described in this thesis is my attempt toward this direction.

Although progress has been made toward understanding the complex responses of plant growth to environmental stresses, in this case, root temperature and water stress, many questions remain unanswered.

Are there linkages among the responses of various plant processes to unfavorable environmental conditions? If there are such linkages, what are their forms and how do they function? For example, is there a linkage among net photosynthesis, partitioning of photosynthates, maintenance of turgor potential, and functioning of root system?

Growth of plants requires all these processes to function in balance. Plant growth is regulated by both turgor potential and the physiological control on properties of cells, such as cell wall extensibility and yielding stress. How does the plant control these parameters in response to various environmental stresses so that balanced growth of the plant as a whole is maintained?

These and many other questions remain to be answered. Our current understanding of the relationship between plants and their environment, although impressive, is incomplete and fragmented. I hope I have made a small contribution in this fascinating field.

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APPENDIX: DATA COLLECTED

Table A1. Leaf area as a function of time in days after transplanting at the indicated combinations of soil water potential and root temperature.

Root temp.	Soil water poten.	Days after transplanting					
		0	2	3	4	5	6(7)*
°C	MPa	----- cm ² /slab -----					
12	-0.03	151.11	186.52	237.86	216.42	273.17	305.24
	-0.06	151.11	189.09	232.42	241.76	246.19	277.20
	-0.10	151.11	197.66	231.94	210.21	255.53	268.36
	-0.15	151.11	207.52	210.30	231.22	228.71	238.05
	-0.25	151.11	166.99	208.00	173.19	211.23	174.33
14	-0.03	129.12	179.36	195.74	234.30	253.32	272.89
	-0.06	129.12	172.93	189.81	218.49	247.04	272.54
	-0.10	129.12	159.60	181.32	183.86	223.71	270.21
	-0.17	129.12	160.16	166.53	174.22	217.02	245.33
	-0.25	129.12	148.71	161.60	174.42	186.71	193.51
17	-0.03	122.54	172.56	206.97	229.48	245.08	283.65
	-0.06	122.54	192.99	190.93	224.43	236.19	264.60
	-0.10	122.54	162.09	185.20	197.52	235.30	267.06
	-0.17	122.54	169.53	182.37	188.55	207.90	260.67
	-0.25	122.54	160.47	193.55	209.90	199.14	251.88
22	-0.03	134.61	173.40	231.40	269.06	262.29	370.53
	-0.06	134.61	168.94	217.18	233.85	245.24	303.90
	-0.10	134.61	182.98	211.49	237.83	243.03	295.74
	-0.17	134.61	182.08	199.66	219.54	221.92	274.66
	-0.25	134.61	155.32	195.26	201.83	215.04	232.35
27	-0.03	122.00	208.16	230.84	232.68	285.78	289.56
	-0.06	122.00	180.27	200.54	246.64	289.10	245.71
	-0.10	122.00	177.28	180.24	235.32	290.90	240.12
	-0.17	122.00	148.92	190.98	192.85	244.09	173.60
	-0.25	122.00	152.34	178.01	179.72	209.67	206.29
29	-0.03	136.24	191.08	211.25	247.41	259.31	263.24
	-0.06	136.24	171.16	204.82	223.89	234.12	246.47
	-0.10	136.24	178.86	193.61	192.83	227.25	224.65
	-0.17	136.24	165.30	177.72	170.90	207.69	221.09
	-0.25	136.24	164.48	163.36	172.17	162.06	176.75
32	-0.03	123.96	153.18	226.47	219.35	243.90	191.53
	-0.06	123.96	143.32	189.73	192.51	211.66	217.12
	-0.10	123.96	171.78	187.00	196.64	160.05	173.94
	-0.17	123.96	193.10	172.20	168.11	172.20	197.23
	-0.25	123.96	144.22	167.88	154.68	166.29	161.56

Table A2. Shoot dry mass as a function of time in days after transplanting at the indicated combinations of soil water potential and root temperature.

Root temp.	Soil water poten.	Days after transplanting					
		0	2	3	4	5	6(7)*
°C	MPa	----- cm ² /slab -----					
12	-0.03	0.52	0.69	0.90	0.87	1.13	1.25
	-0.06	0.52	0.75	0.80	0.89	0.97	1.11
	-0.10	0.52	0.77	0.84	0.80	1.00	1.16
	-0.15	0.52	0.81	0.78	0.93	0.91	1.08
	-0.25	0.52	0.86	0.82	0.71	0.90	0.78
14	-0.03	0.52	0.63	0.71	0.91	0.79	1.10
	-0.06	0.52	0.56	0.73	0.81	0.75	1.03
	-0.10	0.52	0.52	0.62	0.70	0.68	1.00
	-0.17	0.52	0.55	0.59	0.70	0.66	0.96
	-0.25	0.52	0.51	0.59	0.63	0.68	0.80
17	-0.03	0.50	0.62	0.71	0.86	0.90	1.06
	-0.06	0.50	0.75	0.69	0.85	0.88	1.00
	-0.10	0.50	0.58	0.64	0.75	0.85	0.94
	-0.17	0.50	0.58	0.69	0.70	0.77	0.94
	-0.25	0.50	0.58	0.51	0.77	0.59	0.96
22	-0.03	0.53	0.72	0.81	1.02	1.03	1.44
	-0.06	0.53	0.70	0.80	0.86	0.94	1.29
	-0.10	0.53	0.73	0.78	0.92	0.92	1.16
	-0.17	0.53	0.69	0.71	0.82	0.87	1.07
	-0.25	0.53	0.63	0.69	0.84	0.80	1.00
27	-0.03	0.50	0.82	1.00	0.90	1.18	1.23
	-0.06	0.50	0.75	0.91	0.93	1.16	1.18
	-0.10	0.50	0.76	0.87	0.93	1.10	1.16
	-0.17	0.50	0.70	0.83	0.79	1.08	1.09
	-0.25	0.50	0.59	0.76	0.72	0.95	0.87
29	-0.03	0.62	0.71	0.74	0.94	0.96	1.00
	-0.06	0.62	0.67	0.70	0.76	0.85	0.94
	-0.10	0.62	0.64	0.62	0.71	0.85	0.89
	-0.17	0.62	0.64	0.63	0.66	0.74	0.85
	-0.25	0.62	0.60	0.62	0.64	0.70	0.76
32	-0.03	0.49	0.63	0.98	0.88	1.00	0.78
	-0.06	0.49	0.65	0.75	0.71	0.79	0.87
	-0.10	0.49	0.62	0.76	0.75	0.70	0.72
	-0.17	0.49	0.65	0.70	0.72	0.74	0.76
	-0.25	0.49	0.62	0.70	0.62	0.74	0.72

Table A3. Root dry mass as a function of time in days after transplanting at the indicated combinations of soil water potential and root temperature.

