SOME EFFECTS OF SUPRAOPTIMAL TEMPERATURES UPON CREEPING BENTGRASS (AGROSTIS PALUSTRIS HUDS.)

Thesis for the Degree of Ph. D.
MICHIGAN STATE UNIVERSITY
D. THOMAS DUFF
1967

This is to certify that the

thesis entitled

Some Effects of Supraoptimal
Temperatures Upon Creeping Bentgrass
(Agrostis Palustris Huds.)

presented by

D. Thomas Duff

has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Crop Science

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Date June 16, 1967

ABSTRACT

SOME EFFECTS OF SUPRAOPTIMAL TEMPERATURES
UPON CREEPING BENTGRASS
(*Agrostis palustris* Huds.)

by D. Thomas Duff

The detrimental effects of supraoptimal temperatures upon the growth of creeping bentgrass turf result in many problems in the field. Grass vigor is reduced during high temperature periods of the summer season. This study was initiated to elucidate some effects of supraoptimal temperatures upon creeping bentgrass.

Sod pieces of Toronto creeping bentgrass were removed from the field, and placed in the greenhouse and growth chamber for a nine-week establishment period. The grass was then grown at successive light-dark temperature regimes of 20-10, 25-15, 30-20, 35-25 and 40-30 C utilizing a 16-8 hour cycle. Leaf clipping harvests were made once per week at a 1.3 cm cutting height for a four-week period under each temperature regime.

The yield of clippings from a turf was considered as a function of the leaf area removed and the weight per unit area of the leaves. In this study, leaf dry weight per unit area increased lineraly with temperature. Decrease in the dry weight yield of clippings was brought about by decreased leaf area production. At the lower temperatures, leaf area reduction was characterized more by reduced leaf

width than leaf length. At the higher temperature levels, it was influenced more by decreased leaf length than leaf width.

Production of leaf clippings and the level of both 85 per cent ethanol and water soluble carbohydrates in the leaves varied in an inverse manner. Carbohydrate content of clippings was greatest at the highest temperature regime, when clipping yield was lowest. Leaf sheath, stem and stolon tissue contained as much carbohydrate as leaf tissue. Accumulation of carbohydrate in the leaves at high temperature levels could not be attributed to disruption of translocation to lower portions of the plant. Decrease in leaf dry matter production was not attributable to depletion of reserve carbohydrates within the leaf tissue.

Reduction of turf density at the highest temperature regime could not be attributed to carbohydrate depletion within the lower portions of the plant. Plants which had ceased active leaf production and had become chlorotic contained a carbohydrate level equivalent to plants which remained green and still produced new leaves.

Photosynthetic rates were determined manometrically under non-limiting light and carbon dioxide levels. Under these conditions, nonphotochemical reactions limiting photosynthesis were evaluated. Leaves produced at 40-30 C exhibited a greater photosynthetic rate per unit area than those grown at 20-10 C when they were tested at 20, 30 and 40 C. This effect was probably due to quantitative changes

brought about by morphological differences resulting in a greater number of photosynthetic units per unit leaf area. Leaf tissue produced at 40-30 C also exhibited a smaller depression in Q_{10} at 40 C than those leaves grown at 20-10 C. This result was brought about by uncharacterized qualitative changes in leaf tissue grown at 40-30 C. The quantitative and qualitative changes in leaf tissue grown at 40-30 C indicated that adaptive mechanisms were influencing the photosynthetic rate when considered on a per unit area basis of leaves grown at this temperature. Respiration rates were also determined manometrically. Changes similar to those affecting photosynthetic rate were not found.

Although adaptive mechanisms were indicated in the photosynthetic rate per unit area of leaves grown at 40-30 C, much less leaf area was produced. The effects on photosynthetic capability and the ample carbohydrate supply did not result in healthy minature plants. At the 40-30 C temperature regime, many plants died from causes other than those evaluated in this study.

SOME EFFECTS OF SUPRAOPTIMAL TEMPERATURES UPON CREEPING BENTGRASS (*AGROSTIS PALUSTRIS* HUDS.)

By

Dale Thomas Duff

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Crop Science

1967

ACKNOWLEDGMENTS

The author wishes to express his appreciation to Dr. J. B. Beard for his guidance, advice and critical evaluation during the course of this investigation and preparation of the thesis.

In addition, appreciation is expressed to those members of the faculty who generously gave of their time and talents to review and criticize the thesis manuscript during its preparation.

The author also wishes to take this opportunity to thank all those members of the faculty who have generously and unfailingly given their time, advice and assistance during his period of graduate study.

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INTRODUCTION

The growth pattern of cool season grasses in response to temperature has been the object of study in numerous investigations. A definite seasonal trend of rapid growth during the cool period of spring is followed by reduced growth under the influence of warm summer temperatures. The latter period is followed by a secondary increase in growth during the cooler autumn season.

Most grasses utilized for turf in the cool humid region of the United States are classified as cool season. Turf managers in this area are cognizant of a general decline in turf vigor during periods of high summer temperatures. Reduced turf vigor leads to enhanced management requirements during these periods. The turf is less able to resist additional stress placed upon it whether of natural or mechanical origin.

Some workers have attributed the decline in growth at high temperatures to decreased carbohydrate supply within plant tissues. It has been shown that the temperature optimum for photosynthesis is lower than that of respiration. At some point, growth as measured by the rate of dry matter production might be governed by a reduced supply of carbon skeleton for assimilation. Other workers have found little relationship between carbohydrate content and growth rate.

Thus, there is lack of agreement concerning the role of carbohydrate levels in regulating growth rate.

This study was initiated to investigate some of the effects of supraoptimal temperatures upon creeping bentgrass. Clarification of these effects could be of value in developing management practices which would permit the grass to withstand better the stress of summer temperatures.

LITERATURE REVIEW

The influence of temperature upon plant growth has often been studied.

Lundegardh (13) discussed a generalized growth-temperature relationship and pointed out that from low to higher temperatures the Q_{10} value continuously changes. At some point an optimum is reached and above this level, at supraoptimal temperatures, the Q_{10} becomes less than unity. At supraoptimal temperatures, the curve falls rapidly so that at temperatures only slightly above the optimum, growth is greatly reduced. The optimum cannot be considered as a sharply defined point since it is influenced by many other factors of the environment to which a plant may be subjected.

The effect of temperature upon the growth of Kentucky bluegrass was studied by Harrison (9). Grass cultures were grown at 60, 80, and 100 F. Cultures grown at 60 F and supplied with nitrogen produced equivalent clipping weights between 10-day cutting intervals for a 50-day period. Those cultures supplied with nitrogen and grown at 80 F produced more clippings than the 60 F grown the first harvest, but in successive intervals, the clipping yield of the former decreased. Cultures placed at 100 F grew very little the first 10 days, and in subsequent periods, no growth took

place. The effect of the 80 F temperature was time dependent, but the effect of 100 F was shown very quickly.

Stuckey (23) noted the effect of 50, 60, and 80 F soil temperatures upon the growth of Colonial bentgrass. She found both root and top growth were greatest at 60 F with lower amounts at 50 F and the least at 80 F.

Brown (3) found the optimum for herbage production of Kentucky bluegrass to be between 80 and 90 F. Exposure to a constant soil and air temperature of 100 F resulted in severe injury which developed gradually. This temperature did not result in sudden death of the plants. In later work in the field, Brown (4) found that top growth of Kentucky bluegrass reached its peak when mean temperatures reached 60 to 64 F. Herbage production declined at temperatures near or above 80 F.

Sullivan and Sprague (24) studied the effects of four temperature regimes upon the regrowth of perennial ryegrass. All plants were grown at a temperature of 70 F, clipped, and placed under the test temperature. Regrowth was measured periodically for 40 days. Plants placed at 60-70 F night-day temperatures produced the greatest top growth. The least amount was produced at the end of the test period under the 80-90 F temperature regime.

The influence of temperature upon the yield of clippings of creeping bentgrass (Agrostis palustris) was investigated by Jordan (11). He found that of the three

temperatures 60, 70, and 80 F, the greatest clipping yield was at 70 F. Yield at 60 F was somewhat less and that at 80 F considerably less.

