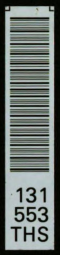

This is to certify that the

thesis entitled

THE EFFECT OF HIGH CROWN AND ROOT TEMPERATURE ON SHOOT AND ROOT GROWTH OF KENTUCKY BLUEGRASS (*Poa pratensis* L.)

presented by

Rafael Angel Yajure

has been accepted towards fulfillment
of the requirements for

Master degree in Crop Science

John E. Kaufmann

Major professor
Dr. John E. Kaufmann

Date April 7, 1980

THE EFFECT OF HIGH CROWN AND ROOT TEMPERATURE ON SHOOT AND ROOT GROWTH OF KENTUCKY BLUEGRASS (*POA PRATENSIS* L.)

by

Rafael A. Yajure

A THESIS

Submitted to
Michigan State University
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DEDICATION

This thesis is dedicated to my parents and those that built a family, Nicomedez, Agrispina, Equenio Lola, Rosa, Isabel, Isabel Maria, Juan, Claudia, Pausolina, Carmen. To those gone for ever. To those that I will never ignore, Juan, Jorge, Aristides, Antero and Santos. To my brothers.

Also I wish to dedicate this thesis to my friends Federico, Marcos and Catalina.

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INTRODUCTION

Temperature and water influence global distribution of plants. Within a region seasonal fluctuations of these environmental parameters often determine sites of adaptation. Grasses, such as Kentucky bluegrass, that are adapted to temperate areas are subjected to periods of drought, and to temperatures above the optimum for sustained growth during the summer season. Descriptive terms such as growth inhibition, growth stoppage, mid-summer depression of growth and dormancy have been used to describe the effects of high temperatures on turfgrass growth in experiments where water is supplied as needed.

Controversy has arisen in determining the site of temperature perception. A widely accepted hypothesis suggest roots rather than shoots are the perception organ. However, it has been long recognized that different parts of the plant may respond differently to temperature. Few experiments have been designed to study the effect of localized temperature on different plant parts. In these experiments growth responses to temperature have been limited to parameters related to leaf growth.

The objectives of this investigation were to determine (a) the site of heat stress perception of Merion Kentucky bluegrass, and (b) how growth of the whole plant including shoots, crowns, rhizomes and roots is affected by independently controlled leaf, crown

and root temperatures when light, water and nutrients are held constant.

The results obtained should assist in understanding whole plant growth responses of grasses grown under heat stress conditions.

LITERATURE REVIEW

Effect of temperature on shoot growth

The optimum temperature for maximum shoot growth does not necessarily mean the optimum temperature for maximum turfgrass quality. Cool season turngrasses such as Kentucky bluegrass (Poa pratensis L.) can sustain high levels of shoot growth under a wide range of temperatures (Brown, 1939; Harrison, 1934).

Optimum temperature for shoot growth of Kentucky bluegrass and other cool season grasses has been reported to be in the range of 60 (15.5 C) to 75 F (23.8 C) by Baker and Jung (1968), Brown (1943), Darrow (1939), and Harrison (1934). Optimum temperature ranges have been shown to be based on shoot growth rates over an extended period of time by Alberda (1957), McKell et al. (1969), and Watschke et al. (1972). These authors have reported that shoot growth decreases as temperature is increased or decreased from the optimum. However, for short time periods shoot growth has been found to be more rapid at slightly above optimum temperatures (Alberda, 1957).

Similar findings have been reported in other cool season grasses such as perennial ryegrass (Lolium perenee L.) by Mitchell (1955), Canada bluegrass (Poa compresa L.) by Hiesey (1953), creeping bentgrass (Agnostis palustris Huds.) by Duff (1967), and annual bluegrass (Poa annua L.) by Hiesey (1953).

Watschke et al (1972) evaluated ten Kentucky bluegrass cultivars grown for two weeks at 23 C day 15 C night after which temperature was changed to 35 C day 25 C night. All cultivars increased in foliar production during the first week at high temperature. However, the decrease in clipping yields were dramatic during the 2nd and 3rd weeks at high temperature. Only four of the six grasses with highest yields during the 4th week of high temperature also had the slightest decline in foliar growth at 35 to 25 C.

In another study Youngner and Nudge (1968) measured the growth of Merion, Fylking and Newport Kentucky bluegrass cultivars when influenced by temperature. The plants were grown at day-night temperature regimes of 27-21, 27-16; 18-12 and 16-7 C. Shoot dry matter production of Merion Kentucky bluegrass was greater than for the other two cultivars. Shoot growth was greatest at the warmer temperature and decreased with decreasing temperature. Sullivan and Sprague (1949) working with Perennial ryegrass found higher dry matter production of shoots when the day-night temperature was 21.1-15.6 C and the lowest at 32.2-26.7 C.

Robson (1973) worked with Tall fescue (Festuca arundinacea) subjected to a constant night temperature of 20 C while day temperature was varied from 10 to 30 C. Likewise, day temperature was held constant at 20 C while night temperatures were varied from 10 to 30 C thus maintaining a constant mean temperature of 20 C in five regimes, 30/10, 25/15, 20/20, 15/25 and 10/30 C. In this study leaf lamina length and area, sheath length, rate of leaf

growth, leaf area ratio, specific leaf area, leaf weight ratio, unit leaf rate, relative rate of leaf area and relative growth rate were found to achieve maximum values in the 25/25 C regime and were more affected by the day temperature than by that of the night temperature. He concludes that when the day temperature was optimal at 25 C, or slightly sub-optimal at 20 C, the optimum night temperature was one equal to that of the day. When the day temperature was markedly suboptimal at 10 or 15 C a higher night temperature favored growth. Only when the day temperature was supraoptimal (above the optimum) at 30 C was a lower night temperature beneficial. These results did not agree with the concept of thermoperiodicity or the response of plants to rhythmic fluctuations in temperature.

However, certain turfgrass species have been reported to exhibit a thermoperiodic response according to other authors previously cited, especially Brown (1939) and Hiesey (1953) when researching Kentucky bluegrass. The findings of McKell et al., (1969) and Watschke, Schmidt and Blaser (1970), also support the concept of thermoperiodicity of this specie.

Baker and Jung (1968) studied the effect of day (from 18.3 to 34.8 C in increasing 3.3 C intervals), and night temperatures (from 1.8 to 18.3 C in increasing 3.3 C intervals) on the dry weight of top growth of Kentucky bluegrass, orchardgrass (Dactylis glomerata L.) and bromegrass (Bromus inermes Leyess). Bluegrass appeared to be very sensitive to night temperatures when the day temperature was 18.3 C. When the day temperature was 21.6 or 24.9 C

more variations in yields were observed due to night temperatures. A night temperature of 8.4 C was reported to be more favorable for orchardgrass and bluegrass when the day temperature was 28.2 or 31.5 C. At the 34.8 C day temperature, none of the night temperatures appeared to favor top growth of bluegrass. This regime yielded the lowest top growth in all the species.

In general, growth of Kentucky bluegrass at 15 C is described as having profuse, long, succulent, bushy shoots while at 35 C as being short, less succulent, rigid with limited production of leaves and reduced bud initiation (Aldous, 1978; Darrow, 1939).

The effect of temperature on tillering

A tiller is a primary lateral shoot that arises intra or extra-vaginally from the stem base with unlimited elongation. More specifically a tiller forms from vegetative bud in the axil of leaf sheaths (Beard, 1973). Tillers are an important component of turf grass density.

Tillers have also been reported to have an optimum temperature range similar to that of the shoot (Alberda, 1957; Brown, 1943; Cooper, 1957; and McKell et al., 1969) or slightly lower than the optimum for shoot growth (Alberda, 1965; Duff, 1967). These authors have reported the number of tillers to be affected proportionally as temperature is increased or decreased from the optimum.

Peterson and Loomis (1948) exposed Kentucky bluegrass plants to 11, 15, and 19 hrs. of light and cool temperatures of 55.8 F(13.2 C) to 61.2 F (16.2), while warm temperatures were 65.4 F (18.6 C)

to 74.7 F (23.7 C). It was concluded that tiller number was affected more by photoperiod than by temperature. Slightly higher number of tillers were found at the 11 hr. light period and cool temperature regime. Tiller number appeared to be independent of temperature. A similar conclusion was reached by Baker and Jung (1968).

Mitchell (1953a) reported the quantity of light to be a chief factor determining tiller number in perennial ryegrass. The number of tillers were nearly quadrupled when light was raised from 700 fc to 2,000 fc (the lowest and highest light intensities used). However, the conclusion was that low light levels, high temperature (26.6 C) or both tend to inhibit bud development from the basal node. In a subsequent study the same author (1953b) stated that inhibition of lateral bud development was induced by either shade, reduction of photoperiod, high temperature or partial defoliation. Environmental conditions in the second study was similar to those in the first.

Using a broader range of temperatures (7.2 to 35 C), Mitchell (1956) determined in a later study that 18.3 to 21.1 C is the optimum range for total shoot growth of perennial ryegrass, cocksfoot (Dactylis glomerata L.) and browntop (Agrostis tenuis Sibth.). However, relatively little change in the growth rate of an individual tiller was noticed over the temperature range when compared to total shoot growth. The percentage increase per day in tiller number of perennial ryegrass peaked at 58 F (14.4 C) and the lowest percentage was found at 95 F (35 C).

Youngner and Nudge (1968) expressed the density of Merion Kentucky bluegrass as the number of tillers per pot and was found to be the highest at the highest temperature and decreased with decreasing temperature. The optimum temperature was found to be different among Merion, Fylking and Newport.

Robson (1973) found the duration of leaf growth of tall fescue (which determines the delay of a successor leaf) and the number of days between the appearance of successive leaves was reduced by raising either the day or the night temperature from 10 to 30 C. High temperature accelerated the leaf appearance rate. Because a tiller develops from the vegetative buds in the axil of the leaf sheath the appearance rate of tillers was also accelerated. However, raising day or night temperatures depressed the tiller number. All the plants used in this study were at the same stage of growth, and had three fully expanded leaves on the stem. The only difference was presence or absence of a tiller in the axil of the leaf. Robson (1973) concluded that if the plant had been compared by chronological, rather than physiological age, a greater rate of tillering at high temperature might have been expected rather than the reduced rate he found for older plants in a previous study (Robson, 1969).

Using radiactive labeled organic compounds, Williams (1964), Marshall and Sagar (1965), and Forde (1966) have traced the fate of assimilates in Phleum pratense L., Lolium multiflorum Lam., and perennial ryegrass, respectively. They were able to show that a fully developed tiller was independent of its parent and sister

tillers for carbohydrate supply. However, under adverse conditions (defoliation or darkening) ^{14}C- assimilates were imported from parts of the plant not affected by the treatment. It has also been reported by Fiveland, Erikson and Seely (1972) for Agropyron repens L. that assimilates were translocated along the rhizome only after defoliation of the main plant.

In an attempt to clarify the relationship between the tiller and the horizontal and erect rhizome, Nyahoza, Marshall and Sagar (1973) supplied $^{14}CO_2$ to the main shoot of Kentucky bluegrass plants and the distribution of ^{14}C assimilates was traced by autoradiography. It was found that although the primary tillers and rhizome tillers of the intact plant appeared to be physiologically independent, the entire tiller-rhizome system reintegrated after defoliation, allowing assimilate distribution.

Robson (1968) argued that when assimilates are in short supply, existing tillers are favored at the expense of new tillers. The same author in a later study (1973) found that perennial ryegrass tiller number was suppressed at high temperature (particularly between 20 and 30 C) and this effect was linked to the lowest content of water soluble carbohydrates (WSC) at those temperatures. However, whether or not WSC decrease with increasing temperatures is doubtful in the light of new findings in this research area (Brown and Blaser, 1970; Martin, 1972; and Duff and Beard, 1974 among others) which indicate an increase rather than a decrease of WSC with increasing temperatures.

The effect of temperature on rhizome and root growth

A rhizome is an extravaginal, secondary lateral shoot that elongates underground. In Kentucky bluegrass a rhizome arises from nodes at the base of the aboveground shoot and from nodes of older rhizomes (Beard, 1973).