Root temp.	Soil water poten.	Days after transplanting					
		0	2	3	4	5	6(7)*
°C	MPa	----- cm ² /slab -----					
12	-0.03	0.32	0.35	0.33	0.38	0.40	0.60
	-0.06	0.32	0.42	0.30	0.44	0.27	0.56
	-0.10	0.32	0.44	0.29	0.37	0.39	0.64
	-0.15	0.32	0.50	0.29	0.38	0.40	0.56
	-0.25	0.32	0.41	0.35	0.37	0.39	0.45
14	-0.03	0.32	0.31	0.37	0.40	0.42	0.44
	-0.06	0.32	0.31	0.31	0.38	0.43	0.42
	-0.10	0.32	0.29	0.31	0.34	0.40	0.45
	-0.17	0.32	0.30	0.33	0.40	0.41	0.46
	-0.25	0.32	0.31	0.37	0.37	0.38	0.39
17	-0.03	0.34	0.43	0.44	0.48	0.45	0.53
	-0.06	0.34	0.47	0.36	0.43	0.48	0.57
	-0.10	0.34	0.33	0.42	0.45	0.53	0.47
	-0.17	0.34	0.35	0.42	0.43	0.42	0.60
	-0.25	0.34	0.34	0.47	0.51	0.49	0.65
22	-0.03	0.35	0.40	0.43	0.48	0.55	0.64
	-0.06	0.35	0.43	0.43	0.45	0.50	0.56
	-0.10	0.35	0.40	0.43	0.47	0.49	0.53
	-0.17	0.35	0.33	0.40	0.46	0.48	0.52
	-0.25	0.35	0.39	0.47	0.48	0.49	0.55
27	-0.03	0.32	0.34	0.40	0.37	0.47	0.44
	-0.06	0.32	0.32	0.37	0.43	0.44	0.44
	-0.10	0.32	0.30	0.33	0.45	0.44	0.45
	-0.17	0.32	0.28	0.34	0.43	0.51	0.44
	-0.25	0.32	0.30	0.37	0.45	0.46	0.43
29	-0.03	0.32	0.26	0.29	0.38	0.33	0.32
	-0.06	0.32	0.25	0.29	0.28	0.35	0.34
	-0.10	0.32	0.25	0.29	0.26	0.34	0.28
	-0.17	0.32	0.25	0.26	0.29	0.32	0.33
	-0.25	0.32	0.24	0.27	0.31	0.35	0.32
32	-0.03	0.32	0.30	0.34	0.39	0.36	0.41
	-0.06	0.32	0.31	0.31	0.33	0.35	0.40
	-0.10	0.32	0.34	0.34	0.33	0.29	0.38
	-0.17	0.32	0.35	0.32	0.33	0.30	0.39
	-0.25	0.32	0.32	0.32	0.31	0.29	0.34

Table B1. The leaf water potential, osmotic potential, and turgor potential as functions of time of day at the root temperature of 12°C and the indicated soil water potential on the third and fifth days after transplanting. The time is in hours and fraction of hours.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_l	π	ψ_p		ψ_l	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.03	6.92	-0.40	-1.00	0.60	6.65	-0.47	-1.11	0.64
	7.38	-0.68	-1.11	0.43	7.07	-0.46	-1.07	0.61
	7.95	-0.52	-1.08	0.56	7.50	-0.56	-1.07	0.51
	8.82	-0.67	-1.02	0.35	8.00	-0.75	-1.12	0.37
	9.92	-0.69	-1.15	0.46	8.10	-0.72	-1.10	0.38
	10.33	-0.65	-1.11	0.46	8.65	-0.74	-1.22	0.48
	11.90	-0.66	-1.14	0.48	10.15	-0.69	-1.15	0.46
	12.30	-0.55	-1.17	0.62	12.07	-0.82	-1.40	0.58
	14.22	-0.75	-1.13	0.38	12.88	-0.87	-1.31	0.44
	14.30	-0.65	-1.07	0.42	14.67	-0.85	-1.16	0.31
	15.87	-0.72	-1.22	0.50	16.73	-0.74	-1.27	0.53
	16.30	-0.65	-1.15	0.50	19.45	-0.71	-1.36	0.65
	19.88	-0.78	-1.31	0.53	20.20	-0.59	-1.17	0.58
	20.37	-0.49	-1.26	0.77	20.52	-0.49	-1.31	0.82
	21.72	-0.41	-1.29	0.88	21.15	-0.44	-1.29	0.85

Table B1. continued.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_l	π	ψ_p		ψ_l	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.06	6.67	-0.42	-1.00	0.58	6.52	-0.45	-1.05	0.60
	7.18	-0.44	-0.98	0.54	6.90	-0.43	-1.04	0.61
	7.72	-0.70	-1.01	0.31	7.25	-0.55	-1.05	0.50
	8.45	-0.67	-1.06	0.39	7.72	-0.70	-1.05	0.35
	9.75	-0.62	-1.08	0.46	8.32	-0.80	-1.14	0.34
	10.08	-0.62	-1.10	0.48	8.72	-0.76	-1.14	0.38
	11.68	-0.74	-1.12	0.38	10.30	-0.72	-1.15	0.43
	12.12	-0.71	-1.10	0.39	12.22	-0.81	-1.16	0.35
	14.00	-0.70	-1.14	0.44	12.45	-0.65	-1.18	0.53
	15.65	-0.80	-1.15	0.35	12.82	-0.78	-1.15	0.37
	16.00	-0.69	-1.23	0.54	14.80	-0.70	-1.24	0.54
	19.65	-0.78	-1.25	0.47	16.90	-0.89	-1.28	0.39
	19.93	-0.75	-1.26	0.51	19.63	-0.86	-1.35	0.49
	20.13	-0.67	-1.25	0.58	20.45	-0.64	-1.21	0.57
	21.53	-0.49	-1.27	0.78	21.28	-0.45	-1.18	0.73

Table B1. continued.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_l	π	ψ_p		ψ_l	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.10	6.50	-0.38	-0.99	0.61	6.58	-0.54	-1.00	0.46
	7.03	-0.41	-1.01	0.60	7.02	-0.52	-1.04	0.52
	7.63	-0.70	-1.05	0.35	7.18	-0.57	-1.03	0.46
	8.35	-0.80	-1.07	0.27	7.62	-0.83	-1.07	0.24
	9.67	-0.76	-0.93	0.17	8.18	-0.97	-1.11	0.14
	10.00	-0.58	-1.08	0.50	8.77	-0.89	-1.12	0.23
	11.58	-0.64	-1.11	0.47	10.22	-0.79	-1.18	0.39
	12.03	-0.74	-1.07	0.33	12.17	-0.75	-1.08	0.33
	13.92	-0.75	-1.14	0.39	12.72	-0.72	-1.12	0.40
	15.55	-0.78	-1.24	0.46	14.73	-0.88	-1.22	0.34
	15.93	-0.80	-1.27	0.47	16.83	-0.82	-1.18	0.36
	19.53	-0.68	-1.26	0.58	19.53	-0.91	-1.32	0.41
	20.07	-0.80	-1.25	0.45	20.27	-0.90	-1.19	0.29
	21.50	-0.46	-1.23	0.77	20.58	-0.71	-1.21	0.50
					21.20	-0.57	-1.18	0.61