Pellet and Roberts (17) grew Kentucky bluegrass in solution culture. They found a decreased growth rate as temperatures increased in the greenhouse regardless of the nutrient level of their culture solution.

The optimum temperature for production of leaf tissue of the cool-season grasses discussed above was generally found to be approximately 60-70 F. Temperatures lower than this order of magnitude resulted in decreased leaf growth as did those above this level.

The type of leaf produced at various temperatures was reported by Sullivan and Sprague (24). They noted that at the 21-day sampling period, leaves at 60-70 F were vigorous in appearance, of good color, and were 5-8 inches long. Those at 50-60 F were second best and were 2-5 inches in length. Leaves of plants at 70-80 F were spindly and lacked vigor. At 80-90 F, leaves were 1-5 inches long and had a very dark green color.

Darrow (5) also reported temperature effects upon leaf development. He found Kentucky bluegrass leaves grown at 15 C soil temperature were long and succulent and that numerous new leaves were produced. At a soil temperature of 35 C, however, the leaves were short and rigid with many of them remaining erect. Leaf production and bud initiation were limited at 35 C.

Sullivan and Sprague (24) reported the percentage dry weight of the new leaf tissue produced in their study. Leaves produced at the 60-70 F temperature regime contained 18.6 per cent dry matter, while those produced at the 80-90 F level contained 23.5 per cent.

Pellet and Roberts (17) found an increase in percentage dry weight with increased temperature. They also found that Kentucky bluegrass cultures supplied with a high level of N, P, and K had a lower percentage dry weight than those receiving a low level.

Although Harrison (9) did not report the percentage dry weight of harvested leaves, he did report green and dry weights of his harvests from which the percentage dry weight can be calculated. On the first cutting date after placing the cultures under the test temperatures, the percentage dry weight was 27.8 at 100 F, 19.5 at 80 F, and 17.0 at 60 F in those plants receiving nitrogen. On the same date, those receiving no nitrogen had a percentage dry weight of 27.6 per cent at 100 F, 23.1 at 80 F, and 20.4 at 60 F.

The chlorophyll content of leaf tissue has been ascertained from the point of view that it might be a limiting factor in the rate of photosynthesis and thus the rate of assimilation. Both Meyer and Anderson (14) and Strain (22) indicated, however, that the chlorophyll content is seldom a limiting factor of photosynthetic rate.

The photosynthetic rate remains constant over a large range in chlorophyll content. Gaastra (7) presented a curve of efficiency of light energy conversion in relation to chlorophyll concentration per unit leaf area. At low concentrations, efficiency increased with increasing chlorophyll concentration, then reached a maximum value and became a non-limiting factor. Leopold (12) also discussed the usually weak quantitative influence of chlorophyll content upon the rate of photosynthesis in the field.

The carbohydrate content of plant tissue has often been studied from many different aspects and points of view and with widely divergent questions being investigated. Certainly, the carbohydrates play a key role in plant metabolism. They provide the major source of carbon skeletons for both catabolic and anabolic reactions.

Brown (4) studied seasonal carbohydrate levels of Kentucky bluegrass in the field. His observations showed that carbohydrates were produced more rapidly than they were used during the cool weather of early spring, the surplus being stored in roots and rhizomes. During the summer period, there was a net loss of carbohydrates from roots and rhizomes. During the autumn period, carbohydrate storage again took place.

Carbohydrate content of various portions of perennial ryegrass was determined by Sullivan and Sprague (24). They found the major portion of carbohydrate was located in the

stubble with smaller amounts in leaves and roots. They also followed the amount of carbohydrate in stubble and roots of plants which were clipped and placed under four temperature regimes during regrowth. At the end of a 40-day period, plants grown at 80-90 F were stunted and had spindly dark green leaves. They attributed this deleterious effect to rapid dissipation of reserve carbohydrates, especially in the roots.

When Harrison (9) placed Kentucky bluegrass under an 80 F temperature, he found the amount of leaf tissue produced between periodic harvests decreased with time. He attributed this effect to exhaustion of reserve carbohydrate.

Beinhart (2) studied the growth of white clover (Trifolium repens L.) at various temperatures in growth chambers and seasonally in the field. He found that the decline in summer branching of the stolons appeared to limit the summer growth of white clover. He concluded, however, that carbohydrate supply was not the limiting factor in summer branching.

When Jordan (11) studied fructose content of creeping bentgrass, he found that carbohydrate accumulation in leaf clippings was an inverse function of their growth.

Green (8) found that temperatures of 80 F and greater appeared to exert an adverse effect on the carbohydrate reserves of the cool season grasses he studied. However, he concluded that under the conditions of his study, the

total carbohydrate level of leaf tissue did not appear to limit growth.

The question of the effect of temperature upon translocation of sucrose in tomato was studied by Went and Engelsberg (27). They found that rate of sugar translocation decreased as the temperature was increased from 8 to 26 C.

In a later paper, Went and Hull (28) reported that carbohydrate transport through the stem of the San Jose Canner tomato became essentially 0 near 30 C.

Swanson and Bohning (25) studied the influence of petiole temperature upon the translocation of sucrose out of the leaf of bean. They found maximum sucrose transport took place between 20 C and 30 C. At petiole temperatures of 5 C to 7.5 C the rate of transport was reduced as much as 50 per cent. From 40 C to 42 C, the transport rate was reduced 100 per cent as compared to the controls.

Hewitt and Curtis (10) found translocation from bean leaves increased when the plants were held for 13 hours at 4, 10, and 20 C. The rate at 30 C nearly equalled that at 20 C. At 40 C there was a marked decrease.

Rabinowitch (18) discussed temperature effects upon the rate of photosynthesis. The rate of photosynthesis is governed not only by temperature but also by light intensity and carbon dioxide supply. When light intensity is low, photosynthetic rate is generally insensitive to change

in temperature. Light controlled or photochemical processes are temperature independent. Under conditions of high light intensity and low carbon dioxide supply, the photosynthetic rate is primarily influenced by the effect of temperature upon the diffusion rate of carbon dioxide. When neither carbon dioxide nor light is limiting, photosynthetic rate increases rapidly in the temperature range near the lower temperature limit. As the temperature is increased further, the rate of increase with temperature decreases until an optimum is reached. Above the optimum, the rate declines rapidly with further temperature increase. Higher plants adapted to moderate climates generally reach the maximum photosynthetic rate in the range of 30-35 C.

Consideration of the effect of temperature upon respiration shows a different relationship than that of photosynthesis (13, 18). The respiratory rate increases with temperature at a rapid pace from temperatures slightly above the minimum for respiration until an optimum is reached. At temperature levels greater than the optimum, the rate decreases rapidly. In many cases, the optimum photosynthetic rate is at a lower temperature than the optimum for respiration. As a result of these effects, a region is reached at high temperatures where net gas exchange becomes less than unity.

The effect of temperature upon the growth of two strains of Chlorella was studied by Sorokin and Myers (20). By culturing and selecting at various temperatures, they

were able to isolate a culture which had a higher optimum for growth than the wild strain with which they started. They found the optimum for the latter was 25-26 C and for the former it was 39 C.

Murata and Iyama (16) in their study of the photosynthetic rate of forage crops found that the season of production of orchard grass influenced the photosynthetic rate. Plants which were grown in July exhibited a greater rate from 20 C through 40 C than those grown in March.

The relationship between carbohydrate levels and plant growth as measured by dry weight production of leaves at various temperatures is still in question. In some studies (4,24) carbohydrate levels decreased as growth was reduced and temperature increased. This correlative relationship shows only that carbohydrate levels and dry weight production vary in a similar manner. In other studies (2, 11) the amount of above ground tissue produced at above optimum temperatures could not be correlated with carbohydrate levels. This result does not provide evidence for the real cause of reduced growth, but the negative relationship does provide evidence that carbohydrate levels are not limiting leaf dry matter production.

Under turf conditions, grass plants are periodically mown to maintain an attractive, uniform appearance. Due to this practice, the leaf tissue present is in a state of continuous turnover. Leaf tissue produced at various

temperature levels may not exhibit the same photosynthetic activity (16).