Rhizomes and roots have been reported to have a similar optimum range of temperature for growth being about 5 to 10 C below that for shoots (Brown, 1939; Brown, 1943; Darrow, 1939; Harrison, 1934; Sprague, 1933; Stukey, 1941; and Youngner, 1961).

Evans and Ely (1935) determined that rhizome development can occur almsot at any time in the year as long as soil temperatures are above 32 F, and that maximum growth rates occur under long day lengths, high light intensity and lower levels of nitrogen. Rhizome growth is reduced by prolonged periods of drought and heat or low temperature stress (Brown, 1943; Etter, 1951; Hanson and Juska, 1961).

Moser, Anderson and Miller (1968) studied rhizome initiation and development of Merion and Windsor Kentucky bluegrass. The plants were exposed to 8, 12, 16 and 18 hr. photoperiods and constant temperatures of 0 to 2 C (cold treated) and 20 to 21 C (not cold treated). It was concluded that a cold treatment is not necessary for rhizome formation. Both initiation and elongation were favored by 16 or 18 hour photoperiod.

Rhizomes are important components of Kentucky bluegrass survival and density. It has been determined that following both winter

and summer dormancy, shoot regrowth is initiated from meristematic regions on rhizomes, and crown of shoots (Olmsted, 1942). Brown (1939) and Harrison (1934) determined that temperatures above 25 C stimulate the emergence of the growing point of Kentucky bluegrass rhizomes above the soil. When the tip of a rhizome is exposed to light or the lower CO_2 concentration of the atmosphere, horizontal growth is inhibited and the internodes adjacent to the tip turn upward. Chlorophyll is then formed in the leaf scales of the tip (Beard, 1973).

It has been previously documented that the optimum temperature range for root growth is 5 to 10 C below that for shoots. The range has been determined to be between 50 F (10 C) to 65 F (18.3 C) for species such as Kentucky bluegrass (Cooper and Calder, 1962; Youngner, 1961), perennial ryegrass (Mitchell, 1955), and creeping bentgrass (Beard and Daniel, 1965).

Youngner and Nudge (1976) found that a soil temperature of 27 C resulted in reduced root dry matter production and root length of Kentucky bluegrass compared to roots growing at 18 C soil temperature. At 32 C there appeared to be no live functioning roots although crowns and leaves were still alive. Defoliation enhanced high temperature suppression of both top and root growth.

Beard and Daniel (1965) found that the growth rate of individual roots and total root production of creeping bentgrass (Agrostis palustris Huds.) was reduced when the plants were exposed to 90 F (32.2 C). Cessation of growth of an individual root appeared to be more rapid as temperatures increased from 60 (15.5 C) to 90 F

(32.2 C). However the rate of root growth on a per day basis was similar in the 60 F (15.5 C) to 80 F (26.4 C) range. In another study the authors (Beard and Daniel, 1966) investigated creeping bentgrass grown in irrigated field conditions and found root temperatures at 6 in. (15 cm) depth highly correlated with root growth. The greatest variation in extremes of temperature occurred at 1 in. (2.54 cm) aboveground. Maximum temperatures of 110 F (43.3 C) were recorded at the soil surface in mid-August. No new root growth was observed from June to November except for two periods when the maximum daily temperature dropped sharply. It was suggested that lower temperatures either initiated root elongation or were required for elongation to occur.

In general, roots growing in the optimum range of temperature are described as white, fleshy, multibranched and thick (Beard and Daniel, 1965; Darrow, 1939; Stukey, 1942). These authors also described root growing at temperatures above the optimum as filamentous spindly, inactive and brown to dark brown in color.

Root distribution as affected by environmental stresses

Another feature of root growth under environmental stress is the ability of the root system to show a compensatory growth. If the growth of one part of the root system is reduced or inhibited, growth of other roots in more favorable conditions is frequently enhanced (Russel, 1977).

Temperature effects on compensatory growth of barley (Hordeum vulgare) roots was examined by Crossett et al. (1975). The root

system of barley plants was divided into two parts, with half of the root system maintained at all combinations of 20 C and 10 C. Air temperature was 15 C throughout and the nutrient supply was constant. The growth of one half of the root system maintained at 20 C (which is a more favorable temperature for root growth) was greater when the temperature of the other half was at 10 C and the growth of one half of the root system at 10 C was less when the temperature of the other half was at 20 C.

A similar compensatory growth capability of the root system has also been reported to occur due to uneven distribution of water in the soil layers, where a growth restriction in part of the root system may lead to increased growth of roots in a moist environment (Ellis et al., 1977; Klepper et al, 1973).

In the case of nutrients, the effects are more striking. Drew (1975) and Drew and Saker (1975), examined the effects of localized supply of phosphate, nitrate, ammonium and potassium on the growth of the seminal root system and the shoots of barley. When seminal roots (axes) were exposed to a localized high concentration of phosphate, initiation and extension of first and second laterals was greater than those receiving very low concentration of phosphate. This resulted in considerable modification of root form, with only a small loss in shoot growth compared with control plants receiving an ample nutrient supply to all parts of the root system. Similar responses were observed with nitrogen but not with potassium where a localized supply caused branching on all remaining parts.

Surface soil temperature effects on shoot and root growth

Evidence concerning the relative importance of soil and air temperatures within the Graminae is conflicting. Allmaras, Burrows and Larson (1964) concluded that root temperature was the main factor controlling shoot growth of corn (Zea mayz L.). Sato and Ito (1969) analyzed growth responses to air and soil temperatures of orchardgrass and perennial ryegrass. It was concluded from these studies that soil temperatures determined growth in terms of plant height, leaf emergence, tiller number, leaf area and dry matter production when the air temperature was either lower or higher than the optimum.

Recently Aldous and Kaufmann (1979) reported supra-optimal temperature to be perceived in the roots. Merion and Nugget Kentucky bluegrass were exposed to air temperatures increased from 22 to 38 in 4 C increments every 2 weeks. The effects of root zone temperature were compared in two conditions, where the root temperatures were controlled at 22 C (CRT) and non-controlled (NRT) where root temperature equilibrated with air temperatures. Though shoot dry matter production was reduced at high temperature (30 to 34 C) significantly higher yields were achieved at CRT when compared to the NRT in both cultivars.

On the other hand, Volden and Blackman (1973) found the relative growth rate, the rate of increase in leaf area, and the net assimilation rate of corn plants were positively dependent on both radiation and mean air temperature. In a recent study Younger and Nudge (1976) found little difference in shoot growth rate of Merion Kentucky

bluegrass at soil temperatures of 13, 18 and 27 C but root length was impaired at 27 C.

In early work Brown (1939) suggested soil temperatures near the surface, rather than air temperatures, were the major temperature regulator of growth. During the summer season temperate plants are exposed to extreme temperatures. Beard and Daniel (1966) reported maximum temperatures of 110 F (43.3 C) at the soil surface in mid-August, in a creeping bentgrass field.

The thermal microclimate of a perennial ryegrass sward was measured in order to study its relationship with crop growth (Peacock, 1975a). The sward was cut at 5 cm and 4 days later on a bright sunny day (May) and with a leaf area index of 0.3, it showed a maximum diurnal temperature of 34 C when measured at 2.5 cm above the soil surface. However, an uncut 55 cm sward, with a leaf index area of 5.6, showed maximum diurnal variation in air temperature at 30 cm where most radiation was intercepted. Daily mean temperature was found highly correlated to leaf extension.

The effect of localized temperatures on the stem apex (crown) of several crop plants has been reported. Schwarz (1972) studied the effect of temperature on tomato seedlings when the crown was exposed to 38 C (warm) and 7 C (cool) compared to control plant exposed to 25 C. The plants were grown in nutrient solution with temperature held constant at 18 C. Greenhouse day air temperatures varied from 22 C to 26 C and from 16 C to 20 C at night. The temperature of the crown of the plants was controlled by a stream of warm or

cool air. Cooling the root crown area to 7 C resulted in increased root weight while shoot weight was not markedly influenced during day time hours. When the crown area roots were exposed to high temperature (38 C) shoot growth was greatly reduced while root weight was only slightly influenced. However similar root crown temperatures (6 C and 35 C) during day and night hours resulted in decreased shoot and root weights. The author suggested that high temperature effects on crowns could reduce or alter translocation of water, nutrients, hormones and assimilates.

Watts (1972) investigated the independent effect of root, apical meristem and shoot temperature on the rate of leaf extension in corn (Zea mays L.) seedlings. In this case high temperature of the apical meristem was controlled with a heating collar placed around the crown of the plants. Low temperature was controlled by passing chilled water through the collar. Roots were grown in either nutrient solution or John Innes No. 1 compost and the temperature was controlled by a water bath.

When the temperature of the apical meristem and region of cell expansion at the base of the leaf was kept at 25 C, increases of leaf extension in response to changes of root and shoot temperature were less pronounced. When the temperature of the meristematic region was changed by increments of 5 or 10 C over a range from 0 to 40 C, and the root and shoot temperature were kept at 25 C, rapid increases in rate of leaf extension were recorded, but the rate declined rapidly between 35 and 40 C. It was concluded that the rate

of leaf extension were controlled at root-zone temperatures of 5 to 35 C by heating or cooling of the meristematic region.

Peacock (1975b) using a similar technique to those used by Watts (1972) exposed the crown region of perennial ryegrass seedlings from 2 to 40 C independent of the temperature to which the rest of the plant was subjected (5 or 15 C) in a growth room experiment. The lowest stem apex temperature (2 C) in the 5 C room was achieved by circulating ethylene glycol solution around the collar but it was not possible to maintain this low temperature in the 15 C room.

Results were presented in terms of a fitted by eye curve which showed the relationship between leaf extension and temperatures in the region of the stem apex. A maximum rate of leaf expansion of about 52 mm per day was achieved at 5 C air and at 28 C apical meristem temperatures. This maximum rate was also achieved at 15 C air and 32 C apical meristem temperatures.

The rate of leaf expansion dropped, although not significantly, from 52 mm to 42 mm when the apical meristem temperature was increased to a range between 34 to 38 C or both air temperatures. Nevertheless, the author concluded that the rate of leaf expansion was dependent on stem apex temperature rather than air temperature.

Peacock (1975b) designed a similar experiment in field condition using heating cables installed below the main rooting zone at a depth of 15 cm by which it was possible to raise the temperature at the soil surface by at least 5 C increments. Response curves of leaf extension plotted against mean temperature in both the control and heated plots showed a closer correspondence with

soil surface temperatures than 5 or 10 cm above the soil surface. This was the case when measurements were done for the spring and autumn season. During the summer period the rate of leaf expansion was affected by water stress even though the crop was irrigated, thus the data was not shown. However, even for the seasons where measurements could be done without confounding effects of water stress; air and soil temperature effects could not be separated.

In the investigation of Peacock (1975b) the effect of high root temperature at high or cool crown temperatures on the rate of leaf expansion or other growth parameters were not evaluated. The possibility that crown might have been dessicated at high crown temperature as a consequence of the technique used was not mentioned by Schwarz (1972). Crossette et al. (1975) found that hot dry air around stem bases of barley seedlings caused tissue dessication and this was related to decreased shoot growth.

On the other hand, the plant material used in other studies cited on the topic, either is not a temperate grass (Watts, 1972) or a Graminae (Schwarz, 1972). Thus, more investigation pertinent to cool season grass growth responses to localized temperatures and adaptation mechanism to heat stress was needed.

MATERIAL AND METHODS

Plant material establishment procedure

Mature sod pieces of Merion Kentucky bluegrass (Poa pratensis L.) were taken from the field and transferred into greenhouse flats. The flats were placed in the greenhouse under an automatic irrigation system. Irrigation was at a frequency of three times a day for three minutes each at equal time intervals. In addition, the plants received about 4 liters per flat of a modified nutrient solution (Hoagland's No. 1 solution) with a 2:1 potassium to nitrogen ratio (Appendix Table 1). The plants were clipped weekly to a height of 4.5 cm for 4 weeks.