Table B1. continued.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_1	π	ψ_p		ψ_1	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.15	6.75	-0.45	-0.97	0.52	6.38	-0.52	-0.98	0.46
	7.32	-0.50	-1.00	0.50	6.80	-0.46	-1.05	0.59
	7.80	-0.86	-1.01	0.15	7.42	-0.66	-0.98	0.32
	8.55	-0.62	-1.12	0.50	7.93	-0.86	-1.13	0.27
	8.67	-0.65	-1.05	0.40	8.43	-0.83	-1.11	0.28
	10.15	-0.69	-1.19	0.50	8.97	-0.91	-1.12	0.21
	11.77	-0.75	-1.12	0.37	10.48	-0.88	-1.15	0.27
	12.20	-0.74	-1.13	0.39	12.37	-0.92	-1.22	0.30
	14.07	-0.80	-1.17	0.37	15.00	-1.06	-1.29	0.23
	15.72	-0.78	-1.15	0.37	17.25	-1.07	-1.36	0.29
	16.12	-0.95	-1.20	0.25	19.77	-0.99	-1.31	0.32
	19.75	-0.84	-1.22	0.38	20.43	-0.89	-1.28	0.39
	20.23	-0.75	-1.24	0.49	20.75	-0.88	-1.29	0.41
	21.60	-0.53	-1.21	0.68	21.47	-0.64	-1.23	0.59
					21.92	-0.53	-1.31	0.78

Table B1. continued.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_l	π	ψ_p		ψ_l	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.25	6.83	-0.52	-1.02	0.50	6.73	-0.69	-0.99	0.30
	7.52	-0.92	-1.14	0.22	6.95	-0.38	-1.09	0.71
	7.88	-0.82	-1.07	0.25	7.35	-0.83	-1.08	0.25
	8.73	-0.78	-1.09	0.31	7.80	-0.82	-1.09	0.27
	9.85	-0.77	-1.07	0.30	8.52	-0.85	-1.22	0.37
	10.25	-0.72	-1.14	0.42	8.87	-0.90	-1.08	0.18
	11.82	-0.70	-1.09	0.39	10.42	-0.93	-1.18	0.25
	12.25	-0.78	-1.05	0.27	12.30	-1.09	-1.27	0.18
	14.17	-0.86	-1.17	0.31	14.87	-1.01	-1.35	0.34
	15.80	-0.90	-1.23	0.33	16.98	-1.01	-1.43	0.42
	16.18	-0.95	-1.20	0.25	19.70	-1.03	-1.43	0.40
	19.80	-0.96	-1.17	0.21	20.38	-1.02	-1.31	0.29
	20.30	-0.88	-1.20	0.32	20.70	-0.94	-1.38	0.44
	21.65	-0.60	-1.21	0.61	21.40	-0.86	-1.38	0.52
					21.85	-0.78	-1.40	0.59
					23.95	-0.57	-1.25	0.68

Table B2. The leaf water potential, osmotic potential, and turgor potential as functions of time of day at the root temperature of 14°C and the indicated soil water potential on the third and fifth days after transplanting. The time is in hours and fraction of hours.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_l	π	ψ_p		ψ_l	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.03	6.65	-0.25	-1.06	0.81	7.23	-0.31	-1.12	0.81
	7.13	-0.24	-1.09	0.85	7.65	-0.40	-1.18	0.78
	7.62	-0.35	-1.11	0.76	8.10	-0.59	-1.21	0.62
	8.07	-0.45	-1.14	0.69	8.65	-0.54	-1.23	0.69
	8.55	-0.42	-1.16	0.74	12.12	-0.59	-1.22	0.63
	9.92	-0.34	-1.14	0.80	14.33	-0.62	-1.17	0.55
	12.48	-0.46	-1.16	0.70	16.20	-0.53	-1.24	0.71
	14.02	-0.54	-1.21	0.67	19.47	-0.58	-1.28	0.70
	15.95	-0.44	-1.19	0.75	20.33	-0.47	-1.26	0.79
	17.98	-0.56	-1.27	0.71	21.08	-0.29	-1.26	0.97
	20.20	-0.45	-1.24	0.79				
	21.52	-0.27	-1.23	0.96				

Table B2. continued.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_l	π	ψ_p		ψ_l	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.06	6.77	-0.30	-1.11	0.81	7.42	-0.51	-1.14	0.63
	7.27	-0.35	-1.11	0.76	7.78	-0.56	-1.20	0.64
	7.72	-0.43	-1.12	0.69	8.23	-0.60	-1.17	0.57
	8.18	-0.55	-1.19	0.64	8.77	-0.57	-1.21	0.64
	8.65	-0.55	-1.16	0.61	12.23	-0.59	-1.26	0.67
	10.05	-0.50	-1.18	0.68	14.47	-0.65	-1.26	0.61
	12.53	-0.61	-1.16	0.55	16.33	-0.65	-1.22	0.57
	14.15	-0.56	-1.19	0.63	19.60	-0.62	-1.26	0.64
	16.05	-0.59	-1.23	0.64	20.45	-0.56	-1.25	0.69
	18.03	-0.61	-1.24	0.63	21.20	-0.35	-1.21	0.86
	20.32	-0.49	-1.35	0.86				
	21.68	-0.30	-1.30	1.00				

Table B2. continued.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_1	π	ψ_p		ψ_1	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.10	6.72	-0.30	-1.12	0.82	7.48	-0.49	-1.16	0.67
	7.22	-0.35	-1.12	0.77	7.85	-0.48	-1.23	0.75
	7.67	-0.48	-1.13	0.65	8.32	-0.82	-1.23	0.41
	8.12	-0.54	-1.17	0.63	8.83	-0.63	-1.17	0.54
	8.60	-0.57	-1.14	0.57	12.33	-0.69	-1.20	0.51
	10.00	-0.47	-1.1	0.71	14.53	-0.60	-1.19	0.59
	12.43	-0.56	-1.17	0.61	16.38	-0.70	-1.26	0.56
	14.10	-0.63	-1.24	0.61	19.65	-0.71	-1.46	0.75
	16.00	-0.63	-1.25	0.62	20.50	-0.50	-1.28	0.78
	17.95	-0.66	-1.23	0.57	21.27	-0.37	-1.29	0.92
	20.25	-0.46	-1.36	0.90				
	21.58	-0.35	-1.23	0.88				