This study was initiated with the goal of elucidating some of the effects of supraoptimal temperatures upon leaf dry matter production and carbohydrate levels in the leaf tissue. In addition, photosynthetic and respiratory rates of leaf tissue produced were determined to investigate the possibility of changes in temperature response of leaves grown at different temperatures.

MATERIALS AND METHODS

Sod pieces of Toronto creeping bentgrass 6.45 square decimeters in area were taken from the field in mid September and placed in boxes 25.4 X 25.4 X 20.3 cm containing a 2-1-1 mixture of soil-sand-peat. They were maintained in the greenhouse three weeks and then transferred to the growth chamber where they were permitted to grow an additional six weeks. This period was considered adequate for the sod to become established and acclimated to the growth chamber.

During establishment, each box received a weekly application of one liter of Hoagland's number two macronutrient solution made up with tap water. On the remaining six days, tap water was added until drainage from the bottom of the boxes occurred.

Leaf growth was harvested at 8:00 AM once per week at a cutting height of 1.3 cm, utilizing hand shears with a pan attached to collect the clippings.

During establishment, the growth chamber was programmed for 20-10 C temperatures during 16-8 hour light-dark cycles. Light was furnished by flourescent lamps supplemented by incandescent bulbs. Intensity at the grass surface was approximately 2,400 foot candles as measured

by a Weston illumination meter, Model 756, utilizing a quartz filter.

Disease infestation was not observed at any time during the course of the study. Insects were controlled by occasional dusting with malathion.

Successive four-week periods were utilized, with temperatures of 20-10, 25-15, 30-20, 35-25, and 40-30 C during 16-8 hour light-dark periods. Experimental determinations were made once per week at any one temperature regime.

Once per week, the grass was clipped to a height of 1.3 cm as previously described and the harvested material frozen and stored at -18 C for future analysis. Leaf harvests were made at the midpoint of the light period in order to avoid diurnal variations in carbohydrate levels. Fertilization and watering procedures and light intensity were as outlined under establishment period.

Chlorophyll extractions of harvested leaf clippings were carried out as given in Official Methods of Analysis, AOAC (1). Approximately 200 mg fresh weight of leaf tissue were macerated in a mortar with quartz sand. Chlorophyll was extracted with 85 per cent acetone and the residue filtered off with a Buchner funnel. The extract was brought to 100 ml final volume and the optical density determined with a Beckman DU spectrophotometer at 660 millimicrons.

A second sample was weighed into glass weighing bottles, dried at 85 C for 24 hours, reweighed, and the percentage dry matter determined so that chlorophyll content could be calculated as percentage dry weight.

Smith and Grotelueschen (19) reported 85 per cent ethanol effective in extracting glucose, fructose, and sucrose from stem base tissue of Agrostis alba L. Their extracts were checked by thin layer chromatography. Very little fructose oligosaccharide was removed with this alcohol concentration. In the present investigation, 85 per cent ethanol was used to extract bentgrass tissue. The carbohydrates thus extracted were considered to be predominately glucose, fructose, and sucrose.

Tissue used for carbohydrate determinations was dried at 85 C for three to four hours. It was then ground in a mortar and returned to the oven for further drying. The total drying time was 24 hours. Approximately 100 mg dried tissue was placed in an 125 ml Erlenmeyer flask and 50 ml 85 per cent ethanol added. The flask was stoppered and shaken for one hour. The sample was removed from the shaker and a small amount of Norit-A added. The sample was filtered through a Buchner funnel utilizing Celite filter aid and the residue washed with additional 85 per cent ethanol. The ethanol was removed in a rotary flash evaporator, at 65 C and the aqueous solution rinsed into an 100 ml volumetric flask with distilled water and brought

to volume. A second sample of approximately 100 mg was extracted with distilled water at room temperature. Similar procedures to the above were used except that the extract was brought to 200 ml final volume without reduction in the flash evaporator.

Colorimetric determination of the carbohydrate contained in the two extracts was carried out according to the anthrone method of Yemm and Willis (29). Concentrated sulfuric acid was diluted by adding 40 ml distilled water to 100 ml acid. The anthrone reagent was made by dissolving 0.2 gram anthrone in 100 ml of the sulfuric acid prepared as above. Fresh reagent was prepared and used each day carbohydrate determinations were made. The reaction was carried out by placing 5 ml anthrone reagent in matched Pyrex test tubes in an ice bath and allowing it to cool for at least 5 minutes. One ml of extract was pipetted on top of the anthrone solution. The solutions were mixed and again cooled 5 minutes. Color was developed in a boiling water bath for 10 minutes and the test tubes returned to the ice bath for a 5-minute cooling period. Optical density was read with a Coleman Junior spectrophotometer at 620 millimicrons, and the carbohydrate content determined by reference to a standard curve. Duplicate determinations of each extract were made. Duplicate standards of 10, 20, 40, and 60 micrograms fructose were also run each time in order to be certain the reaction remained on the standard curve.

On the same day harvests were made, one box was removed from the growth chamber and taken to the laboratory. Photosynthetic and respiratory rate determinations were made at the temperature of the light period under which the plants were grown.

Photosynthetic rate determinations were made by standard Warburg manometric techniques (26). The last fully unrolled leaf was excised from individual plants. Then leaves were arranged in the center well of a flask containing 0.1 ml distilled water. Three ml of buffer was placed in the flask outside the center well to serve as a source of carbon dioxide during the experimental run. The buffer was made by adding 6.72 grams sodium bicarbonate to 100 ml saturated sodium borate solution. Calculated atmospheric carbon dioxide concentration within the flasks was 15 per cent. Light intensity measurements showed 3,200 foot candles transmitted through the bottom of the Warburg apparatus as measured with a Weston illumination meter, model 756 utilizing a quartz filter.

Four flasks containing leaves plus two checks were used for each run. All flasks were placed in the water bath and allowed to equilibrate 20 minutes. The manometers were then brought to the reference point and closed off. Readings were taken at 15-minute intervals over a two-hour period.

At the end of the run, flasks were removed from the manometers and leaf area of the tissue determined by measuring the length and midpoint width of all leaves used. Leaves were then placed in glass weighing bottles, dried at 85 C for 24 hours and weighed.

Preliminary determinations showed no difference between the photosynthetic rate at 3,200 foot candles and 2,600 foot candles light intensity (Appendix Table XVII). The system was considered to be at light saturation at 3,200 foot candles. Preliminary determinations of the effect of the calculated carbon dioxide level were also made (Appendix Table XVIII). Carbon dioxide supply was not considered to be limiting in the photosynthetic rate determinations with the buffer system used.

Respiratory rates were also determined in the Warburg apparatus. Light was excluded by a black velvet cloth draped over the top and fitted over the bottom of the apparatus. Twenty-five leaves similar to those used in the photosynthetic rate determination were excised and placed in the Warburg flask. Two-tenths ml of 10 per cent potassium hydroxide were placed in the center well. A 2 cm X 2 cm piece of filter paper was folded and placed in the center well to increase absorption area. Determinations were made in a manner similar to that described above and the tissue dried and weighed.

Statistical analyses were carried out according to methods outlined in Steele and Torrie (21).

RESULTS

The bentgrass grew quite vigorously under the 20-10 C temperature regime. Leaf tissue was a good, green color and new leaves were produced rapidly. One week after clipping, the leaves were beginning to bend toward an horizontal orientation. The turf was dense and was similar to the kind of growth observed in the field in late spring and early summer.

Very few visual differences were noted between grass grown at 25-15 C and that produced at 20-10 C. The plants appeared quite healthy and the turf vigorous.

Under the 30-20 C temperature regime, the grass did not appear to be adversely affected. The plants were vigorous and the turf dense with no visible evidence of thinning. Color did not appear different from that of the lower temperatures.

Beginning with the 35-25 C temperature level, a striking difference in growth of the turf was noted. Leaves were much more upright in growth habit and did not bend towards the horizontal. They had a bristle-like appearance when harvested. No distinct color differences could be seen when compared with leaves grown at the lower temperatures.