After this acclimatation period to greenhouse conditions, the sod pieces were broken into tillers having equal number of leaves. the tillers were then placed in waxed cups 10 cm diameter and 8 cm deep, containing below a 50-50 mixture of silica sand 1 cm deep layer of vermiculite. Holes were punched in the bottom of the waxed cup to provide drainage.

The cups with the plants were then transferred to a growth chamber which was maintained at 22 C day 16 C night for another 4 weeks. The growth chamber was set on a 16 hr. photoperiod with

a photosynthetically active radiation (PAR) level of 1200 $mEm^{-2}sec^{-1}$ and total radiation of 40 Wm^{-2} from mercury and sodium lamps.[1]

The cups were rotated every day according to a predetermined randomized plan to avoid environmental variation that may have occurred in the chamber. Every day at the beginning of the photoperiod, each cup received 100 ml of the same modified nutrient solution plus 100 ml of tap water 6 hrs. after the photoperiod began, and again 3 hrs. before it ended. The tillers were considered established when new tillers developed from the parent plants which occurred at the end of the third week. The plants were again clipped and kept under this management until a tiller was placed under temperature treatment.

Method for Temperature Treatment of Plants

A system was developed in order to control leaf, crown and root temperature independently from each other.

Leaf temperature control

Leaf temperature was provided by a walk-in environmental growth chamber maintained at 22 C day, 16 C night and a photoperiod of 16 hrs. Light source was from fluorescent tubes and heavy duty incandescent bulbs. Light was measured with a Lambda Li-170 Quantum/Radiometer/Photometer at the turf canopy height. PAR was measured at 1200 $mEm^{-2}sec^{-1}$ and 40 Wm^{-2} at the middle point of the growth chamber. The temperature of the air surrounding the leaves and in

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[1]SunBrella Bench lighting fixture. Environmental Growth Chambers. Chagrin Falls, Ohio.

the turf canopy was measured with a thermometer placed both above and in the canopy at the base of the emerging shoot from the insulating chamber of the crowns. These temperatures were consistent with growth chamber air temperature, except where the crown was exposed to a higher temperature than the leaves. In this case the temperature in the turf canopy was one degree centigrade higher.

Crowns temperature control chambers

A total of 16 chambers for crown temperature control (CTCC) were made each from two "U" shaped plexiglass boxes, encased internally and externally with closed cell Nalgene foam [2], which provided thermal insulation from surroundings. An illustration of the characteristics and dimensions for one of these chambers is shown in Figure 1.

Two copper pipes were glued to the bottom of the "U" shaped plexiglass boxes, through which temperature controlled water was circulated by a pump. The copper pipes were connected by their inlets and outlets to the respective cool or hot water manifold and drainage pipes with tygon tubing.

The CTCC were arranged 8 on top of each styrofoam ice chest that was the mist media environment for root growth. Each CTCC was used as a replicate for a treatment, thus each chest held two treatments each with four replicates.

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[2]Nalgene clean sheets, white cross-linked polyethylene foam, 12 in wide 1/8 in thick from Nalge Sybrom Corporation. Rochester, N. Y. 14602.

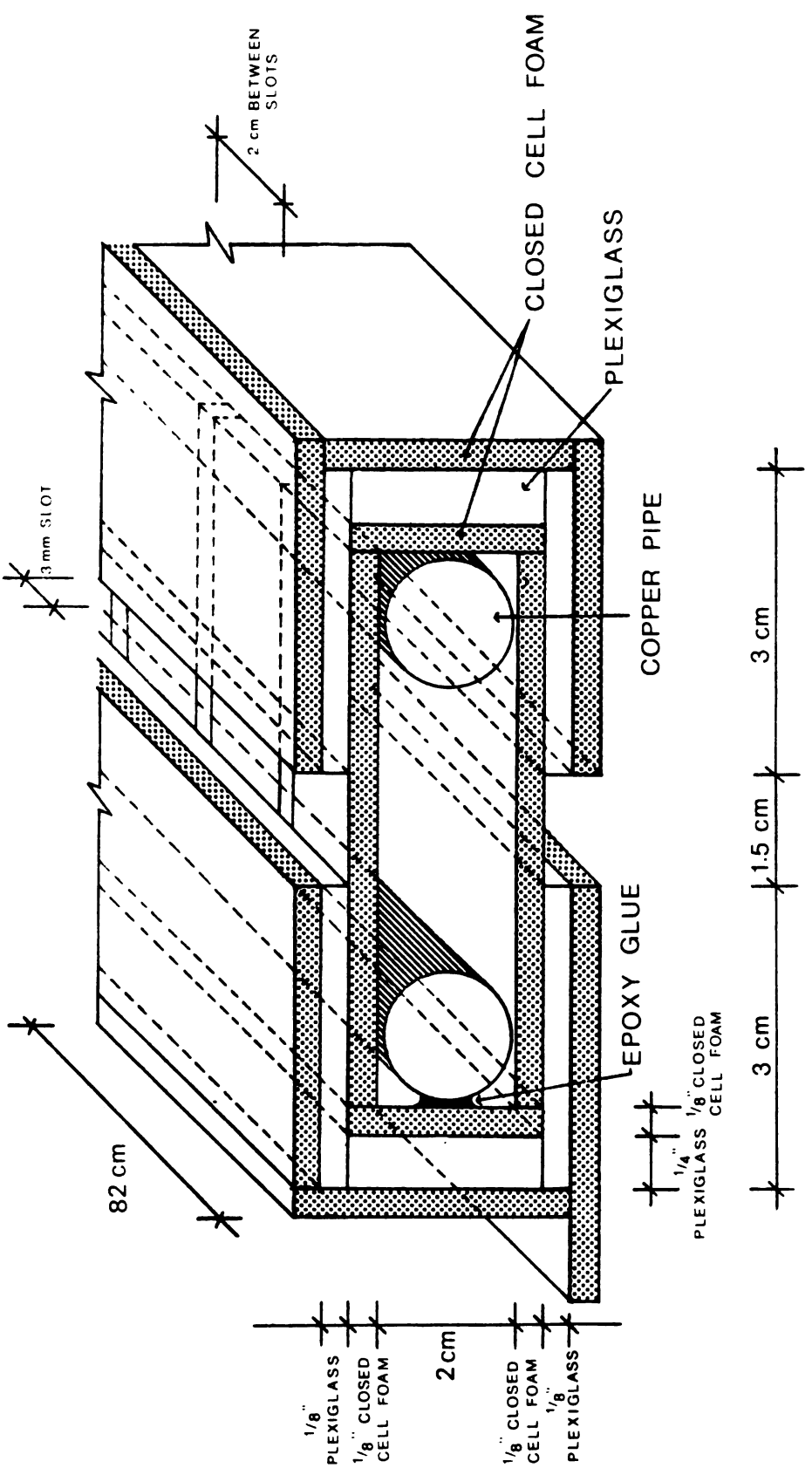

Figure 1.--Crown temperature control chamber (CTCC) Diagram and dimensions of the chamber.

A total of 32 slots were cut with a razor blade in the closed cell foam of each CTCC. These slots were 3 mm wide, at a 2 cm spacing and 8 cm from the ends of the chamber. One tiller was inserted in each of the slots and held in place in a bed of vermiculite inside the CTCC (Figure 2). The vermiculite moistened by the mist coming from the root environment provided a media resembling that of natural thatch conditions where rhizomes and roots often develop.

Crown temperatures were monitored by inserting mercury thermometers in the inlets, outlets and the space between the copper pipes that was filled with vermiculite. A gradient of ± 1 C was detected between the ends of each CTCC. Thus water circulating at 22 C or 34 C during the day in the temperature controlled water baths was actually one degree centigrade higher or lower, respectively in the CTCC. This depended on the root media temperature on which the CTCC was placed on top.

Root temperature control

Two styrofoam ice chest boxes 43 cm wide x 73 cm long x 34 cm high were cut along one of the longitudinal axes. The excised walls of each box were then taken apart and the remaining three-sided edge of each box glued to the other with silicone sealant glue. It resulted in a single box with internal dimensions 64 cm wide x 71 cm long x 34 high (Figure 3). Two of these boxes were built to enclose either one of the cool or hot root temperature environments. A hole was made at one of the corners in the bottom of each box to provide drainage.

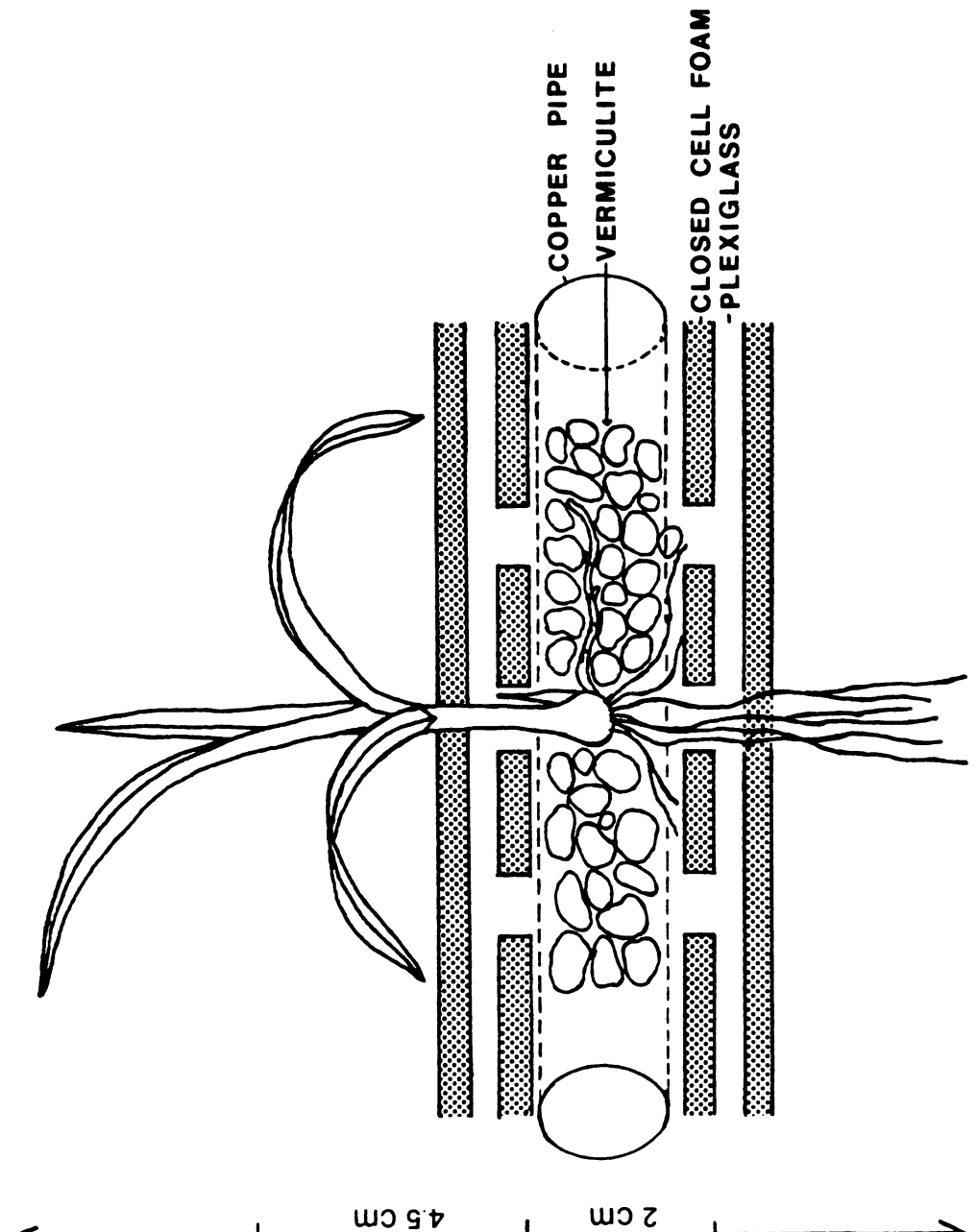

Figure 2.--Tiller placement in the crown temperature control chamber and harvesting dimensions for different plant components.