Table B2. continued.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_1	π	ψ_p		ψ_1	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.17	6.87	-0.35	-1.12	0.77	7.05	-0.40	-1.18	0.78
	7.35	-0.40	-1.14	0.74	7.58	-0.60	-1.19	0.59
	7.77	-0.51	-1.15	0.64	8.02	-0.65	-1.22	0.57
	8.23	-0.62	-1.17	0.55	8.58	-0.71	-1.24	0.53
	8.70	-0.69	-1.15	0.46	12.07	-0.77	-1.19	0.42
	10.08	-0.58	-1.28	0.70	14.25	-0.74	-1.17	0.43
	12.58	-0.69	-1.27	0.58	16.15	-0.80	-1.25	0.45
	14.22	-0.65	-1.30	0.65	19.42	-0.69	-1.34	0.65
	16.10	-0.71	-1.32	0.61	20.27	-0.56	-1.31	0.75
	18.08	-0.70	-1.37	0.67	21.02	-0.50	-1.28	0.78
	20.38	-0.50	-1.23	0.73				
	21.72	-0.35	-1.28	0.93				

Table B2. continued.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_l	π	ψ_p		ψ_l	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.25	6.92	-0.39	-1.11	0.72	7.33	-0.44	-1.18	0.74
	7.40	-0.49	-1.16	0.67	7.72	-0.59	-1.17	0.58
	7.83	-0.67	-1.16	0.49	8.17	-0.85	-1.27	0.42
	8.30	-0.95	-1.30	0.35	8.72	-0.74	-1.25	0.51
	8.78	-0.85	-1.19	0.34	12.17	-0.79	-1.26	0.47
	10.15	-0.79	-1.28	0.49	14.42	-0.82	-1.29	0.47
	12.65	-0.83	-1.26	0.43	16.28	-0.88	-1.20	0.32
	14.12	-0.90	-1.24	0.34	19.53	-0.77	-1.31	0.54
	16.15	-0.90	-1.32	0.42	20.40	-0.80	-1.34	0.54
	18.13	-0.96	-1.24	0.28	21.13	-0.60	-1.31	0.71
	20.45	-0.79	-1.38	0.59				
	21.77	-0.54	-1.29	0.75				

Table B3. The leaf water potential, osmotic potential, and turgor potential as functions of time of day at the root temperature of 17°C and the indicated soil water potential on the third and fifth days after transplanting. The time is in hours and fraction of hours.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_l	π	ψ_p		ψ_l	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.03	6.72	-0.21	-1.10	0.89	6.62	-0.20	-1.10	0.90
	6.92	-0.30	-1.07	0.77	7.23	-0.43	-1.11	0.68
	7.45	-0.31	-1.12	0.81	7.80	-0.48	-1.12	0.64
	7.90	-0.44	-1.13	0.69	8.28	-0.71	-1.13	0.42
	8.37	-0.47	-1.13	0.66	8.77	-0.50	-1.17	0.67
	9.02	-0.35	-1.13	0.78	10.50	-0.47	-1.10	0.63
	10.77	-0.43	-1.18	0.75	11.93	-0.70	-1.20	0.50
	12.50	-0.50	-1.17	0.67	12.05	-0.59	-1.11	0.52
	14.35	-0.59	-1.18	0.59	13.65	-0.65	-1.11	0.46
	14.55	-0.52	-1.12	0.60	15.03	-0.69	-1.14	0.45
	15.80	-0.50	-1.21	0.71	16.38	-0.72	-1.25	0.53
	16.77	-0.63	-1.25	0.62	18.92	-0.70	-1.26	0.56
	19.20	-0.56	-1.34	0.78	20.08	-0.63	-1.31	0.68
	20.27	-0.49	-1.17	0.68	20.53	-0.50	-1.24	0.74
	20.60	-0.44	-1.25	0.81	21.52	-0.32	-1.29	0.97
	21.80	-0.26	-1.34	1.08	23.57	-0.32	-1.23	0.91
					2.17	-0.26	-1.17	0.91
					4.17	-0.25	-1.13	0.88

Table B3. continued.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_l	π	ψ_p		ψ_l	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.06	6.50	-0.35	-1.16	0.81	6.83	-0.24	-1.10	0.86
	7.20	-0.31	-1.12	0.81	7.62	-0.31	-1.13	0.82
	7.68	-0.44	-1.18	0.74	8.08	-0.57	-1.16	0.59
	8.13	-0.45	-1.15	0.70	8.57	-0.62	-1.16	0.54
	8.82	-0.48	-1.18	0.70	9.03	-0.59	-1.15	0.56
	10.53	-0.57	-1.19	0.62	10.73	-0.62	-1.22	0.60
	11.10	-0.45	-1.12	0.67	12.20	-0.74	-1.21	0.47
	12.25	-0.64	-1.16	0.52	13.95	-0.72	-1.20	0.48
	14.08	-0.67	-1.25	0.58	15.25	-0.76	-1.19	0.43
	15.72	-0.71	-1.22	0.51	16.67	-0.71	-1.24	0.53
	16.55	-0.70	-1.29	0.59	16.97	-0.76	-1.23	0.47
	19.02	-0.53	-1.39	0.86	19.12	-0.72	-1.32	0.60
	20.08	-0.50	-1.40	0.90	20.32	-0.56	-1.39	0.83
	20.45	-0.48	-1.34	0.86	20.75	-0.60	-1.19	0.59
	21.65	-0.27	-1.35	1.08	21.72	-0.34	-1.29	0.95
	21.90	-0.22	-1.38	1.16	23.47	-0.34	-1.27	0.93
					2.03	-0.28	-1.19	0.91
					4.10	-0.29	-1.14	0.85