Soon after the plants were placed under the 35-25 C temperature treatment, the stand of plants appeared to decrease in density. After the initial period, no further apparent thinning took place.

Growth habit of plants at the 40-30 C temperature regime assumed a distinctly upright, bristle-like appearance. Leaves produced at this temperature appeared to have a darker green color than those produced at lower temperatures.

Turf density definitely decreased at the highest temperature level. The effect was noted in all boxes in the growth chamber. Some plants died, but no definite positional pattern could be noted in any of the boxes. The plants were kept at the 40-30 C level for four weeks as they were for the previous temperature treatments. At the end of this period, all but two boxes were discarded. The two remaining boxes were placed under a 20-10 C temperature regime and watered, fertilized and clipped as before. At the end of two weeks, the surviving plants appeared healthy, but the turf did not fill in and became dense until an additional two-week period had passed.

The width of leaves produced at five temperature levels is presented in Table 1. The data presented are from measurements taken when leaf area was determined during the photosynthetic rate studies. Essentially equal numbers of leaves produced at 20-10 and 25-15 C were in the 1.0-1.5 mm

and >1.5 mm width classes. When temperature was increased to the 30-20 C level, there was a distinct decrease in leaf width. None of the leaves measured were more than 1.5 mm wide. The width of leaves grown at 35-25 C was quite similar to that of leaves grown at 30-20 C. Leaves grown at 40-30 C were distinctly narrower than those produced at any other temperature regime.

Leaf length at five temperature regimes is presented in Table 2.

TABLE 1.--The number of leaves out of 160 falling in three width classes when grown at five temperature regimes.

Temperature Regime Grown	Leaf Width Class, mm		
	<1.0	1.0-1.5	>1.5
20-10 C	0	144	16
25-15 C	0	142	18
30-20 C	58	102	0
35-25 C	60	100	0
40-30 C	130	30	0

TABLE 2.--The number of leaves out of 160 falling in four length classes when grown at five temperature regimes.

Temperature Regime Grown	Leaf Length Class, mm			
	6-10	11-15	16-20	21-25
20-10 C	0	6	78	76
25-15 C	0	4	88	68
30-20 C	0	3	79	78
35-25 C	0	58	102	0
40-30 C	62	98	0	0

As in the case of leaf width, there was essentially no change in leaf length between 20-10 and 25-15 C. Nearly equal numbers of leaves fell in the three longer length classes at the three lower temperature regimes. Increasing the temperature to 35-25 C resulted in shorter leaves than were produced at lower temperatures. There was a large reduction in leaf length at the 40-30 C temperature level.

Percentage dry weight increased gradually from the 20-10 to the 30-20 C temperature level, then increased more sharply between the 30-20 and 35-25 C regimes (Table 3). A very definite increase in percentage dry weight was found when temperature was increased from 35-25 to 40-30 C. Percentage dry weight increased 44 per cent between the two levels. Although there was an increasing trend in percentage dry weight at the higher temperatures, Duncan's test of the means showed the sharp increase at the highest temperature to be the only one significantly different at the 1 per cent level. The average percentage dry weight for the four lower temperature levels was 22.1 per cent. Dry weight percentage of the leaf tissue grown at 40-30 C was 34.4 per cent, an increase of 61 per cent.

Weight per unit area of the leaf tissue increased from the lowest temperature regime to the highest (Table 4). Although Duncan's range test showed that not all means were significantly different, analysis of the treatment sums of squares showed that the portion due to linearity was highly

significant and deviation from linearity was nonsignificant (Appendix Table VI).

TABLE 3.--Percentage dry weight of leaf tissue produced under five temperature regimes.

Temperature Regime	Percentage Dry Weight	Duncan's Test of Means*
20-10 C	20.6	a
25-15 C	21.6	a
30-20 C	22.4	a
35-25 C	23.9	a
40-30 C	34.4	b

*Means containing the same letter in the third column are not significantly different at the 1 per cent level.

TABLE 4.--Milligrams dry weight per square centimeter of leaf area produced under five temperature regimes.

Temperature Regime Grown	Milligrams Dry Weight per Square Centimeter	Duncan's Test of Means*
20-10 C	1.7	a
25-15 C	2.1	b
30-20 C	2.1	b
35-25 C	2.4	bc
40-30 C	2.6	c

*Means containing the same letter in the third column are not significantly different at the 1 per cent level.

There was a gradual decrease in dry matter production from the 20-10 to the 30-20 C temperature level (Table 5).

TABLE 5.--Dry weight of clippings, grams per 25.8 square decimeters per week at five temperature regimes.

Temperature Regime Grown	Clipping Yield	Duncan's Test of Means*
20-10 C	13.4	a
25-15 C	12.9	a
30-20 C	11.4	a
35-25 C	8.4	b
40-30 C	3.1	c

*Means containing the same letter in the third column are not significantly different at the 1 per cent level.

When the results were subjected to Duncan's multiple range test, however, the decrease was nonsignificant at the 1 per cent level. When the temperature was increased to 35-25 C, weekly dry matter production of new leaf tissue was reduced significantly. The average value for dry weight of clippings for the three lowest temperature regimes was 12.6 grams, and that of the 35-25 C regime was 8.4 grams, a decrease of 33 per cent. Comparison of the dry matter produced among the first three temperature levels versus the 40-30 C regime shows a decrease of 75 per cent in new leaf production. When temperature was increased from 35-25 to 40-30 C, leaf dry matter production was decreased 64 per cent.

Chlorophyll content per mg dry weight of harvested leaf tissue showed a general increase from the 20-10 C temperature regime to the 25-15 C level (Table 6).

TABLE 6.--Chlorophyll content of leaf clippings, micrograms per milligram dry weight at five temperature regimes.

Temperature Regime Grown	Chlorophyll, Micrograms per Milligram Dry Weight	Duncan's Test of Means*
20-10 C	8.7	a
25-15 C	9.3	ab
30-20 C	10.3	b
35-25 C	10.4	b
40-30 C	6.7	c

*Means containing the same letter in the third column are not significantly different at the 1 per cent level.

The amount of chlorophyll decreased markedly in the tissue produced at 40-30 C. When the means of chlorophyll content were subjected to Duncan's range test, the content at the 20-10 C regime was significantly less than that at 30-20 and 35-25 C. The amount present in the 40-30 C grown tissue was significantly less than that present in tissue produced at any of the other temperatures. The quantity present at the intermediate temperatures, although showing a slight increase, was not significantly different.

The observation that leaves produced at the highest temperatures appeared to be a dark green color did not agree with the decrease in chlorophyll content found on a weight basis. Chlorophyll content per unit area was then calculated from the dry weight per unit area and chlorophyll per unit weight data (Table 7). The marked decrease in chlorophyll content shown on a dry weight basis at the

highest temperature level was not found when the content was changed to an area basis. There was a slight decrease, but the amount present on this basis was still greater than that found at the lowest temperature regime.

The amount of 85 per cent ethanol soluble carbohydrate in the leaf tissue was very similar at all temperature regimes from 20-10 to 35-25 C (Table 8). Duncan's Test of

TABLE 7.--Chlorophyll content, micrograms per square centimeter of leaf area at five temperature regimes.

Temperature Regime Grown	Chlorophyll Content, Micrograms per Square cm
20-10 C	15.0
25-15 C	20.4
30-20 C	22.5
35-25 C	25.1
40-30 C	17.9

TABLE 8.--85 per cent ethanol soluble carbohydrate content of leaf tissue produced under five temperature regimes: percentage of dry weight of tissue.

Temperature Regime Grown	Percentage Carbohydrate	Duncan's Test of Means*
20-10 C	5.2	a
25-15 C	5.2	a
30-20 C	5.1	a
35-25 C	5.7	a
40-30 C	8.1	b

*Means containing the same letter in the third column are not significantly different at the 1 per cent level.

the treatment means showed the differences to be nonsignificant at the 1 per cent level. The average content of leaves produced at the four lower temperature regimes was 5.3 per cent of the dry weight. The 40-30 C grown leaf tissue contained 8.1 per cent on the same basis, an increase of 53 per cent.