Figure 3.--Illustration of the system designed to independently control crown and root temperatures of Kentucky bluegrass.

DEVICE FOR CROWN TEMPERATURE CONTROL
To copper pipes (3/8" ID)
COPPER CAP
PLASTIC CONNECTORS
on top of styrofoam box
Copper manifold (1 1/4" ID)
COPPER "T" 1 1/4" ID WITH 3/8" ID REDUCTION END
MOTOR
WOOD SUPPORT
SHAFT
inlet
outlet
SPITNHER
COPPER COIL
To pumps
WATER BATH
HOT WATER CONTAINER
To copper coil inlet
To hot water manifold
To cool water manifold
1 1/4" ID
PUMPS
WOOD SUPPORT
COOL WATER CONTAINER
Nutrient solution drainage hole
PVC Drainage pipe (1 1/4" ID)
To hot or cool water container
COOLING UNIT

At the bottom of each box, a 3/8 in internal diameter (I.D.) copper coil was placed, through which water circulated for temperature control of the nutrient solution, mist and roots. Root temperature was monitored by inserting mercury thermometers at different depths in boxes. The copper coil provided for constant temperature for both the nutrient solution and the mist.

Nutrient Solution Misting System

The system was similar to that used by Zobel, Tredici and Torrey (1976). A 9 cm wide x 78 cm long x 2 cm thick wood support was placed about 1 cm from the top of each box, and holding a fractional horsepower motor[3] with 1.4 Hp, 3450 rpm, 0.6 amp and 115 volts. A stainless steel shaft 25 cm long with 1.3 cm outside diameter (O.D.) at one end was made and attached to the motor shafts. At the smaller diameter end of the shaft a plastic spinner[4] was attached with epoxy glue. The top of the spinner was immersed 2 cm into the nutrient solution at all times. The spinner was placed at the middle of each box to provide for even distribution of the mist. It was necessary to use an aspirator in order to obtain desirable distribution in the upper center portion of the root chamber. The aspirator was also used to keep the roots moist when the nutrient solution was exchanged. For this the aspirator inlet tube was withdrawn from the nutrient solution and immersed into a 50 ml beaker containing fresh nutrient solution.

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[3]Howard Electric Company, 4801 Bellevue, Detroit, MI 48207.

[4]Northern Electric Co., P.O. Box 469, Waynesboro, Miss. 39367.

Cool and Hot Water Circulation System

Each of 2 manifolds were built with a 1-1/4 in. internal diameter (I.D.), 80 cm long copper pipe caped at one end. A 3/8 in. (I.D.) reduction "T" at the other end provided the outlet to the copper coil in each mist box. The other inlet of the "T" was connected to the respective pump for cool or hot water by a 1-1/4 in. I.D. hose.

All along the 80 cm long copper pipe, pairs of holes were made 1/4 in. diameter, 4 cm apart from each other and 8 cm away from the next pair of holes. A 3 cm long 1/4 in. (O.D.) copper tube was soldered in each hole. All other junctions were prepared in the same manner. Each pair of these manifold outlets were connected to the corresponding CTCC with tygon tubing and plastic connectors. Laboratory clamps on the tubing allowed for withdrawing of any CTCC at any time from the system. All copper pipes and hoses were insulated with flexible foam rubber-like insulation pipes 1-1/2 in. (I.D.) to reduce heat exchange.

Source of cool and hot water

A cooling unit[5] and a water bath[6] were placed on the floor of the growth chamber (Figure 3). The coil of the cooling unit was immersed in a 43 cm wide, 73 cm long and 34 cm high styrofoam ice chest which was used as the container for cool water. Holes were

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[5]Constant Flow Portable Cooling Unit with microtol controlling thermostat. Blue M Electric Company, Blue Island, Illinois 60406.

[6]Refrigerated shaker water bath. Model MSB-3222A-1. Blue M Electrical Company, Blue Island, Illinois 60406.

made in the lid of the ice chest for drainage hoses and the coil head. The container needed to be filled with water once only, throughout the investigation.

The cooling unit maintained a 20 C constant water temperature, which varied up to 22 C during the day and 18 C during the night.

The water bath unit temperature was adjusted to 34 C. A timer was set to automatically turn off the water bath during the 8 hr. night period. In this way, the water heated to 34 C during the day slowly dissipated its heat to a temperature of 24 C in about 6 hours.

The water at 20 C and 34 C was then circulated to the respective manifolds by two pumps.[7]

Growth Chamber Procedure

The plants were again broken into single tillers and the sand and vermiculite washed off the roots with water. The tillers were trimmed to five leaves and placed into a CTCC as shown in Figure 2. A total of 32 tillers were placed in each CTCC.

Sources of environmental variation were reduced by alternating cool and hot CTCC on top of the boxes. Thus, each treatment had at least one replicate adjacent to the spinner motor mount.

Additionally the 32 plants on each CTCC were divided into 4 sections of 8 plants. Only 2 sections chosen at random in each

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[7]Teel Laundry Tray Pump. Dayton Electric Mfg. Co., 5959 W. Howard St., Chicago, Illinois 60648.

device constituted the experimental unit on which dry weights and innovation number were measured. The remaining 16 plants were used for leaf extension measurements.

After one week of acclimation the plants were clipped again and the temperature regimes imposed. The dry weight of the clippings was statistically analyzed and no significant differences in growth were detected.

The four crown-root temperature regimes were 22-22 C day and 18-18 C night, 22-34 C day 18-24 C night, 34-22 D day 24-18 C night and 34-34 C day 24-24 C night. The treatments were imposed for a 5 week period. Only day temperature is given in the data tables and figures.

Growth Response Measurements

Growth responses to the crown and root temperature regimes were determined by measuring dry weight of clippings, stubble, crowns, crown-region roots, rhizomes, rooting chamber roots and the total dry weight of the plant. By relating the dry weight of the roots to that of the shoots, root/shoot ratios were calculated. From a subsample of four plants drawn from each replicate, the number of crown-tillers, rhizome-tillers, and rhizomes were recorded. The rate of leaf extension was also measured.

Clippings above 4.5 cm were harvested weekly at the beginning of the photoperiod. The clippings were placed in labeled paper bags, dried in a forced-air oven at 80 C for 24 hours and the weights recorded after the tissue cooled in a dessicator. Total accumulated

dry weight of clippings was calculated by adding the weekly yields of clippings. The time between harvest of clippings and drying did not exceed one hour. After the fifth weekly harvest of clippings, the CTCC's were removed from the growth chamber, placed into double plastic bags and transferred to the laboratory.

Roots growing in the rooting chamber were cut from the rest of the plant with a razor blade at the lower side of the insulating chamber for crowns (see Figure 2). The excised roots of the 16 plants were then cut in 5 cm sections to determine distribution with depth. Since roots in the high mist chamber root temperature did not extend longer than 35 cm, comparisons were done up to this depth. In treatments where roots extended longer than 35 cm, the dry weight of remaining sections were added and recorded as depth greater than 35 cm.

Stubble consisted of material above the CTCC including stems, leaf sheaths, new and old leaves and tillers (see Figure 2).

The dry weight of material growing in the CTCC was determined after the number of tillers were counted. The crown was considered to be stem bases and 2 or 3 mm of roots growing in the crown chamber. Total shoot dry weights were calculated by adding the dry weight of crowns and stubble components to the total accumulated dry weight of clippings.

Crown-region roots were roots that grew in the CTCC. The vermiculite was washed off from these roots and dry weight was determined. The dry weight of crown-region roots and rooting chamber roots were added to determine the total dry weight of the root system.

Rhizomes were considered to be extravaginal secondary shoots growing horizontally from the crown tissue. A rhizome with at least 2 young leaves was considered a rhizome-tiller. The rhizome-tiller weight was added to the rhizomes that had not developed into tillers to give the total rhizome dry weight.

Total dry weight of the plant was determined by adding the total dry weight of clippings accumulated during the 5 week period to the dry weight of all plant parts.

The number of rhizomes, rhizome-tillers and crown tillers was counted from a subsample of 4 plants per replicate. Crown-tillers were considered to be those visible tillers growing as extravaginal shoots developed from the meristematic tissues at the crown.

The total number of rhizomes was calculated by adding rhizome and rhizome-tiller numbers. The total number of tillers likewise, was the total of crown-tillers and rhizome tillers. The total number of innovations resulted from adding the total number of tillers to the number of rhizomes. After counting, each plant was added to the remaining 12 plants of each replicate for the determination of the dry weight of the different plant component previously described.

In order to analyze the relationship between roots and shoots two separate root/shoot ratios were calculated. One included both dry weight of crown-region and rooting chamber roots compared to the total shoot dry weight. In the second root/shoot ratio, crown-region roots were not included. Both ratios were calculated since

crown-region roots did not grow in direct contact with the nutrient solution mist, and in some cases were exposed to a different temperature regime than roots growing in the rooting chamber. Thus a significant contribution of crown-region roots to shoot growth, if any, could be detected by not including its weight into the total dry weight of roots.

The rate of leaf extension was measured daily on the youngest visible leaf not more than 15 mm long; from its tip to the ligule of the youngest fully expanded leaf which was used as a datum point. The data was recorded during the second and fourth week after temperature regimes were imposed.

Values stated in tables or shown in figures are the mean of four replications. Analysis of variance was used to detect significant differences and Duncan's Multiple Range test was used for mean separation.

RESULTS

The Effect of Crown and Root Temperature on Dry Weight Production

Clippings

The data in Figure 4 shows the effect of the temperature regimes on weekly clipping yield. Dry weight of clippings did not differ significantly at the different temperature regimes at the end of the first week (Figure 4a).

In the next two weeks clipping growth greatly increased in all treatments except at 34-34 C and significant differences were detected among temperature treatments (Figures 4b and 4c). At the end of the second week higher yields were found for plants with the crown exposed to the lower temperature (22-22 C and 22-34 C regimes). However, plants at high crown temperature but with cool root temperature (34-22 C regime) had statistically similar yields. The lowest yields were from those plants with both the crown and roots at the higher temperature (34-34 C regime).

During the third week the 22-34 C regime had the greatest yields but it did not differ significantly from the 22-22 C or 34-22 C regimes. The 34-34 C regime showed again the lowest yield and differed significantly only from the 22-34 C regime.