Table B3. continued.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_l	π	ψ_p		ψ_l	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.10	6.77	-0.24	-1.11	0.87	6.77	-0.28	-1.06	0.78
	6.97	-0.27	-1.05	0.78	7.50	-0.47	-1.14	0.67
	7.52	-0.34	-1.11	0.77	7.98	-0.80	-1.10	0.30
	7.95	-0.44	-1.11	0.67	8.48	-0.83	-1.22	0.39
	9.12	-0.53	-1.16	0.63	8.97	-0.71	-1.21	0.50
	10.83	-0.50	-1.16	0.66	10.67	-0.78	-1.18	0.40
	11.17	-0.47	-1.09	0.62	12.12	-0.80	-1.20	0.40
	12.60	-0.66	-1.28	0.62	13.87	-0.91	-1.19	0.28
	14.42	-0.57	-1.12	0.55	14.18	-0.83	-1.11	0.28
	15.88	-0.67	-1.25	0.58	15.17	-0.81	-1.19	0.38
	16.87	-0.96	-1.33	0.37	16.57	-0.99	-1.29	0.30
	17.10	-0.63	-1.12	0.49	16.88	-0.85	-1.16	0.31
	19.27	-0.60	-1.31	0.71	19.03	-0.81	-1.30	0.49
	20.35	-0.53	-1.48	0.95	20.25	-0.64	-1.31	0.67
	20.67	-0.49	-1.33	0.84	20.68	-0.74	-1.27	0.53
	21.85	-0.31	-1.33	1.02	21.67	-0.38	-1.28	0.90
					23.68	-0.40	-1.20	0.80
					2.27	-0.34	-1.18	0.84
					4.30	-0.32	-1.15	0.83

Table B3. continued.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_l	π	ψ_p		ψ_l	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.17	6.65	-0.40	-1.18	0.78	6.70	-0.27	-1.00	0.73
	7.35	-0.45	-1.07	0.62	7.02	-0.47	-0.97	0.50
	7.85	-0.40	-1.12	0.72	7.37	-0.52	-1.11	0.59
	8.28	-0.65	-1.21	0.56	7.87	-0.73	-1.15	0.42
	8.97	-0.56	-1.16	0.60	8.38	-0.94	-1.13	0.19
	10.72	-0.69	-1.18	0.49	8.85	-0.77	-1.22	0.45
	12.43	-0.88	-1.24	0.36	10.57	-0.86	-1.18	0.32
	12.78	-0.71	-1.16	0.45	12.00	-0.86	-1.17	0.31
	14.28	-0.69	-1.16	0.47	13.75	-0.91	-1.21	0.30
	15.70	-0.76	-1.22	0.46	15.10	-1.02	-1.21	0.19
	16.68	-0.80	-1.29	0.49	16.47	-0.86	-1.26	0.40
	17.03	-0.61	-1.16	0.55	16.83	-0.96	-1.17	0.21
	19.17	-0.61	-1.27	0.66	18.97	-0.84	-1.34	0.50
	20.20	-0.59	-1.54	0.95	20.17	-0.99	-1.33	0.34
	20.55	-0.59	-1.39	0.80	20.60	-0.85	-1.31	0.46
	21.75	-0.30	-1.29	0.99	21.58	-0.48	-1.28	0.80
					23.77	-0.34	-1.22	0.88
					2.35	-0.34	-1.17	0.83
					4.40	-0.34	-1.08	0.74

Table B3. continued.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_l	π	ψ_p		ψ_l	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.25	6.57	-0.22	-1.05	0.83	6.95	-0.34	-1.08	0.74
	6.83	-0.26	-0.98	0.72	7.73	-0.54	-1.21	0.67
	7.27	-0.35	-1.11	0.76	8.20	-0.93	-1.19	0.26
	7.80	-0.49	-1.09	0.60	8.67	-0.94	-1.24	0.30
	8.20	-0.73	-1.09	0.36	9.10	-0.86	-1.25	0.39
	8.88	-0.69	-1.16	0.47	10.80	-0.94	-1.28	0.34
	10.63	-0.72	-1.13	0.41	12.28	-1.06	-1.28	0.22
	12.33	-0.75	-1.15	0.40	14.02	-0.87	-1.24	0.37
	14.18	-0.85	-1.20	0.35	14.10	-1.06	-1.31	0.25
	15.60	-0.78	-1.20	0.42	15.33	-1.16	-1.33	0.17
	16.62	-0.71	-1.15	0.44	16.72	-1.14	-1.40	0.26
	16.98	-0.79	-1.09	0.30	19.22	-1.04	-1.42	0.38
	19.12	-0.86	-1.25	0.39	20.38	-1.10	-1.47	0.37
	20.17	-0.65	-1.32	0.67	20.80	-0.79	-1.31	0.52
	20.50	-0.62	-1.20	0.58	21.78	-0.60	-1.26	0.66
	21.72	-0.39	-1.26	0.87	23.85	-0.36	-1.12	0.76
					2.45	-0.58	-1.16	0.58
					4.50	-0.42	-1.15	0.73

Table B4. The leaf water potential, osmotic potential, and turgor potential as function of time of day at the root temperature of 22°C and the indicated soil water potential on the third and fifth days after transplanting. The time is in hours and fraction of hours.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_l	π	ψ_p		ψ_l	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.03	6.85	-0.28	-1.23	0.95	6.82	-0.30	-1.18	0.88
	7.32	-0.20	-1.11	0.91	7.37	-0.59	-1.21	0.62
	7.72	-0.40	-1.11	0.71	7.87	-0.71	-1.28	0.57
	8.12	-0.46	-1.24	0.78	8.75	-0.60	-1.26	0.66
	8.73	-0.40	-1.15	0.75	10.20	-0.58	-1.29	0.71
	10.73	-0.51	-1.15	0.64	11.73	-0.67	-1.30	0.63
	12.23	-0.50	-1.26	0.76	13.18	-0.71	-1.29	0.58
	13.77	-0.50	-1.17	0.67	14.82	-0.87	-1.31	0.44
	15.33	-0.56	-1.31	0.75	15.05	-0.83	-1.29	0.46
	16.92	-0.65	-1.35	0.70	16.85	-0.68	-1.38	0.70
	18.88	-0.70	-1.38	0.68	18.90	-0.78	-1.41	0.63
	19.82	-0.52	-1.27	0.75	19.65	-0.70	-1.45	0.75
	20.72	-0.44	-1.43	0.99	20.72	-0.55	-1.45	0.90
	21.73	-0.20	-1.28	1.08	21.65	-0.27	-1.37	1.10
					23.48	-0.27	-1.11	0.84
					2.15	-	-1.04	
					3.93	-	-1.00	

Table B4. continued.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_1	π	ψ_p		ψ_1	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.06	6.95	-0.23	-1.14	0.91	6.93	-0.20	-1.29	1.09
	7.47	-0.38	-1.26	0.88	7.47	-0.40	-1.23	0.83
	7.85	-0.51	-1.08	0.57	7.98	-0.59	-1.17	0.58
	8.28	-0.58	-1.30	0.72	8.38	-0.73	-1.35	0.62
	8.93	-0.66	-1.27	0.61	8.90	-0.69	-1.32	0.63
	10.88	-0.65	-1.32	0.67	10.33	-0.68	-1.30	0.62
	12.37	-0.69	-1.21	0.52	11.85	-0.69	-1.32	0.63
	13.87	-0.79	-1.24	0.45	13.37	-0.73	-1.32	0.59
	15.50	-0.80	-1.22	0.42	14.98	-0.69	-1.26	0.57
	17.07	-0.75	-1.39	0.65	16.97	-0.72	-1.41	0.69
	19.55	-0.79	-1.40	0.61	19.02	-0.86	-1.49	0.63
	20.00	-0.77	-1.44	0.67	19.73	-0.59	-1.38	0.79
	20.83	-0.66	-1.46	0.80	20.83	-0.52	-1.52	1.00
	21.82	-0.24	-1.47	0.23	21.77	-0.34	-1.44	1.10
					23.55	-0.30	-1.09	0.79
					2.15	-	-1.01	-
					3.95	-	-1.01	-