The water soluble carbohydrate content showed a response similar to the 85 per cent ethanol soluble fraction (Table 9). A significant increase in water soluble carbohydrate content was found in leaf tissue produced at 40-30 C. The average water soluble carbohydrate content of tissue produced under the four lower temperature regimes was 6.5 per cent of the dry weight. Leaves grown at 40-30 C contained 9.8 per cent, an increase of 51 per cent.

In addition to leaf carbohydrate determinations, the amount present in stem and stolon tissue was ascertained for the lowest and highest temperature regimes (Table 10). Carbohydrate analyses were made on distinctly different appearing plants at the 40-30 C level. In one instance, plants which retained a green leaf color were used, but in the second, chlorotic plants were selected.

The amount of water soluble carbohydrate found in the stem and stolon tissue grown at 20-10 C was somewhat lower than the average value found in leaf tissue of plants grown under the same temperature regime. As previously stated, however, the water soluble content was found to be quite variable and the content found in the stem and stolon

tissue was within the range of values previously determined for bentgrass leaf tissue.

TABLE 9.--Water soluble carbohydrate content of leaf tissue produced under five temperature regimes: percentage of dry weight of tissue.

Temperature Regime Grown	Percentage Carbohydrate	Duncan's Test of Means*
20-10 C	6.1	ab
25-15 C	6.3	ab
30-20 C	5.7	a
35-25 C	7.8	b
40-30 C	9.8	c

*Means containing the same letter in the third column are not significantly different at the 1 per cent level.

TABLE 10.--Water soluble carbohydrate content of stem and stolon tissue, per cent of the dry weight.

Temperature Regime Grown	Visual Plant Appearance	Per Cent Water Soluble Carbohydrate
20-10 C	Green	5.2
40-30 C	Green	10.7
40-30 C	Chlorotic	11.9

The water soluble carbohydrate content of stem and stolon tissue of green plants grown at the 40-30 C temperature regime was somewhat higher than in leaf tissue of plants grown at this temperature level. Again, however,

the values determined were within the range of those determined for leaf tissue.

In the chlorotic plants, the water soluble carbohydrate content of stem and stolon tissue was greater than that found in leaf tissue. The values in this case were all greater than any value found for green plants when water soluble carbohydrate content of leaf tissue was determined.

Cumulative O_2 and CO_2 production of leaf tissue grown at 20-10, 30-20 and 40-30 C and tested at the light temperature is presented in Figures 1 and 2. The figures presented show how tissue produced under the three temperature regimes reacted when tested at the temperature under which they were grown. As has been shown, tissue produced under various temperature regimes was not equivalent. The figures presented do not represent the change in photosynthetic rate per unit area of any one tissue over a range of temperatures. The usual Q_{10} relationship used to compare photosynthetic rates of tissue at different temperature levels is not a valid mode of comparison in this case. The photosynthetic and respiratory rates per unit area of leaf tissue grown at the indicated temperatures and tested in the Warburg apparatus at the light period temperature are represented. Neither photosynthetic nor respiratory measurements made in the highly artificial environment of the Warburg apparatus represent how the tissue was capable of

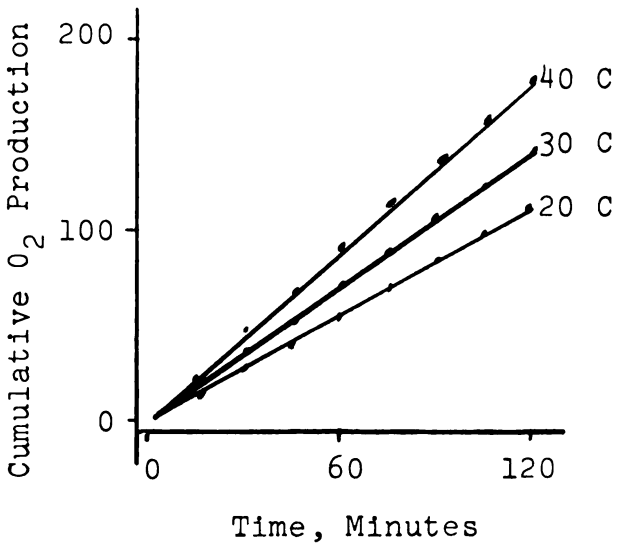

Figure 1.--Cumulative O_2 Production of Leaves Grown and Tested at the Indicated Temperatures. Microliters per Square Centimeter.

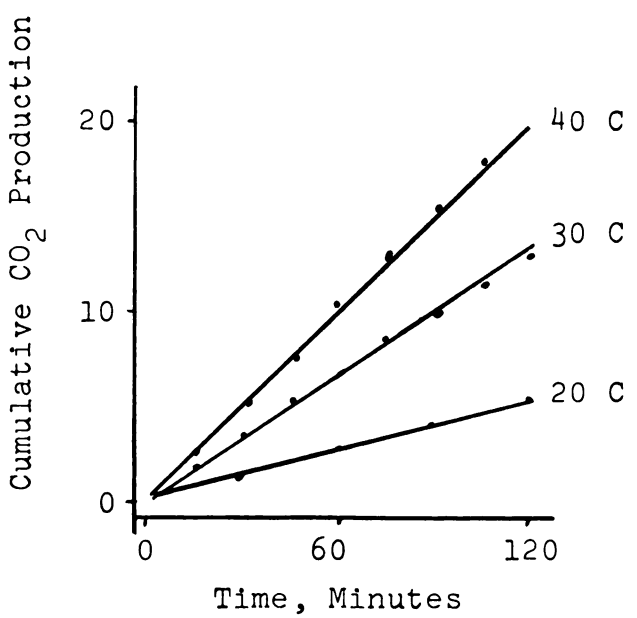

Figure 2.--Cumulative CO_2 Production of Leaves Grown and Tested at the Indicated Temperatures. Microliters per Square Centimeter.

reacting to the conditions extant in the growth chamber. The data are presented and must be interpreted within the framework of these restrictions.

Photosynthetic rates of tissue grown and tested at the temperature levels indicated ranked as 40>30>20 C. Respiratory rates ranked in the same order. Rates of tissue grown and tested at the highest temperature level continued to be greater than those of tissue grown and tested at lower temperatures.

It has been pointed out that leaf tissue grown at the various temperature regimes was continuously changing as the temperature levels increased. So that the results of the previous study could be interpreted, the photosynthetic rates per unit area of tissue grown at 20-10 and 40-30 C were determined at 20, 30 and 40 C as a control experiment (Table 11). The ranking of activity was 30>40>20 C in tissue grown at both 20-10 and 40-30 C. The photosynthetic rates of tissue produced at the two temperature levels were also significantly different when they were tested at the same temperature.

In order to compare the response of photosynthetic activity to temperature in leaves produced at the two temperature regimes, the rates were placed on a relative basis. The means of the rates at 20 C were assigned the value 1.0 and rates at 30 and 40 C are shown relative to this base rate (Table 12). The relative rates were the

TABLE 11.--Photosynthetic rate of leaf tissue grown at 20-10 and 40-30 C and tested at the indicated temperatures: microliters per square centimeter per hour.

Temperature Regime Grown	Test Temperature		
	20 C	30 C	40 C
20-10 C	55.3	80.9	61.0
40-30 C	68.1	95.2	88.5
t Test Value*	5.297**	3.808**	4.792**

*Value of t test for significance between means at the indicated temperatures.

TABLE 12.--Relative photosynthetic rate per unit area of leaves grown at 20-10 and 40-30 C and tested at the indicated temperatures.

Temperature Regime Grown	Test Temperature		
	20 C	30 C	40 C
20-10 C	1.00	1.46	1.10
40-30 C	1.00	1.40	1.30
t Test Value*		1.003	2.143*

*Value of t test for significance between means at the indicated temperatures.

same at 30 C in both tissues. At 40 C, however, the relative rate of leaf tissue grown at 40-30 C was greater than that of tissue grown at 20-10 C.