During the fourth week (Figure 4d) the data shows significantly higher clipping yields in the 22-22 C regime, and similarly

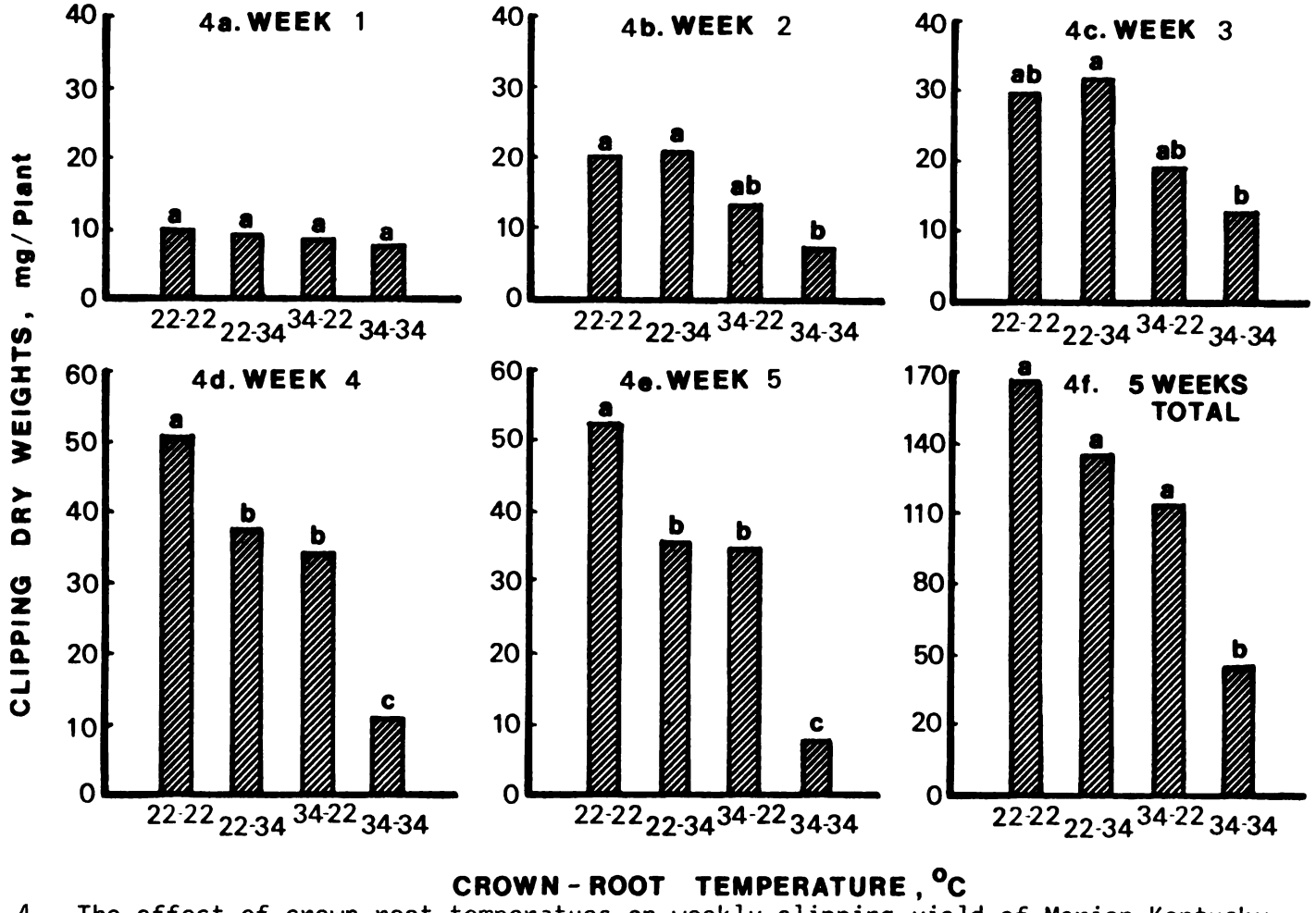

Figure 4.--The effect of crown-root temperatues on weekly clipping yield of Merion Kentucky bluegrass. Bars within the same week having common letters are not significantly different at the 5% level by Duncan's Multiple Range Test.

reduced yields when either crowns or roots were exposed to high temperature (34-22 C or 22-34 C regimes). Plants with both crowns and roots at high temperature had again the lowest yields and differed to all others. At the end of the fifth week (Figure 4e), the statistical pattern of clipping yields was identical to those from the previous week indicating shoot growth had stabilized.

The data in Table 1 and Figure 4f shows the total accumulated dry weight of clippings over the five week period. When either crowns or roots were exposed to the high temperature (34-22 C or 22-34 C) regimes, total accumulated dry weight of clippings did not differ significantly from each other or from plants having both crowns and roots at the cooler temperature (22-22 C regime). However, when both the crown and the roots were subjected to the high temperature (34-34 C regime) the total accumulated dry weight of clippings was significantly reduced.

Stubble and Crowns

Stubble dry weights did not differ significantly among all temperature regimes. Yields were almost identical except for those from the 34-34 C regime which had the lowest weight (Table 1). This regime seemed to have the higher proportion of dead to living leaf tissue, but this aspect was not measured in this study.

Crowns of plants exposed to the cooler temperature (22-22 C and 22-34 C regimes) had significantly higher dry weights than those crowns exposed to the higher temperature in the 34-22 C and 34-34 C regimes (Table 1). Thus, high crown temperatures appeared to exert a negative effect on crown development.

TABLE 1.--The effect of crown and root temperature on clipping, stubble, crown, rhizome and root dry weight of Merion Kentucky bluegrass grown in a 22C growth chamber for 5 weeks.

Temperature (C) Crown-Root	Dry Weight (mg/plant)						
	Clippings	Stubble	Crowns	Shoot Total	Rhizomes	Roots	Plant Total
22-22	165.6a*	214.8a	77.2a	457.6a	22.5a	229.7a	709.8a
22-34	134.7a	217.5a	83.7a	435.7a	19.0a	132.3b	587.2a
34-22	113.5a	215.5a	49.8b	378.8ab	6.8b	163.1b	548.7a
34-34	44.4b	178.6a	34.8b	257.8b	2.4b	52.9c	313.1b

* Means having common letters within the same column are not significantly different at the 5% level by Duncan's Multiple Range Test.

Total Shoot

Crowns at cool temperature yielded the highest shoot dry weights regardless of root temperature (Table 1). Reduced shoot weight occurred when crowns were exposed to a higher temperature than roots (34-22 C regime) although the reduction was not significant. Significantly lower shoot dry weights were found when both crowns and roots were at the high temperature (34-34 C regime). The latter and the 34-22 C regime however were found not significantly different.

Shoots of plants with their crowns exposed to the cooler temperature showed an upright growth habit, bearing leaves dark green in color and a vertical orientation. Shoots at the high crown and root temperatures showed a stunted growth habit. Their leaves were growing more horizontally than vertically and had a higher proportion of chlorotic leaves with a green-brown color and waxed appearance but still alive and functioning. Plants at the warm crown and cool root regime, had shoot with similar characteristics to those with cool crowns, although the amount of chlorotic leaves was apparently higher.

Rhizome and Total Root

High crown temperature greatly suppressed dry weight production of rhizomes. Plants with the crown exposed to the higher temperature, yielded statistically less rhizome dry weights than those with the crown at the cooler temperature regardless of the root temperature (Table 1). Rhizomes of plants growing at the high crown temperature appeared to be less thicker and shorter than those from plants at the cooler crown temperature.

Maximum total root dry weights were obtained where both crowns and roots were at the cooler temperature. The root dry weight yields from this regime were significantly higher than all others. When either the crown or the root were exposed to the higher temperature in the 22-34 C and 34-22 C regimes, yields did not differ significantly from one another. However, plants subjected to the 34-34 C crown and root temperature regime yielded a significantly lower dry weight (Table 1). An expanded description of root distribution with depth will be discussed later in Figure 5.

Total Dry Weight of the Plant

Plants at all temperature regimes yielded statistically equal total dry weights except the 34-34 C regime which had the lowest dry weights (Table 1). Plants growing with both crowns and roots at cooler temperature (22-22 C) yielded about 55% more dry weight than those with both crowns and roots at the higher temperature (34-34 C regime), and about 21% more than those with either one of these plant parts at the high temperature (22-34 C and 34-22 C regimes).

Crown-region Root

The data in Figure 5 shows the dry weight of roots initiated in the crown region (2-0 cm) and root dry weight distribution by depth.

Initiation of new roots was significantly enhanced by the cooler crown temperature. Plants growing at the 22-22 C regime and those at the 22-34 C regimes had the highest crown-region root yields (Figures 5a and 5b). Crown-region roots for the 22-34 C regime treatment accounted for about 45% of its total root dry weight, while in

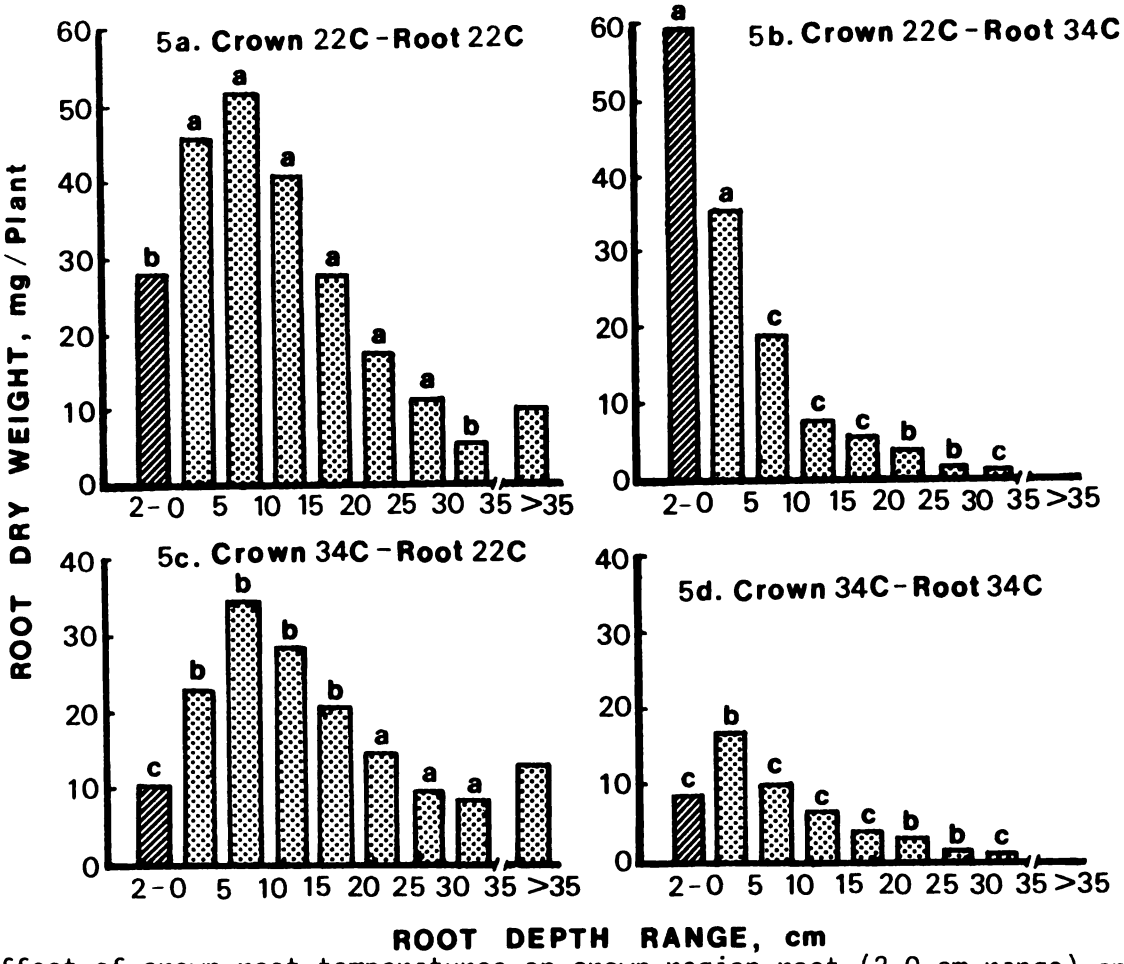

Figure 5.--The effect of crown-root temperatures on crown-region root (2-0 cm range) and rooting chamber root dry weights in Merion Kentucky bluegrass.
Bars within the same rooting depth range having common letter are not significantly different at the 5% level by Duncan's Multiple Range Test.

the 22-22 C regime these roots were 27% of the total dry weight of its root system. Crown-region roots of these two regimes were significantly different from one another and to the other regimes.

Significantly reduced root weight in the crown region was found in regimes involving high crown temperatures (34-22 C and 34-34 C). Crown-region roots accounted for only 17% of the total dry weight of roots in the 34-22 C regime and only 6% in the 34-34 C regime (Figures 5c and 5d).

Rooting Chamber Root Dry Weight

Most of the root dry weight was localized in the first 15 cm of depth. Plants growing at the 22-22 C, 22-34 C, 34-22 C and 34-34 C regimes had 58.8%, 45.5%, 52.4% and 67.1% of their roots at this depth respectively.

The data in Figures 5a to 5d shows the distribution by depth of rooting chamber root weights in 5 cm sections. For the first 5 cm of depth, significant differences in dry weights were found between plants growing at cool crown temperature and those at warm crown temperature regardless of root temperature. Cooler crown temperatures rather than cooler root temperature encouraged greater root dry weights at this depth.