Table B4. continued.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_1	π	ψ_p		ψ_1	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.10	6.90	-0.35	-1.32	0.97	6.62	-0.26	-1.16	0.90
	7.38	-0.29	-1.13	0.84	7.23	-0.24	-1.11	0.87
	7.78	-0.43	-1.19	0.76	7.70	-0.61	-1.13	0.52
	8.18	-0.65	-1.32	0.67	8.10	-0.75	-1.23	0.48
	8.85	-0.57	-1.20	0.63	8.62	-0.73	-1.26	0.53
	10.82	-0.71	-1.25	0.54	10.05	-0.78	-1.25	0.47
	12.28	-0.71	-1.38	0.67	11.60	-0.71	-1.22	0.51
	13.80	-0.72	-1.40	0.68	13.07	-0.75	-1.19	0.44
	15.40	-0.73	-1.44	0.71	14.70	-0.76	-1.19	0.43
	16.97	-0.78	-1.42	0.64	16.75	-0.82	-1.24	0.42
	18.97	-0.79	-1.47	0.68	18.73	-0.79	-1.35	0.56
	19.85	-0.61	-1.41	0.80	19.53	-0.64	-1.37	0.73
	20.77	-0.60	-1.41	0.81	20.62	-0.55	-1.31	0.76
	21.78	-0.22	-1.28	1.06	21.50	-0.40	-1.35	0.95
					23.65	-0.37	-1.04	0.67
					2.15	-	-1.00	-
					3.95	-	-1.02	-

Table B4. continued.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_l	π	ψ_p		ψ_l	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.17	6.73	-0.35	-1.17	0.82	6.75	-0.27	-1.25	0.98
	7.25	-0.41	-1.29	0.88	7.30	-0.37	-1.22	0.85
	7.58	-0.49	-1.12	0.63	7.75	-0.68	-1.18	0.50
	7.97	-0.53	-1.24	0.71	8.17	-0.84	-1.28	0.44
	8.58	-0.69	-1.25	0.56	8.68	-0.85	-1.29	0.44
	10.57	-0.70	-1.22	0.52	10.13	-0.82	-1.23	0.41
	12.12	-0.75	-1.19	0.44	11.67	-0.92	-1.31	0.39
	13.52	-0.75	-1.19	0.45	13.13	-1.00	-1.30	0.30
	15.18	-0.79	-1.35	0.56	14.77	-0.99	-1.32	0.33
	16.77	-0.75	-1.25	0.50	16.78	-0.97	-1.38	0.41
	18.75	-0.75	-1.31	0.56	18.82	-1.10	-1.44	0.34
	19.72	-0.65	-1.38	0.73	19.60	-0.96	-1.40	0.44
	20.58	-0.51	-1.34	0.83	20.67	-0.75	-1.47	0.72
	21.60	-0.35	-1.40	1.05	21.60	-0.45	-1.45	1.00
					23.70	-0.37	-1.04	0.67
					2.15	-	-1.02	-
					3.95	-	-1.03	-

Table B4. continued.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_l	π	ψ_p		ψ_l	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.25	6.78	-0.37	-1.14	0.77	6.87	-0.20	-1.21	1.01
	7.18	-0.45	-1.25	0.80	6.98	-0.35	-1.09	0.74
	7.65	-0.52	-1.26	0.74	7.43	-0.41	-1.22	0.81
	8.03	-0.61	-1.23	0.62	7.93	-0.86	-1.33	0.47
	8.65	-0.70	-1.29	0.59	8.30	-0.92	-1.33	0.41
	10.63	-0.73	-1.33	0.60	8.98	-0.87	-1.29	0.42
	12.17	-0.82	-1.24	0.42	10.27	-0.85	-1.40	0.55
	13.60	-0.81	-1.30	0.49	11.80	-0.97	-1.40	0.43
	15.27	-0.86	-1.29	0.43	13.27	-0.96	-1.33	0.37
	16.85	-0.90	-1.28	0.38	14.92	-1.05	-1.41	0.36
	18.82	-0.90	-1.43	0.53	16.92	-1.01	-1.41	0.40
	19.77	-0.85	-1.48	0.63	18.95	-1.13	-1.39	0.26
	20.52	-0.90	-1.42	0.52	19.68	-0.97	-1.56	0.59
	21.67	-0.40	-1.34	0.94	20.77	-0.77	-1.48	0.71
					21.71	-0.55	-1.36	0.81
					23.60	-0.48	-1.05	0.57
					2.15	-	-1.05	-
					3.95	-	-1.07	-

Table B5. The leaf water potential, osmotic potential and turgor potential as functions of time of day at the root temperature of 27°C and the indicated soil water potential on the third and fifth days after transplanting. The time is in hours and fraction of hours.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_l	π	ψ_p		ψ_l	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.03	6.80	-0.27	-1.21	0.94	6.85	-0.25	-1.10	0.85
	7.35	-0.29	-1.20	0.91	7.23	-0.39	-1.14	0.75
	7.77	-0.43	-1.17	0.74	7.73	-0.66	-1.17	0.51
	8.17	-0.54	-1.16	0.62	8.08	-0.68	-1.18	0.50
	8.60	-0.52	-1.11	0.59	8.55	-0.64	-1.27	0.63
	10.23	-0.55	-1.18	0.63	10.25	-0.60	-1.19	0.59
	10.55	-0.54	-1.24	0.70	12.28	-0.54	-1.23	0.69
	12.68	-0.56	-1.19	0.63	13.73	-0.58	-1.17	0.59
	14.35	-0.70	-1.22	0.52	15.15	-0.68	-1.29	0.61
	15.67	-0.62	-1.27	0.65	16.68	-0.71	-1.23	0.52
	17.32	-0.62	-1.27	0.65	19.30	-0.75	-1.26	0.51
	19.33	-0.66	-1.32	0.66	19.90	-0.76	-1.14	0.38
	20.38	-0.50	-1.33	0.83	20.62	-0.67	-1.31	0.64
	21.57	-0.33	-1.26	0.93	21.65	-0.30	-1.37	1.07
					23.30	-0.35	-1.28	0.93
					2.17	-0.25	-1.21	0.96
					4.27	-0.25	-1.18	0.93