The respiratory rates per unit area of leaf tissue grown at 20-10 and 40-30 C were also determined at 20, 30 and 40 C (Table 13). The ranking of activity was 40>30>20 as was found in the initial test when leaf tissue was tested at the light period temperature under which the plants were grown. In contrast to the photosynthetic rate, no difference was found between tissue grown at the two temperature regimes when tested at the same temperature.

The effects of increasing the temperature level were manifested within one week upon leaf dry matter production (Appendix Table I) and percentage dry weight (Appendix Table III). The effects were not time dependent through the course of the four-week period the plants were held under a given temperature regime. The same time response was found for dry weight per square centimeter, chlorophyll content, and water soluble carbohydrate content (Appendix Tables V, VII, IX and XI respectively).

TABLE 13.--Respiratory rate of leaf tissue grown at 20-10 and 40-30 C and tested at the indicated temperatures: microliters per square centimeter per hour.

Temperature Regime Grown	Test Temperature		
	20 C	30 C	40 C
20-10 C	2.8	6.9	9.3
40-30 C	3.0	6.7	9.8
t Test Value*	1.007	0.615	0.764

*Value of t test for significance between means at the indicated temperatures.

DISCUSSION OF RESULTS

Growth of an autotrophic green plant such as creeping bentgrass entails a catenary series of processes. In order for the end product, dry weight, to accumulate, all must be capable of reaching a delicate balance within the living system. Stress upon the system may effect one, a few, or many of the processes involved. The final effect may well be the same, whether few or many are affected. All are inter-dependent and reduction of the rate of any single process may conceivably reduce the amount of product formed.

Production of leaf dry matter in this study followed the same general type of pattern as previously reported for cool season grasses (3, 5, 9, 23). More new leaf tissue was produced at the 20-10 C temperature regime than at any of the others studied. A gradual decrease was found from the 20-10 C level to the 30-20 C. When the temperature was raised further, a precipitous decrease in dry matter production took place. At 40-30 C, very little new leaf growth was produced between harvests.

Change in leaf dry matter production can come about through modification of leaf area and leaf dry weight per unit area. Leaf area of a grass is a function of leaf width or length or a combination of both.

In this study, leaf width was found to decrease as temperature increased from 20-10 to 30-20 C. Leaf length, however, changed very little. Dry weight per unit area increased between these temperature regimes. A small decrease in leaf dry matter production resulted. The decrease in leaf width was to some extent offset by the increased weight per unit area.

At the higher temperatures both leaf width and leaf length decreased markedly. Dry weight per unit area continued to increase. The resultant was a highly significant decrease in dry matter production at 35-25 and 40-30 C. The precipitous decrease in leaf area produced overshadowed the upward trend in dry weight per unit area. Change in leaf length, width, and dry weight per unit area have a multiplicative effect upon the dry weight of leaf tissue produced.

Change in leaf width had its greatest influence in decreasing dry matter production at the lower temperature regimes. Conversely, a small decrease in leaf width coupled with a large decrease in leaf length plus reduction of turf density resulted in reduced dry matter production at the highest temperatures.

The turf as a whole was much less vigorous at higher temperatures. Such turf in the field would be less resistant to disease and insect attack or weed encroachment, and would be less able to recover from damage caused by

use of the turf. The less vigorous plants would have a reduced ability to recover from or resist stress placed upon them by another factor of the environment whether natural or mechanical.

On a dry weight basis, chlorophyll content decreased sharply at the 40-30 C temperature level. However, percentage dry weight increased sharply, thus confounding the chlorophyll determination. Visual observation of the tissue produced, however, indicated that leaves at the highest temperature appeared to retain their green coloration. The amount of chlorophyll per square centimeter of leaf area was then calculated. On this basis, the large decrease in chlorophyll content was not present as it was on a weight basis. On an area basis, there was more chlorophyll present at the 40-30 C than at the 20-10 C level. The large decrease in chlorophyll content per milligram dry weight was probably more apparent than real because of other changes which were taking place in the tissue at the highest temperature regime. On either basis, the production of leaf dry matter could not be equated with chlorophyll content of the leaf tissue.

Carbohydrate production is the resultant of a series of reactions which must take place in sequential order. Not only must photosynthetic carbon reduction take place, but the product must be transported from the site of synthesis to the non-photosynthetic portions of the plant

which are dependent upon the green portions for a supply of respiratory substrate. If the supply of carbohydrate becomes depleted, the autotrophic plant will exhibit a decreased growth rate because of the decreased supply of respiratory carbon skeleton.

Carbohydrate levels within the leaf tissue of the creeping bentgrass of this study varied very little from the 20-10 to the 30-20 C level. Production of leaf tissue decreased slightly between these regimes, but the trend was statistically nonsignificant at the 1 per cent level.

Dry matter production was significantly reduced at the 35-25 C temperature regime. The amount of 85 per cent ethanol soluble carbohydrate, increased slightly as did the amount of water soluble carbohydrate.

At the highest temperature, there was a highly significant decrease in leaf tissue production and a highly significant increase in 85 per cent ethanol soluble carbohydrate content, water soluble carbohydrate content, and percentage dry weight of harvested leaf tissue. The amount of water soluble carbohydrate increased 51 per cent at 40-30 C compared to the mean of that found at the lower temperature regimes. On the same basis, percentage dry weight increased 61 per cent. The increase in percentage dry weight was largely accounted for by increase in carbohydrate content. None of the other components of the dry weight were determined, therefore, the data do not show what made up the remainder of the dry weight not accounted for by carbohydrate.

The finding that carbohydrate content of leaf tissue increased at the highest temperature prompted investigation of the content in lower leaf sheath, stem, and stolon. The cause of the increased leaf carbohydrate content could have been a breakdown in translocation of material from the leaf to lower portions of the plant. This investigation showed that the amount of water soluble carbohydrate in tissues of the lower portion of green plants was of the same order of magnitude as that found in the leaves. This finding was interpreted as showing that translocation of carbohydrate from leaves to lower portions of the plant was not disrupted.

The amount of water soluble carbohydrate present in the lower portion of plants which were becoming visibly chlorotic at the highest temperature was also investigated. Although these plants were visibly harmed in that they were not actively growing and were turning yellow, the amount of water soluble carbohydrate present was of the same order of magnitude as that found in green plants at the same temperature.

At no temperature regime could the amount of carbohydrate present be directly equated with dry matter production of new leaf tissue. Rather, the two were inversely related. When leaf dry matter production was at its greatest, carbohydrate content of both leaf and lower portions of the plant was at its lowest. Conversely, when

leaf dry matter production was at its ebb, carbohydrate content was at its peak.

Photosynthetic rates were determined manometrically. Photosynthetic oxygen production was evaluated in an environment where neither carbon dioxide nor light limited activity. Under these conditions, the temperature dependent, nonphotochemical reactions of photosynthesis were evaluated.

The photosynthetic rate per unit area of leaves grown at 20-10, 25-15 and 40-30 C was determined at the light period temperature. The results of this study indicated a steadily increasing rate per unit area from the lowest temperature to the highest. However, this result conflicted with the results of other investigators who have reported the effect of this temperature level on the photosynthetic rate of grasses. In their studies, Murata and Iyama (16) found a reduction of photosynthetic rate at 40 C, as did Miller (15). It has been shown in the previous discussion that numerous changes were taking place in the leaf tissue produced as the temperature was increased. This evidence indicated that changes were taking place which made the base, leaf area, a significant variable due to qualitative and/or quantitative changes within the leaf as temperature increased. The photosynthetic activity of leaves produced at 20-10 and 40-30 C was determined at 20, 30 and 40 C as a control experiment to elucidate the

steadily increasing photosynthetic rate found in the previous study. Leaves grown at 40-30 C exhibited a greater photosynthetic rate per unit area than those grown at 20-10 C when both tissues were tested at 20, 30 and 40 C. This effect may have been caused by morphological changes within the leaf tissue produced at the two temperature regimes. One possible change is indicated indirectly by the observed change in leaf size as temperature was increased. Each cell produced at 40-30 C, although physically smaller than those produced at 20-10 C, would be expected to retain a certain level of autonomy. A greater number of the smaller cells would be present per unit leaf area. Because of the greater number of cells per unit area, there may have been a quantitatively greater concentration of photosynthetically active units per unit leaf area. This larger number of phyotsynthetic units per unit leaf area would be capable of exhibiting a greater photosynthetic rate per unit area of leaf even if the rate per photosynthetic unit was the same in both tissues. El-Sharkawy and Hesketh (6) noted that there seemed to be an inverse relationship between cellular diameter and photosynthetic rate. They suggested that the reason for the relationship observed was due to a surface to volume factor.