In the 5 to 10 cm depth and all subsequent depths, cool root temperatures rather than cool crown temperatures resulted in higher root dry weights. Root branching was greatly enhanced at this depth by cool root temperature. When the dry weights of the 5 to 10 cm depth were analyzed, it was found that plants with roots growing at

the cooler root temperature (22-22 C and 34-22 C regimes) not only had significantly higher root dry weights than the other regimes, but also higher root weights from the previous 5 cm section (Figures 5a and 5c). Plants exposed at the higher root temperature (22-34 C and 34-34 C regimes) had reduced root dry weights at this depth when compared to the previous 5 cm section.

The distribution of dry weight of root in the remaining depths was related to root elongation from the nodal axes and branches. Root of plants at the high root temperature extended only to a depth of 30-35 cm, while root of plants growing at the cool root temperature extended to a 50-55 cm depth. The latter are shown in Figure 5 as greater than 35 cm.

Roots growing in the cool root environment were more numerous, thicker, multibranched, and exhibited profuse root hairs development. These roots also had a healthy pale white color. Roots growing in the warm environment, on the contrary, were filamentous with little branching and few root hairs. These roots exhibited a dark brown color and were apparently unfunctional.

Root/Shoot Ratios

The data in Table 2 shows the results of root/shoot (R/S) ratios. In one analysis crown-region roots and rooting chamber roots were combined. In the second analysis crown-region roots were omitted.

When crown-region roots were included significantly higher R/S ratios were found at the 22-22 C and 34-22 C regimes. A significantly reduced R/S ratio was found at the 34-34 C regime which was lower but did not differ significantly from the 22-34 C regime.

TABLE 2.--The effect of crown and root temperature on root/shoot ratios of Merion Kentucky bluegrass grown in a 22C growth chamber for 5 weeks.

Temperature (C) Crown-Root	Tissue Analyzed	
	With crown-region roots	Without crown-region roots
22-22	0.51a*	0.45a
22-34	0.30b	0.17b
34-22	0.43a	0.43a
34-34	0.21b	0.17b

*Means having common letters within the same column are not significantly different at the 5% level by Duncan's Multiple Range Test.

In the second analysis higher R/S ratios were obtained from plants growing at the cooler root temperature. Plants with roots at higher temperature had equally reduced R/S ratios.

The Effect of Crown and Root Temperature on Tiller, Rhizomes and Total Number of Innovations

Crown-tillers appeared to be more affected by a combination of both crown and root high temperatures than for any of those alone (Table 3). The highest number of crown-tillers resulted from plants with both the crown and the roots at the cooler temperature 22-22 C regime, but it did not differ from the number of crown-tillers produced by plants having either the crown or the root at the high temperature (22-34 C or 34-22 C regimes). However, about three more tillers per plant resulted when the roots were kept cooler than the crown (34-22 C regime) than when the crown was kept cooler than the roots (22-34 C regime).

Rhizome-tillers followed a similar pattern to crown-tillers. The highest number of rhizomes developing into tillers were found in the crown and root cooler temperature regime (22-22 C). Plants with either the crown or the root exposed at the high temperature did not differ significantly from each other (22-34 C and 34-22 C regimes). However, the 22-34 C regime differed significantly from the 22-22 C regime. The lowest number of rhizomes developing into tillers were again found in the 34-34 C regime. In other words, higher root temperature rather than higher crown temperature affected rhizome-tiller production. The total number of tillers also reflected

TABLE 3.--The effect of crown and root temperature on the number of innovations per plant of Merion Kentucky bluegrass grown in a 22C growth chamber for 5 weeks.

Temperature (C) Crown-Root	Number of Innovations per Plant					
	Crown Tillers	Rhizome Tillers	Total Tillers	Rhizomes	Total Rhizomes	Total Innovations
22-22	25.4a*	5.8a	31.2a	5.9a	11.7a	37.1a
22-34	19.7ab	3.1b	22.8bc	3.3b	6.4b	26.1b
34-22	22.1a	3.8ab	25.9ab	0.6c	4.4b	26.5b
34-34	15.4b	1.4c	16.8c	0.1c	1.5c	16.9c

*Means having common letters within the same column are not significantly different at the 5% level by Duncan's Multiple Range Test.

the trend observed in the previous categories. High root temperature rather than high crown temperature affected tiller production. Significantly higher total number of tillers were obtained from plant temperature regimes with the roots at the cooler root temperature (22-22 C and 34-22 C regimes) than at the high root temperature regimes (22-34 C and 34-34 C) regardless of crown temperatures. The 22-34 C regime did not differ significantly from the 34-34 C and 34-22 C regimes but it did differ from the 22-22 C regime.

The number of rhizomes appeared to be greatly reduced by high crown temperatures. Maximum number of rhizomes were obtained when the crown was kept cool (22-22 C and 22-34 C regimes) regardless of root temperatures. Crowns subjected to high temperature (34-22 C and 34-34 C regimes) essentially showed no rhizome development at the end of the fifth week. These differed significantly from all others.

The total number of rhizomes showed a distinct trend. Higher total number of rhizomes were found in regimes with the crown at the cooler temperature than in the regimes with the crown at the higher temperature (22-22 C and 22-34 C regimes versus 34-22 C and 34-34 C regimes respectively). However, the number at the 34-22 C regime was significatnly lower than that for the 22-22 C regime but not from the 22-34 C regime. The 34-34 C regime had the lowest total number of rhizomes and differed to all others.

The total number of innovations indicates the total number of tillers and rhizomes that developed from crowns. The 22-22 C regime had the highest number of innovations and differed significantly

to all other regimes. Plants with either crowns and roots at high temperature showed reduced number of innovations when compared to the 22-22 C regime. Plants with both crowns and roots at high temperature had a greater reduction of innovations and differed significantly from all other treatments.

The Effect of Crown and Root Temperature on Leaf Extension Rate

The data in Table 4 shows the results for rate of leaf extension. During the second week, a significantly higher rate of leaf extension was found in plants growing at the cool crown temperature (22-22 C and 22-34 C) regimes than those at high crown temperature (34-22 C and 34-34 C regimes).

During the fourth week only those plants at the 22-22 C regime had a significantly high rate of leaf extension. Plants with either crowns or roots at high temperature had equally reduced rate of leaf extension. Plants with both crowns and roots at high temperature (34-34 C regime) had the lowest rate and differed from all others.

TABLE 4.--The effect of crown and root temperature on leaf extension rate of Merion Kentucky bluegrass growth in a 22C growth chamber for 5 weeks.

Temperature (C) Crown-Root	Leaf Extension Rate (mm/day) During Week 2	During Week 4
22-22	6.8a*	7.0a
22-34	7.1a	6.1b
34-22	5.7b	5.6b
34-34	5.6b	3.3c

*Means having common letters within the same column are not significantly different at the 5% level by Duncan's Multiple Range Test.

DISCUSSION

Shoots of Merion Kentucky bluegrass were maintained at day-night temperatures consistent with its optimum range for growth (22-16 C). The temperature of crowns and roots were independently controlled near the optimum (20°-18 C) or above the optimum (34-24 C) range for growth giving 4 crown-root temperature combinations.

In experiments cited in the literature, where root temperature has been controlled separate from air temperature, it has usually been concluded that the 'root' is the primary perception organ of heat stress resulting in reduced shoot growth. In most of these investigations the experimental conditions were such that the whole 'root' system (including crowns) was exposed to the same high or low temperature. In this investigation crown temperatures were controlled separately from root temperature, and at no time did a moisture or nutrient deficiency occur.

When the dry matter production of the shoot system was analyzed (Table 1, shoot total) a significant reduction in shoot dry weight was found only when both crowns and roots were exposed to high temperature (34° C). A reduced shoot weight was found in plants at the high crown and cool root temperature regime (34-22 C) but it did not differ significantly from those at cool crown temperature (22-22 C and 22-34 C regimes). This would suggest a combination of both high crown and root temperature was required to

promote shoot growth reduction. However, the fact that the highest shoot dry weight in a per plant basis was obtained from plants with cooler crowns regardless of root temperature, suggested that the meristematic tissue of the shoot apex is the site of heat stress perception.

This conclusion is also supported by the results obtained from the analysis of weekly dry weight production of clippings (Figures 4a to 4e), clippings total accumulated (Figure 4f and Table 1) and crown dry weight (Table 1). The results from the crown-region roots (Figures 5a to 5d) and rate of leaf extension analysis (Table 4) also support this conclusion.

A large increase in clipping yields was found for all treatments during the initial three weeks, although lower yields were detected at high crown or high root temperature. Alberda (1957) found this same rapid increase in growth and suggested it may be due to plant adaptation to high root temperature for short periods of time.

As yields stabilized during the remaining two weeks, only those plants with both crowns and roots exposed to cool temperature (22 C) had significantly higher clippings yield. Plants with both crowns and roots at high temperature (34 C) had significantly reduced yield of clippings, but when either one of these tissues were exposed to that temperature (Figures 4d and 4e) the reduction was less. This would suggest again a combination of both high crown and root temperature to promote reduced clippings yield. However, a similar reasoning to that for shoots leads to the conclusion that the shoot apex is the site of heat stress perception. The total production

of clippings (Figure 4f and Table 1) also showed higher yields from plants with crowns exposed to cool temperature regardless of root temperature. The results from the analysis of crowns dry weight also confirm the conclusion in reference. A significantly higher crown dry weight was found where crowns were cooler than roots (Table 1).

The results from the crown-region roots evaluation (Figures 5a to 5d) not only supported that conclusion but also showed reduced initiation of new roots when the crown was exposed to high temperature. Thus, root initiation appeared to be enhanced at cool crown temperature. The literature reviewed on this topic (Brown, 1939; Beard and Daniel, 1966) gave no conclusive proof for this. Throughton (1965) found that differences in the relative growth rate of the root was due to variations in the size of individual roots rather than to differences in root number. In this investigation root initiation was determined by dry weight of roots growing in the crown region rather than by root number.

The fact that the stubble component (Table 1) did not differ significantly among all temperature regimes, also suggested that the differences found in clipping yields could be due to a reduction in leaf growth. Peacock (1972) in perennial ryegrass and Watts (1973) in corn, found a reduced rate of leaf extension at high crown temperature in growth chamber experiments where crown temperature was controlled distinctly from air and root temperatures.

Actually, the rate of leaf extension (Table 4) followed the same pattern showed by clippings in both periods of adaptation to

high temperature (second week) and stabilization of dry weight yields (fourth week) under heat stress. During the second week cooler crowns than roots seemed to control leaf extension rate. However, at the fourth week only plants with both crowns and roots exposed to the cool temperature (22-22 C regime) had a significantly higher rate of leaf extension. The opposite was true for the 34-34 C regime. Plants with either crowns or roots at high temperature (34 C) had equally reduced rate of leaf extension. If an equally reduced rate had been found between the 34-34 C and 22-34 C regimes the conclusion would have been that root temperature controlled the rate of leaf extension. But the latter instead had a significantly higher rate than that at the 34-34 C regime. Thus, cool crown temperature rather than cool or high root temperature appeared to be controlling the rate of leaf extension.

These results while showing the shoot apex (crowns) is the site of heat stress perception also support those of Peacock (1972) in perennial ryegrass for the site of temperature perception. The basic difference is that Peacock's work included both cool and high crown temperature at cool root temperature but not at high root temperature. Thus, a site of heat stress perception (rather than the generalized concept of a site of temperature perception) was not clearly elucidated in his investigation.

The term growth has been applied to quantitative changes occurring during development and it may be defined as an irreversible change in the size of a cell, organ or whole organism. Size in this context refers to as a dimension, volume, weight or all of them.

Troughton (1963) using nondestructive methods (determination of the volume of shoots or single tillers and roots by water displacement instead of weights) and allometric relationships between the growth of shoots and roots grown in optimum conditions, determined that there was a direct relationship between tiller number and number of leaves. Latter, the author (1965) using the same technique found that the relative growth rate of the shoot system depends on the growth of its components, the tiller number and their size. It was also mentioned in the literature cited that a fully developed tiller (an aerial shoot plus roots) is physiologically independent from parent and sister tillers but that under defoliation stress the whole system (tillers and rhizome-tillers) reintegrated (Nyahoza, Marshall and Sagar, 1975).