Table B5. continued.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_l	π	ψ_p		ψ_l	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.06	6.85	-0.25	-1.09	0.84	6.90	-0.27	-1.09	0.82
	7.40	-0.41	-1.11	0.70	7.32	-0.40	-1.09	0.69
	7.85	-0.57	-1.12	0.55	7.80	-0.60	-1.16	0.56
	8.23	-0.58	-1.14	0.56	8.13	-0.74	-1.16	0.42
	8.68	-0.55	-1.14	0.59	8.60	-0.63	-1.16	0.53
	10.30	-0.51	-1.17	0.66	10.33	-0.77	-1.09	0.32
	10.60	-0.55	-1.16	0.61	12.38	-0.80	-1.17	0.37
	12.73	-0.55	-1.18	0.63	13.78	-0.67	-1.14	0.47
	14.42	-0.69	-1.22	0.53	15.22	-0.85	-1.17	0.32
	15.72	-0.65	-1.30	0.65	16.75	-0.72	-1.17	0.45
	17.37	-0.70	-1.24	0.54	19.38	-0.75	-1.23	0.48
	19.45	-0.75	-1.31	0.56	19.95	-0.70	-1.28	0.58
	20.43	-0.47	-1.26	0.79	20.67	-0.40	-1.24	0.84
	21.73	-0.25	-1.23	0.98	21.68	-0.26	-1.17	0.91
					23.62	-0.31	-1.29	0.98
					2.32	-0.27	-1.20	0.93
					4.35	-0.26	-1.19	0.93

Table B5. continued.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_l	π	ψ_p		ψ_l	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.10	6.73	-0.25	-1.10	0.85	6.73	-0.26	-1.17	0.91
	7.30	-0.39	-1.07	0.68	7.48	-0.47	-1.07	0.60
	7.67	-0.45	-1.11	0.66	7.92	-0.67	-1.13	0.46
	8.10	-0.56	-1.13	0.57	8.32	-0.81	-1.22	0.41
	8.53	-0.63	-1.11	0.48	8.75	-0.69	-1.18	0.49
	10.17	-0.55	-1.13	0.58	10.18	-0.62	-1.18	0.56
	10.50	-0.58	-1.16	0.58	12.22	-0.69	-1.21	0.52
	12.60	-0.68	-1.19	0.51	13.67	-0.71	-1.16	0.45
	14.28	-0.66	-1.16	0.50	15.10	-0.84	-1.21	0.37
	15.60	-0.61	-1.22	0.61	16.63	-0.78	-1.24	0.46
	17.27	-0.77	-1.14	0.37	19.25	-0.74	-1.28	0.54
	19.22	-0.60	-1.27	0.67	19.80	-0.85	-1.38	0.53
	20.33	-0.73	-1.26	0.53	20.55	-1.00	-1.24	0.24
	21.60	-0.35	-1.20	0.85	21.52	-0.51	-1.30	0.79
					23.28	-0.31	-1.31	1.00
					2.13	-0.28	-1.11	0.83
					4.23	-0.27	-1.09	0.82

Table B5. continued.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_l	π	ψ_p		ψ_l	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.17	6.90	-0.28	-1.13	0.85	6.80	-0.28	-1.14	0.86
	7.50	-0.50	-1.13	0.63	7.53	-0.50	-1.19	0.69
	7.92	-0.61	-1.21	0.60	7.98	-0.81	-1.19	0.38
	8.30	-0.70	-1.17	0.47	8.38	-0.89	-1.20	0.31
	8.77	-0.65	-1.20	0.55	8.87	-0.75	-1.18	0.43
	10.35	-0.56	-1.16	0.60	10.52	-0.82	-1.18	0.36
	10.67	-0.71	-1.13	0.42	12.53	-0.87	-1.30	0.43
	12.80	-0.77	-1.21	0.44	13.93	-1.00	-1.31	0.31
	14.48	-0.70	-1.19	0.49	15.40	-0.99	-1.28	0.29
	15.78	-0.71	-1.22	0.51	16.90	-0.94	-1.33	0.39
	17.43	-0.85	-1.29	0.44	19.52	-0.85	-1.44	0.59
	19.52	-0.77	-1.21	0.44	20.00	-0.96	-1.37	0.41
	20.48	-0.66	-1.27	0.61	20.80	-0.70	-1.43	0.73
	21.72	-0.45	-1.31	0.86	21.60	-0.45	-1.34	0.89
					23.53	-0.31	-1.17	0.86
					2.22	-0.29	-1.10	0.81
					4.33	-0.28	-1.09	0.81

Table B5. continued.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_l	π	ψ_p		ψ_l	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.25	6.97	-0.36	-1.11	0.75	6.78	-0.40	-1.14	0.74
	7.57	-0.52	-1.18	0.66	7.42	-0.71	-1.17	0.46
	7.98	-0.79	-1.18	0.39	7.85	-0.80	-1.22	0.42
	8.38	-0.90	-1.14	0.24	8.25	-0.96	-1.24	0.28
	8.83	-0.81	-1.19	0.38	8.70	-1.13	-1.29	0.16
	10.42	-0.86	-1.22	0.36	10.58	-1.01	-1.24	0.23
	10.72	-0.88	-1.20	0.32	12.47	-0.99	-1.28	0.29
	12.85	-0.83	-1.31	0.48	13.87	-1.04	-1.27	0.23
	14.55	-0.82	-1.34	0.52	15.32	-1.05	-1.29	0.24
	15.83	-0.92	-1.23	0.31	16.82	-1.04	-1.32	0.28
	17.50	-1.00	-1.29	0.29	19.45	-1.02	-1.40	0.38
	19.58	-1.09	-1.36	0.27	19.98	-1.05	-1.37	0.32
	20.55	-0.84	-1.39	0.55	20.73	-0.87	-1.42	0.55
	21.77	-0.55	-1.24	0.69	21.75	-0.56	-1.30	0.74
					23.47	-0.50	-1.30	0.80
					2.18	-0.39	-1.26	0.87
					4.30	-0.38	-1.19	0.81