In order to compare the response of photosynthetic activity to temperature in leaf tissue grown at 30-20 and 40-30 C, the observed rates were placed on a relative basis.

The relative photosynthetic rate of leaf tissue grown at the two temperatures was quite similar at 30 C compared to 20 C. The Q_{10} of both tissues was essentially the same between 20 and 30 C. In both tissues, the relative rate at 40 C was less than that at 30 C, therefore the Q_{10} between 30 and 40 C was less than unity in both. At 40 C, the relative rate of leaf tissue grown at 40-30 C was greater than that of tissue grown at 20-10 C. The depression in Q_{10} value of leaf tissue grown at 40-30 C was less than the depression in leaves grown at 20-10 C. This difference in the depression of Q_{10} between 30 and 40 C is a qualitative difference in the leaf tissue grown at the two temperatures.

These results indicate that adaptive mechanisms of both a quantitative and qualitative nature played a role in influencing the photosynthetic activity per unit area of leaves grown at the various temperature levels. These postulated adaptive mechanisms affected the results observed in the initial study. The steadily rising photosynthetic rate per unit area of leaf was occasioned by continuous changes within the leaf leading to different photosynthetic capability per unit area of leaves grown at the various temperature levels.

Similar effects of the influence of the temperature under which the leaf tissue was produced was not evidenced for the respiratory rate. The respiratory rate was still

increasing at the highest temperature in all tissues tested. The rate per unit area of leaves grown at 20-10 and 40-30 C was essentially equal.

Adaptive mechanisms affecting the photosynthetic rate per unit area were indicated in this study. The total amount of net photosynthesis is a function of both the photosynthetic rate per unit area and the amount of leaf area present. The amount of leaf area produced at the higher temperatures was much less than that produced at the lower temperatures. The total amount of photosynthesis and thereby growth would be much lower at the high temperature regime.

If only the effects measured in this study affected the growth of bentgrass plants at high temperature, the plants might be expected to survive quite well. The plants might be much smaller, but photosynthetic capability and carbohydrate levels were adequate. The diametrically opposite result was observed. When the temperature was increased to the 40-30 C level, the turf became thinner in stand due to death of plants. The results of this study do not provide evidence for the cause of plant death at the 40-30 C level.

SUMMARY

Some effects of above optimum temperatures upon the growth of creeping bentgrass were investigated.

The amount of dry matter produced as measured by weekly harvests of leaf tissue decreased slightly from the 20-10 C regime through the 25-15 and 30-20 C. When the temperature was increased further to 35-25 C, a sharp decrease in dry matter production took place. At 40-30 C, very little new leaf tissue was produced between harvests.

Reduction in dry matter production came about through the action of three separate effects, leaf length, leaf width, and leaf weight per unit area. Decrease in leaf width was the most important at the lower temperature regimes. The effect was nearly countered by increased leaf dry weight per unit area. At the higher temperatures of 35-25 and 40-30 C there was a precipitous decrease in leaf length. Dry weight per unit area continued to increase at these temperatures but was overshadowed by the large decrease in leaf length.

The dry weight percentage of leaf tissue increased slightly as temperature was increased above 20-10 C until at 40-30 C a large and highly significant increase took place.

Dry weight per unit area trended upward linearly from the lowest temperature to the highest.

The amount of 85 per cent ethanol soluble carbohydrate and water soluble carbohydrate remained essentially the same at 20-10, 25-15 and 30-20 C. A slight increase was noted in both fractions at 35-25 C. A highly significant increase was found in both carbohydrate fractions at 40-30 C.

The content of water soluble carbohydrate present in leaf sheath, stem and stolon tissue was on the same order of magnitude as that found in leaf tissue grown at the same temperature.

When leaves grown at 20-10, 30-20 and 40-30 C were tested for cumulative O_2 and CO_2 production in the Warburg apparatus at the light period temperatures under which they were grown, activity ranked as 40>30>20 for both.

When leaves grown at 20-10 C were tested at 20, 30 and 40 C, the ranking was 30>40>20 for photosynthetic rate and 40>30>20 for respiratory rate. Leaves grown at 40-30 C exhibited the same ranking of activity.

Comparison of relative photosynthetic rates of leaves grown at 20-10 C with those produced at 40-30 C and tested at 20,30 and 40 C indicated that quantitative and qualitative changes were taking place within the leaf tissue. These changes indicated that adaptive mechanisms influenced the photosynthetic rate per unit area in leaf tissue grown at the highest temperature level.

Although ample carbohydrate was found in leaf tissue grown at the highest temperature, and adaptive mechanisms

for photosynthetic rate per unit area were indicated, plants died at the highest temperature. The effects measured in this study did not account for their death.

CONCLUSIONS

The following conclusions were drawn from the results of the study.

1. Decrease in leaf dry matter production was dependent upon decrease in leaf width and leaf length. Leaf width was more important at the lower temperatures. Leaf length was more important at the higher temperatures.
2. Decrease in leaf dry matter production could not be equated with a change in chlorophyll content of the leaf tissue on either a dry weight or area basis.
3. Diminished leaf dry matter production could not be equated with leaf content of either 85 per cent ethanol or water soluble carbohydrate.
4. Indreased carbohydrate content of leaf tissue at 40-30 C could not be accounted for by disruption of transport out of the leaf into lower portions of the plant.
5. Reduction of turf density at 40-30 C could not be attributed to depleted carbohydrate reserves in chlorotic appearing plants.

6. Morphological changes within the tissue of leaves grown at 40-30 C resulted in a quantitative increase in the photosynthetic rate per unit area compared to leaves grown at 20-10 C.
7. Uncharacterized qualitative changes in the leaf tissue grown at 40-30 C resulted in a smaller depression of Q_{10} of photosynthetic rate per unit area at 40 C than in leaves grown at 20-10 C.
8. The results of this study do not provide evidence for the cause of death of plants at 40-30 C. Metabolic derangements not investigated resulted in plant death and a thinner turf at this temperature level.

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LITERATURE CITED

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APPENDIX

APPENDIX TABLE 1.--Leaf dry matter production, grams per 25.8 square decimeters.

Temperature Regime	Replication (Week)				Sum	Mean
	1	2	3	4		
20-10 C	12.62	15.76	14.96	10.47	53.80	13.45
25-15 C	13.54	13.04	13.08	12.25	51.91	12.98
30-20 C	12.36	11.77	11.88	9.77	45.78	11.45
35-25 C	7.91	10.72	6.38	8.63	33.64	8.41
40-30 C	2.88	5.16	2.08	2.12	12.24	3.06
Sum	49.31	56.45	48.37	43.24	197.37	

APPENDIX TABLE II.--Analysis of variance, leaf dry matter production, grams per 25.8 square decimeters.

Source	df	SS	MS	F
Total	19	331.84		
Replications	3	17.74	5.91	3.50
Treatments	4	293.84	73.46	43.47**
Linear Effect	1	256.99	256.99	152.07**
Quadratic Effect	1	31.68	31.68	18.75**
Residual Effect	2	5.17	2.59	1.53
Error	12	20.26	1.69	

APPENDIX TABLE III.--Per cent dry weight of harvested leaf clippings.

Temperature Regime	Replication (Week)				Sum	Mean
	1	2	3	4		
20-10 C	21.19	21.68	19.76	19.99	82.62	20.66
25-15 C	22.76	20.45	22.01	21.27	86.49	21.62
30-20 C	21.81	22.22	22.45	23.12	89.60	22.40
35-25 C	23.78	24.12	23.58	24.12	95.60	23.90
40-30 C	29.38	33.79	37.36	37.26	137.79	34.45
Sum	118.92	122.26	125.16	125.76	492.10	

APPENDIX TABLE IV.--Analysis of variance, per cent dry weight of harvested leaf clippings.