On these basis and in connection with this investigation, tillers (crown-tiller, rhizome-tiller or both) can be seen as the primary source of dry weight production for the shoot system. But it still remains to be determined what caused the reduced shoot growth at high crown temperature.

When the total number of tillers was analyzed (Table 3) it was found that tiller number appeared to be affected by high root temperature rather than by high crown temperature. The same was true for its components, crown-tillers and rhizome-tiller. However, from the analysis of dry weight of clippings, crowns and rate of leaf extension it was concluded that high crown temperature caused reduction in the dry weight or rate of these components. The stubble component

showed weight reduction only when both crowns and roots were exposed to high temperature.

Thus it appears likely that differences in total shoot growth found at high crown temperature (Table 1) were due primarily to reduced tiller size and secondarily to the reduction in tiller number. If a lower number of crown-tillers, rhizome-tillers or both had been found in the 34-22 C regime rather than the 22-34 C regime (Table 3), a higher dry weight of crowns would have been expected for the 34-22 C regime. But the latter instead showed significantly lower crown dry weight. The reduction in total shoot growth found in the 34-34 C regime resulted from a reduction in both tiller size (weight plus rate of leaf extension) and number. The 22-22 C regime, a better condition for shoot growth, exhibited the greatest shoot growth. The reasoning also agrees with the established conclusion that the meristematic tissue localized at the crown is the site of heat stress perception.

Beard (1973) and Harrison (1934) have reported that temperatures above 25 C stimulate emergence of the growing point of Kentucky bluegrass above the soil. A comparison of the total number of rhizomes, rhizome-tillers and rhizomes in Table 3 support that concept. High temperature in the crowns stimulated rhizome buds to turn up and once exposed to light, leaf development was promoted by light induced chlorophyll formation. This would explain why there was no apparent rhizome development in both treatments involving high crown temperature. As a rhizome developed from a secondary bud at

the crown it partially developed during the acclimation period and once exposed to high temperature, it converted into a rhizome-tiller. This would also explain why the dry weight of rhizomes (Table 1) was found reduced at high crown temperature.

The fact that a higher rhizome-tiller number was found in the 34-22 C regime than the 34-34 C regime suggested a combination between high root temperatures and a key factor from the roots affecting rhizome development. The same would hold for the number of crown-tillers (Table 3) since the 34-22 C regime had a significantly higher number of crown-tillers than the 34-34 C regime.

The data shown in Table 2 when summarized under the total number of innovations resulted in an overview of the picture previously presented. If the data had been analyzed only under this category, the different potentialities of the plant detected by partitioning of its components would have been obscured.

It has been mentioned before that the number of crown tillers and rhizome-tillers appeared to be reduced by high root temperature rather than high crown temperature. It was suggested a combination between root temperature and some key factor from the roots. Repression of inhibition of bud development has been shown to be controlled by endogenous growth regulators. Early work by Leopold (1949) suggested that auxins may play a role in tiller development and tiller initiation.

Recently Aldous (1978) using hypobaric ventilation (which reduced ethylene and other gases to subnormal levels) concluded that

bud growth may be influenced by kinetin stimulated ethylene production. A common feature of these growth regulators is the release of axillary buds from apical dominance.

On the other hand, Yeh, Matches and Larson (1976) reported high temperature in the field and growth chamber (31/17 C) favored the accumulation of endogenous auxin in stem bases of Tall fescue. This was related to the inhibition of tiller initiation in early summer. It has been shown in this study that a higher number of tillers were found at high crown and low root temperatures than the reverse. Thus bud development may in fact be controlled by temperature effects on root hormone levels to a greater extent than by crown temperature.

These partial results, however, do not fully explain the observed differences in growth when the plant is seen as a whole integrated with its parts (total dry weight of the plant, Table 1). Only those plants with both crowns and roots at high temperature showed significantly reduced total plant dry weight. Thus, a comprehensive view to the overall growth of the plant is a necessity.

The compensatory growth mechanism exhibited by the root system would explain these results. When the root system was separated into crown-region roots and rooting chamber roots this mechanism was evident. Where high temperature impaired root growth by reducing length and dry weight, root initiation and growth was promoted in the crown region where temperature was more favorable (Figure 5b).

This also explains why the total dry weight of roots in the 22-34 C and 34-22 C regimes were found to be not statistically different (Table 1).

Likewise, where high crown temperature suppressed initiation of roots (Figures 5c and 5d) in the crown region, roots growing in the cooler rooting chamber exhibited greater elongation and branching. This branching primarily compensated for the lack of new root initiation under these conditions which was evident when weight of roots at different layers were compared. Higher root dry weights were found at deeper layers (5 to 15 cm) than those nearby the crowns (0-5 cm). This suggests that branching of roots was the primary reason for continued shoot growth under high crown and low rooting chamber root temperature. In the more extreme condition where both crowns and roots were at high temperature, length and branching of roots was greatly affected. In this case, the compensatory effect did not operate and both shoot and root growth was significantly less (Table 1). Whether or not the higher number of rhizome-tillers (Table 3) found in the 34-22 C regime than in the 34-34 C regime was a compensatory response or rather a direct effect of high crown temperature was not clear.

Similar compensatory growth mechanism in response to temperature have been reported in the literature by Crossett et al., 1975 in barley (Hordeum vulgaie) and to water by Garwood and Williams (1967) in perennial ryegrass (Lolium perenne). A partial explanation for these compensatory responses has been found in 'source-sink' relationships. Unfavorable conditions in part of the plant

causes some 'sink' to be removed or reduced, with the supply of metabolites to those which remain being thereby increased.

The results from the analysis of root/shoot ratios (R/S) confirm the compensatory growth response (Table 2). This was particularly shown for the R/S ratio from the 22-34 C regime. This treatment showed greatly reduced rooting chamber root dry weights (Figure 5b) and yet had comparable shoot growth (Table 1 and Figures 4a to 4f) to the highest shoot dry matter producer treatment (22-22 C regime). The role of crown-region roots in supplying water and nutrients required for shoot growth was evident when these roots were not included in the second R/S ratio analysis. The result was equal R/S ratio to the 34-34 C regime, the lowest shoot dry matter producer treatment.

Although some exceptions have been reported (Troughton, 1960), it is generally recognized that the root/shoot ratio decreases with increasing temperature (Brown, 1939; Darrow, 1939; Sullivan and Sprague, 1949). Our results support this view since decreased root/shoot ratios were found when either crowns or the entire root system (including the crowns) were exposed to high temperature.

Thus, it can be hypothesized that a mechanism exists by which photosynthate and minerals are partitioned into those plant parts growing in a favorable environment in order to maintain a balanced functional economy for the entire plant. These results from the root/shoot ratio and other data in this thesis support this hypothesis. The cause(s) triggering this mechanism of course, remain unknown. One of the most important drawbacks is the fact that we are working

with weight ratios, whereas, what we are really concerned with are activity ratios. These can be elucidated only by analytical procedures. Thus, further research is needed in this area.

One last consideration must be made. In this investigation an approximate 2:1 potassium (K) to nitrogen (N) ratio was used. Normal fertilization practices recommend, instead, a 2:1 N to K ratio in field conditions for Kentucky bluegrass. This was done with the aim of prolonging growth of shoots in treatments where a high temperature on crowns and roots was expected to cause death of plants, and thus impairing the comparisons throughout the experimental period.

The basis for the change in the N to K balance lied in current research on the role of K in improving heat tolerance of turfgrass plants. Pellet and Roberts (1963) found that the combination of high K with high N resulted in increased resistance of Kentucky bluegrass to high temperature over that grown on high N and low K. Recently, Christians et al. (1979) reported more K (144 ppm) than N (125 ppm) was required for maximum shoot growth of Merion Kentucky bluegrass. The most desirable characteristics for Merion occurred at the N concentration of 96 ppm and phosphorous concentration of less than 2 ppm when K was 196 ppm. In that experiment temperature for shoot growth was held within the optimum range (22 C day 18 C night).

In this investigation, even though K was in a higher concentration than N, the latter was kept still high for normal fertilization practices. This change in the N to K balance might have had some effect in the phisiology of the plant and should be considered in

interpreting the result obtained. However, at the light of the new findings previously cited, it is possible that future fertilization practices for the summer season may include higher K rates than N. In this context, the results reported in this thesis concerning heat stress and the nutritional status of the plants used, may provide some insights for further research.

This investigation indicates the merestematic tissue localized at the shoot apex to be the perception organ for heat stress. Differences between these results and results previously published (Aldous and Kaufmann, 1979; Allmars, Burrow and Larson, 1964; Nudge, 1976; Sato and Ito, 1969; Slavov, 1972, Volden and Blackman, 1973) supporting an opposite conclusion, are due to the fact that crown temperatures were not separated from air or 'root' temperatures.

Reduction in the total growth of the plant at high temperature occurred only when both crowns and roots were exposed to high temperature. However, the plant appeared to exert compensatory growth mechanisms when either crowns or roots were exposed to high temperatures which enabled it to maintain sustained growth.

CONCLUSIONS

1. When air temperature was held within the optimum range for shoot growth (22-16 C day-night), significantly higher clipping dry weights resulted from plants with crowns exposed to cool temperature (22 C), regardless of root temperature (22 or 34 C).
2. The 5 week total accumulated dry weight of clippings was significantly reduced only when both crowns and roots were at high temperature (34^{o}C).
3. Dry weight of stubble was not significantly altered among all temperature regimes.
4. Crown dry weights were significantly reduced when exposed to high crown temperature regardless of root temperature.
5. Shoot growth reduction at high crown temperature resulted mainly from reduced tiller size. Under high crown and high root temperatures, reduction in both tiller size and number caused a significant decrease in shoot growth.
6. The meristematic tissue localized at the shoot apex (crowns) appeared to be the perception site of heat stress in Merion Kentucky bluegrass.
7. Tiller number appeared to be decreased by high root temperature rather than by high crown temperature.
8. Rhizome-tiller growth was enhanced by high crown temperature.

9. High crown temperature decreased rhizome dry weight. When the root was also at high temperature, the rhizome number was reduced.
10. Both tiller and rhizome development was reduced by high root temperature and appeared to be controlled by some root factor such as growth hormones.
11. The total dry weight of the plant appeared to be significantly reduced only when both crowns and roots were exposed to high temperature.
12. Cooler root temperature overcame the detrimental shoot growth effect of high crown temperature.
13. Initiation of new roots was promoted by cool crown temperature and suppressed by high crown temperature. The latter effect was overcame by a cooler root temperature causing greater length and branching.
14. Root/shoot ratios were significantly decreased by high root temperature.
15. Crown-region roots at 22 C were able to support shoot growth when rooting chamber roots were impaired at high root temperature (34 C).
16. When either roots or crowns were kept cool and the other was under heat stress compensatory growth of roots enabled the plant to sustain yields comparable to those where crowns and roots were in the cool environment.
17. The N to K ratio used might have had some effects on the phisiology of the plant, influencing the responses reported.

LITERATURE CITED

Alberda, T. 1957. The effect of cutting, light intensity and night Temperature on growth and stubble carbohydrate content of Lolium perenne L. Pl. Soil. 8: 199-230.

_____. 1965. The influence of temperature, light intensity and nitrate concentration on dry matter production and chemical composition of Lolium perenne L. Neth J. agric. Sci. 13: 355-60.

Aldous, E. D. 1978. Regulation of bud growth in Kentucky bluegrass (Poa pratensis L.) as influenced by temperature, ethylene and kinetin. Ph.D. Thesis. Michigan State University, East Lansing. pp. 1-86.

Aldous, D. E. and J. E. Kaufmann. 1979. Role of root temperature on shoot growth of two Kentucky bluegrass cultivars. Agron. J. 71: 545-547.

Allmaras, R. R., W. C. Burrows, and W. E. Larson. 1964. Early growth of corn as affected by soil temperature. Soil Sci. Amer. Proc. 28: 271-275.