Table B6. The leaf water potential, osmotic potential, and turgor potential as functions of time of day at the root temperature of 32°C and the indicated soil water potential on the third and fifth days after transplanting. The time is in hours and fraction of hours.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_l	π	ψ_p		ψ_l	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.03	6.62	-0.23	-0.97	0.74	6.73	-0.18	-1.02	0.84
	7.22	-0.33	-1.02	0.69	7.30	-0.53	-1.03	0.50
	7.63	-0.51	-1.05	0.54	7.75	-0.85	-1.08	0.23
	8.13	-0.55	-1.06	0.51	8.22	-0.70	-1.08	0.38
	8.60	-0.54	-1.08	0.54	8.68	-0.79	-1.03	0.24
	10.20	-0.69	-1.13	0.44	10.60	-0.95	-1.15	0.20
	11.75	-0.61	-1.09	0.48	12.43	-0.73	-1.06	0.33
	13.13	-0.74	-1.09	0.35	13.40	-0.92	-1.13	0.21
	15.05	-0.78	-1.04	0.26	15.27	-0.90	-1.18	0.28
	16.18	-0.74	-1.14	0.40	16.67	-0.82	-1.10	0.28
	18.85	-0.66	-1.27	0.61	18.67	-0.81	-1.18	0.37
	19.48	-0.70	-1.28	0.58	19.58	-1.00	-1.24	0.24
	20.62	-0.43	-1.16	0.73	20.67	-0.71	-1.17	0.46
	21.57	-0.29	-1.21	0.92	21.62	-0.32	-1.16	0.84
					0.83	-0.39	-1.16	0.77

Table B6. continued.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_l	π	ψ_p		ψ_l	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.06	6.78	-0.25	-0.98	0.73	6.85	-0.38	-1.08	0.70
	7.35	-0.44	-1.04	0.60	7.42	-0.35	-1.00	0.65
	8.30	-0.57	-1.04	0.47	7.90	-0.87	-1.09	0.22
	8.72	-0.63	-1.05	0.42	8.35	-0.90	-1.11	0.21
	10.37	-0.72	-1.10	0.38	8.82	-0.60	-1.16	0.56
	11.92	-0.78	-1.12	0.34	10.75	-0.89	-1.17	0.28
	13.25	-0.87	-1.18	0.31	12.57	-0.86	-1.14	0.28
	15.15	-0.84	-1.15	0.31	13.55	-0.95	-1.23	0.28
	16.30	-0.86	-1.17	0.31	15.40	-0.85	-1.16	0.31
	18.95	-0.84	-1.17	0.33	16.82	-0.86	-1.29	0.43
	19.60	-0.80	-1.21	0.41	18.80	-0.89	-1.36	0.47
	20.72	-0.71	-1.26	0.55	19.68	-0.85	-1.20	0.35
	20.83	-0.69	-1.22	0.53	20.78	-0.84	-1.13	0.29
	21.68	-0.35	-1.30	0.95	21.85	-1.14	-1.33	0.19
					0.58	-0.40	-1.04	0.64

Table B6. continued.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_l	π	ψ_p		ψ_l	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.10	6.52	-0.29	-0.99	0.70	6.90	-0.44	-1.06	0.62
	7.15	-0.42	-1.06	0.64	7.48	-0.70	-1.05	0.35
	7.57	-0.62	-1.04	0.42	7.98	-0.90	-1.12	0.22
	8.07	-0.78	-1.00	0.22	8.43	-0.92	-1.19	0.27
	8.50	-0.76	-1.09	0.33	8.88	-0.89	-1.09	0.20
	10.12	-0.73	-1.04	0.31	10.83	-0.90	-1.21	0.31
	11.67	-0.78	-1.11	0.33	12.65	-0.99	-1.29	0.30
	13.07	-0.89	-1.18	0.29	13.62	-0.93	-1.33	0.40
	14.98	-0.87	-1.11	0.24	15.48	-1.12	-1.47	0.35
	16.13	-0.91	-1.17	0.26	16.90	-0.94	-1.43	0.49
	18.78	-0.62	-1.25	0.63	18.87	-0.98	-1.61	0.63
	19.45	-0.91	-1.29	0.38	19.75	-0.99	-1.32	0.33
	20.58	-0.60	-1.23	0.63	20.85	-1.15	-1.25	0.10
	21.52	-0.35	-1.20	0.85	21.93	-0.95	-1.27	0.32
					0.92	-0.45	-1.06	0.61

Table B6. continued.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_l	π	ψ_p		ψ_l	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.17	6.87	-0.27	-0.94	0.67	6.97	-0.40	-1.18	0.78
	7.43	-0.50	-1.04	0.54	7.53	-0.59	-1.09	0.50
	7.90	-0.55	-1.05	0.50	8.07	-0.86	-1.23	0.37
	8.38	-0.61	-1.04	0.43	8.50	-0.85	-1.23	0.38
	8.78	-0.57	-1.07	0.50	8.97	-0.91	-1.23	0.32
	10.43	-0.83	-1.12	0.29	10.90	-0.84	-1.28	0.44
	11.98	-0.81	-1.10	0.29	12.72	-1.01	-1.28	0.27
	13.30	-0.79	-1.05	0.26	13.72	-1.01	-1.31	0.30
	15.20	-0.91	-1.13	0.22	15.55	-0.89	-1.34	0.45
	16.38	-0.94	-1.19	0.25	16.98	-1.15	-1.40	0.25
	19.02	-0.87	-1.28	0.41	18.95	-1.16	-1.42	0.26
	19.65	-0.96	-1.30	0.34	19.83	-1.09	-1.49	0.40
	20.78	-0.63	-1.26	0.63	20.90	-1.16	-1.39	0.23
	21.75	-0.39	-1.14	0.75	22.02	-0.87	-1.17	0.30
					0.67	-0.48	-1.04	0.56

Table B6. continued.

Soil water pot.	Time of day	Day 3			Time of day	Day 5		
		ψ_1	π	ψ_p		ψ_1	π	ψ_p
MPa		----- MPa -----				----- MPa -----		
-0.25	6.70	-0.34	-0.96	0.62	6.78	-0.30	-1.08	0.78
	7.28	-0.51	-1.03	0.52	7.37	-0.75	-1.20	0.45
	7.70	-0.54	-1.08	0.54	7.83	-0.95	-1.19	0.24
	8.22	-0.75	-1.08	0.33	8.28	-0.95	-1.21	0.26
	8.65	-0.67	-1.07	0.40	8.77	-0.94	-1.11	0.17
	10.28	-0.85	-1.14	0.29	10.67	-1.01	-1.21	0.20
	11.83	-0.84	-1.14	0.30	12.50	-1.09	-1.33	0.24
	13.20	-0.95	-1.11	0.16	13.48	-1.03	-1.21	0.18
	15.10	-1.03	-1.19	0.16	15.35	-0.94	-1.41	0.47
	16.25	-1.04	-1.22	0.18	16.77	-1.04	-1.41	0.37
	18.90	-1.08	-1.35	0.27	18.73	-1.08	-1.42	0.34
	19.55	-1.03	-1.24	0.21	19.65	-1.16	-1.44	0.28
	20.67	-0.75	-1.29	0.54	20.72	-1.16	-1.49	0.33
	21.63	-0.44	-1.18	0.74	21.77	-1.08	-1.23	0.15
					0.75	-0.65	-1.11	0.46