Source	df	SS	MS	F
Total	19	556.07		
Replications	3	5.90	1.97	0.55
Treatments	4	506.90	126.73	35.20**
Linear Effect	1	356.71	356.71	99.09**
Quadratic Effect	1	98.83	98.83	27.45**
Cubic Effect	1	34.13	34.13	9.48**
Residual Effect	1	17.23	17.23	4.79
Error	12	43.25	3.60	

APPENDIX TABLE V.--Leaf dry weight, mg per square centimeter.

Temperature Regime	Replication (Week)				Sum	Mean
	1	2	3	4		
20-10 C	1.60	1.71	1.81	1.76	6.88	1.72
25-15 C	2.05	2.06	2.31	2.32	8.74	2.19
30-20 C	2.18	2.19	2.16	2.18	8.71	2.18
35-25 C	2.38	2.55	2.42	2.27	9.62	2.41
40-30 C	2.89	2.69	2.70	2.39	10.67	2.67
Sum	11.10	11.20	11.40	10.92	44.62	

APPENDIX TABLE VI.--Analysis of variance, leaf dry weight, mg per square centimeter.

Source	df	SS	MS	F
Total	19	2.20		
Replications	3	0.02	0.007	0.35
Treatments	4	1.94	0.49	24.50**
Linear Effect	1	1.79	1.79	89.50**
Residual Effect	3	0.15	0.05	2.50
Error	12	0.24	0.02	

APPENDIX TABLE VII.--Chlorophyll content of harvested leaf clippings, micrograms per mg dry weight.

Temperature Regime	Replication (Week)				Sum	Mean
	1	2	3	4		
20-10 C	8.78	8.48	8.88	8.91	35.05	8.76
25-15 C	9.08	9.18	8.97	10.15	37.38	9.35
30-20 C	10.37	10.53	10.46	9.97	41.33	10.33
35-25 C	10.05	9.25	11.47	10.99	41.76	10.44
40-30 C	6.97	5.77	7.32	6.82	26.88	6.72
Sum	45.25	43.21	47.10	46.84	182.40	

APPENDIX TABLE VIII.--Analysis of variance, chlorophyll content of harvested leaf clippings, micrograms per mg dry weight.

Source	df	SS	MS	F
Total	19	42.06		
Replications	3	1.92	0.64	2.21
Treatments	4	36.60	9.15	31.55**
Linear Effect	1	3.58	3.58	12.34**
Quadratic Effect	1	22.45	22.45	77.41**
Cubic Effect	1	7.17	7.17	24.72**
Residual Effect	1	3.40	3.40	11.72**
Error	12	3.54	0.29	

APPENDIX TABLE IX.--Content of 85 per cent ethanol soluble carbohydrate in harvested leaf clippings. Per cent of dry weight.

Temperature Regime	Replication (Week)				Sum	Mean
	1	2	3	4		
20-10 C	4.5	5.0	4.9	6.3	20.7	5.2
25-15 C	5.5	5.6	5.5	4.1	20.7	5.2
30-20 C	4.6	4.8	5.0	5.8	20.2	5.1
35-25 C	5.9	6.0	5.7	5.1	22.7	5.7
40-30 C	8.0	9.1	7.9	7.4	32.4	8.1
Sum	28.5	30.5	29.0	28.7	116.7	

APPENDIX TABLE X.--Analysis of variance, content of 85 per cent ethanol soluble carbohydrate in harvested leaf clippings. Per cent of dry weight.

Source	df	SS	MS	F
Total	19	32.81		
Replications	3	0.50	0.17	0.35
Treatments	4	26.58	6.65	13.48**
Linear Effect	1	16.13	16.13	33.60**
Quadratic Effect	1	7.98	7.98	16.63**
Residual Effect	2	2.47	1.24	2.58
Error	12	5.73	0.48	

APPENDIX TABLE XI.--Content of water soluble carbohydrate in harvested leaf clippings. Per cent of dry weight.

Temperature Regime	Replication (Week)				Sum	Mean
	1	2	3	4		
20-10 C	6.8	5.8	5.0	6.9	24.5	6.1
25-15 C	7.4	6.8	6.2	4.9	25.3	6.3
30-20 C	5.4	5.7	5.3	6.5	22.9	5.7
35-25 C	8.8	7.8	7.2	7.2	31.0	7.8
40-30 C	9.5	10.8	9.7	9.4	39.4	9.8
Sum	37.9	36.9	33.4	34.9	143.1	

APPENDIX TABLE XII.--Analysis of variance, content of water soluble carbohydrate in harvested leaf clippings. Per cent dry weight.

Source	df	SS	MS	F
Total	19	55.35		
Replications	3	2.44	0.81	1.33
Treatments	4	45.65	11.41	18.70**
Linear Effect	1	31.51	31.51	51.65**
Quadratic Effect	1	10.32	10.32	16.91**
Residual Effect	2	3.82	1.91	3.13
Error	12	7.26	0.61	

APPENDIX TABLE XIII.--Photosynthetic rate of leaves grown at the indicated temperature regime and tested at the light period temperature extant. Microliters per square centimeter per hour.

Temperature Regime	Replication (Week) 1	2	3	4	Sum	Mean
20-10 C	55.84	59.78	55.17	50.51	221.30	55.33
25-15 C	62.50	66.15	63.73	72.61	264.99	66.25
30-20 C	68.35	72.75	73.16	70.78	285.04	71.26
35-25 C	79.75	78.16	70.97	79.05	307.93	76.98
40-30 C	92.03	92.71	89.03	80.23	354.00	88.50
Sum	358.47	369.55	352.06	353.18	1433.26	

APPENDIX TABLE XIV.--Analysis of variance, photosynthetic rate of leaves grown at the indicated temperature regime and tested at the light period temperature extant. Microliters per square centimeter per hour.

Source	df	SS	MS	F
Total	19	2,699.86		
Replications	3	38.35	12.78	0.67
Treatments	4	2,432.81	608.20	31.91**
Linear Effect	1	2,376.84	2,376.84	124.70**
Residual Effect	3	55.97	18.66	0.98
Error	12	228.70	19.06	

APPENDIX TABLE XV.--Respiratory rate of leaves grown at the indicated temperature regime and tested at the light period temperature extant. Microliters per square centimeter per hour.

Temperature Regime	Replication (Week)				Sum	Mean
	1	2	3	4		
20-10 C	2.52	2.51	2.87	3.31	11.21	2.80
25-15 C	5.11	4.94	5.62	5.25	20.92	5.23
30-20 C	5.59	6.18	6.24	6.79	24.80	6.20
35-25 C	9.74	9.53	9.24	7.71	36.22	9.05
40-30 C	10.63	9.76	10.26	8.49	39.14	9.79
Sum	33.59	32.92	34.23	31.55	132.29	

APPENDIX TABLE XVI.--Analysis of variance, respiratory rate of leaves grown at the indicated temperature regime and tested at the light period temperature extant. Microliters per square centimeter per hour.

Source	df	SS	MS	F
Total	19	137.07		
Replications	3	0.79	0.26	0.54
Treatments	4	130.51	32.63	67.98**
Linear Effect	1	126.59	126.59	263.73**
Residual Effect	3	3.92	1.31	2.73
Error	12	5.77	0.48	

APPENDIX TABLE XVII.--Photosynthetic rate at three temperatures and two light intensities.

Test Temperature	Photosynthetic Rate, Microliters per Square cm per Hour	
	2600 fc	3200 fc
20 C	24.60	25.96
30 C	32.33	31.20
40 C	24.93	23.92

APPENDIX TABLE XVIII.--Photosynthetic rate of leaves at three calculated carbon dioxide levels and 30 C. Microliters per mg dry weight per hour.

Calculated per cent Carbon Dioxide Concentration	Photosynthetic Rate
1.5	22.77
7.2	18.73
20.5	23.63