Baker, B. S., and G. A. Jung. 1968. Effect of environmental conditions on the growth of four perennial grasses. I. Response to controlled temperature. Agron. J. 60: 155-158.

Beard, J. B. 1973. Turfgrass: science and culture. Prentice-Hall, Inc., Englewood, N.J. p. 658.

Beard, J. B., and W. H. Daniel 1965. Effect of temperature and cutting on the growth of creeping bentgrass (Agrostis palustris. Huds.) roots. Agron. J. 57: 249-250.

_____. 1966. Relationship of creeping bentgrass (Agrostis palustris Huds.) root growth to environmental factors in the field. Agron. J. 58: 337-339.

Brown, E. M. 1939. Some effects of temperature on the growth and chemical composition of certain pasture grasses. Mo. Agric. Exp. Stn. Res.Bull. 299 pp. 1-60.

Brown, E. M. 1943. Seasonal variations in the growth and chemical composition of Kentucky bluegrass. Mo. Agric. Exp. Stn. Res. Bull. 360.

Christians, N. E., D. P. Martin, and J. F. Wilkinson. 1979. Nitrogen, Phosphorous, and Potassium effects on quality and growth of Kentucky bluegrass and Creeping bentgrass. Agron. J. 71: 564-567.

Cooper, J. P. 1957. Developmental analysis of population in the cereals and herbage grasses. II. Response to low-temperature vernalization. J. Agric. Sci. 49: 361-383.

Cooper, J. P., and D. M. Calder. 1962. Flowering response of herbage grasses. Rep. W. Pl. Breed. Sta. 1961. pp. 20-22.

Crossett, R. N., D. J. Campbell, and H. E. Stewart. 1975. Compensatory growth in cereal root systems. Pl. Soil. 42: 673-683.

Darrow, R. A. 1939. Effect of soil temperature, pH and nitrogen nutrition on the development of Poa pratensis L. Bot. Gaz. 101: 109-127.

Drew, M. C. 1975. Comparison of the effect of localized supply of phosphate, nitrate, amonium and potassium on the growth of the seninal root system, and the shoot, in barley. New Phytol. 75: 479-490.

Drew, M. C., and L. R. Saker. 1975. Nutrient supply and the growth of the seminal root system in barley. II. Localized, compensatory increases in lateral root growth and rates of nitrate uptake when nitrate supply is restricted to only part of the root system. J. exp. Bot. 26: 79-90.

Duff, D. T. 1967. Some effect of supraoptimal temperatures upon creeping bentgrass (Agrostis palustris Huds.). Ph.D. Thesis Michigan State University. pp. 1-61.

Duff, D. T. and J. B. Beard. 1974. Supraoptimal temperature effects upon Agrostis palustris. Part II. Influence on carbohydrate levels, photosynthetic rate, and respiration rate. Physiol. Plant. 32: 18-22.

Ellis, F. B., J. G. Elliot, B. T. Barnes, and K. R. Howse. 1977. Comparison of direct drilling, reduced cultivation and ploughing on the growth of cereals. II. Spring barley on a sandy loam soil: Soil physical conditions and root growth. J. Agri. Sci. 89: 631-642.

Etter, A. G. 1951. How Kentucky bluegrass grows. Annals of the Missouri Botanical Garden. 38: 293-376.

Evans, M. W., and J. E. Ely. 1935. The rhizomes of certain species of grasses. J. Amer. Soc. Agron. 27: 791-797.

Forde, B. J. 1966. Trnaslocation in grasses. IV. Perennial ryegrass and couch grass. N. Z. J. Bot. 4: 496-514.

Fiveland, T. J., L. C. Erickson, and C. I. Seely. 1972. Translocation of ^{14}C-assimilates and 3-amino-1, 2, 4-triazole and its metabolites in Agropyron repens. Weed Res. 12: 155-163.

Garwood, E. A., and T. E. Williams. 1967. Soil water use and growth of a grass sward. J. Agri. Sci. 68: 281-292.

Hanson, A. A., and F. V. Juska. 1961. Winter root activity in Kentucky bluegrass (Poa pratensis L.) Agron. J. 53: 372-374.

Harrison, C. M. 1934. Responses of Kentucky bluegrass to variations in temperature, light, cutting and fertilizing. Plant Physiol. 6: 43-72.

Hiesey, W. M. 1953. Growth and development of species and hybrids of Poa under controlled temperatures. Am. J. Bot. 4: 205-221.

Klepper, B., H. M. Taylor, M. G. Huck, and E. L. Fiscus. 1973. Water relations and growth of cotton in drying soil. Agron. J. 65: 307-310.

Leopold, A. C. 1949. The control of tillering in grasses by auxin. Am. J. Bot. 36: 437.

MacKell, C. M., V. B. Youngner, F. J. Nudge, and I. J. Chatterton. 1969. Carbohydrate accumulation of coastal bermuda grass and Kentucky bluegrass in relation to temperature regimes. Crop Sci. 9: 534-537.

Marshall, C., and G. R. Sagar 1965. The influence of defoliation on the distribution of assimilates in Lolium multiflorum Lam Ann. Bot. 29: 365-370.

Martin, D. P. 1972. The influence of temperature, cultural factors, and analytical techniques on carbohydrate levels in turfgrass. Ph.D. Thesis. Michigan State University. East Lansing. p. 1-89.

Mitchell, K. J. 1953a. Influence of light and temperature on the growth of ryegrass (Lolium spp.). I. Pattern of vegetative development. Physiol. Plant. 6: 21-46.

_____. 1953b. Influence of light and temperature on the growth of ryegrass (lolium spp.). II. The control of lateral bud development. Physiol. Plant. 6: 425-443.

_____. 1955. Growth of pasture species. II. Perennial ryegrass (Lolium perenne), cocksfoot (Dactylis glomerata) and paspalum (Paspalum dilatatum). N. Z. J. Sci. Tech. 37: 8-26.

_____. 1956. Growth of pasture species under controlled environment. I. Growth at various levels of constant temperature.

Moser, L. E., S. R. Anderson, and R. W. Miller. 1968. Rhizome and tiller development in Kentucky bluegrass as influenced by photoperiod, cold treatment and variety. Agron. J. 60: 632-635.

Nyahoza, F., C. Marshall, and G. R. Sagar. 1973. The interrelationship between tillers and rhizomes of Poa pratensis L. - An autoradiographic study. Weed Res. 13: 304-309.

Olmsted, C. E. 1942. Growth and development of range grasses. II. early development of Boutelova curtipendula as affected by drought periods. Bot. Gaz. 103: 531-542.

Peacock, J. M. 1975a. Temperature and leaf growth in Lolium perenne. I. The thermalmicroclimate: its measurement and relation to crop growth. J. Appl. Ecol. 12: 99-114.

_____. 1975b. Temperature and leaf growth in Lolium perenne. II. The site of temperature perception. J. Appl. Ecol. 12: 115-123.

Pellet, H. M., and E. C. Roberts. 1963. Effects of mineral nutrition and high temperature induced growth retardation of Kentucky bluegrass. Agron. J. 55: 473-476.

Peterson, M. L., and W. E. Loomis. 1949. Effects of photoperiod and temperature on growth and flowering of Kentucky bluegrass. Pl. Physiol. 24: 31-43.

Robson, M. J. 1969. Light, temperature and the growth of grasses. A. Rep. Grassld Res. Inst. 1968, 111-23.

_____. 1973. The effect of temperature on the growth of S.170 tall fescue (Festuca arundinacea). II. independent variation of day and night temperatures. J. Anal. Ecol. 10: 93-105.

Russell, R. S. 1977. Plant root systems: their function and interaction with the soil. McGraw-Hill, London, Maidenhead, Berkshire, England, p. 298.

Schwarz, M. 1972. Short communication. Influence of root crown temperature on plant development. Plt. Soil. 37: 435-439.

Sprague, H. B. 1933. root development of perennial grasses and its relation to soil conditions. Soil Sci. 36: 189-209.

Sprauge, V. G., H. Neuberger, W. H. Orgell, and A. V. Dodd. 1954. Air temperature distribution in the microclimatic layer. Agron. J. 46: 105-108.

Stuckey, I. H. 1941. Seasonal growth of grass root. Amer. J. Bot. 28: 486-491.

_____. 1942. Influence of soil temperature on the development of colonial bentgrass. Pl. Physiol. 17: 116-122.

Sullivan, J. T., and V. G. Sprague. 1949. The effect of temperature on the growth and composition of the stubble and roots of perennial ryegrass. Plant Physiol. 24: 706-719.

Troughton, A. 1960. Further studies on the relationship between root and shoot systems of grasses. J. Brit. Grassl. Soc. 15: 41-47.

_____. 1963. A comparison of five varieties of Lolium perenne with special reference to the relationship between the root and shoot systems. Euphytica. 12: 49-56.

_____. 1965. Intra-varietal variation in Lolium perenne. Euphytica 14: 59-66.

Voldeng, H. D., G. E. Blackman. 1973. The influence of seasonal changes in solar radiation and air temperature on the growth in the early vegetative phase of Zea mays. Ann. Bot. 37: 553-563.

Watts, W. R. 1972. Leaf extension in Zea mays. II. Leaf extension in response to independent variation of the temperature of the apical meristem, of the air around the leaves and the root zone. J. exp. Bot. 23: 713-721.

Watschke, T. L., R. E. Schmidt, and R. E. Blaser. 1970. Responses of some Kentucky bluegrasses to high temperature and nitrogen fertility. Crop Sci. 10: 372-376.

Watschke, T. L., R. E. Schmidt., E. W. Carson, and R. E. Blaser. 1972. Some metabolic phenomena of Kentucky bluegrass under high temperature. Crop sci. 12: 87-90.

Williams. R. D. 1964. Assimilation and translocation in perennial grasses. Ann. Bot. 28: 419-426.

Youngner, V. B. 1961. Growth and flowering of Zoysia species in response to temperature, photoperiods, and light temperatures. Crop Sci. 1: 91-93.

Youngner, V. B., and F. J. Nudge. 1968. Growth and carbohydrate storage of three Poa pratensis L. strains as influenced by temperature. Crop Sci. 8: 455-457.

Youngner, V. B.,and F. J. Nudge. 1976. Soil temperature, air temperature and defoliation effects on growth and nonstructural carbohydrates of Kentucky bluegrass. Agron. J. 68: 257-260.

Yeh, R. Y., A. G. Matches, R. L. Larson. 1966. Endogenous growth regulators and summer tillering of Tall fescue. Crop Sci. 16: 409-413.

Zobel, R. W., P. Del Trici, and J. G. Torrey. 1976. Method for growing plants aeroponically. Plant Physiol. 57: 344-346.

APPENDIX

APPENDIX TABLE 1.--Composition of the nutrient solution.

Chemical	ml. stock solution per liter of nutrient solution	Parts per million (ppm) of element in nutrient sol.
[1] M-KH_2PO_4	1	K: 39.1; P: 30.9
M-KNO_3	6	K: 234; N: 84
M-$Ca(NO_3)_2$	3	Ca: 120; N: 74
M-$MgSO_4$	2	Mg: 48; S: 64
[2] Micronutrients	gr/H of H_2O	ppm
H_3BO_3	2.86	B: 0.5
$Mn_2 \cdot 4H_2O$	1.81	Mn: 0.5
$ZnSO_4 \cdot 7H_2O$	0.22	Zn: 0.05
$CuSO_4 \cdot SH_2O$	0.08	Cu: 0.02
$H_2MoO_4 \cdot H_2O$	0.02	Mo: 0.01
Sequestrene 330Fe(10%Fe)*		Fe: 5

[1] M stands for Molar concentration.

[2] Composition of stock solution. One mililiter per liter of nutrient solution was used.

* Iron was supplied with Sequestrene 330Fe, a chelate product containing 10%Fe. The iron chelate stock solution was prepared by dissolving 50g sequestrene in distilled water brought to 1 liter volume. One mililiter of stock solution per liter of nutrient solution twice a week.