EFFECTS OF SOIL TEMPERATURE GRADIENT ON GROWTH AND CARBOHYDRATE AND NUTRIENT ELEMENT LEVELS IN THREE WARM-SEASON TURFGRASSES

By

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A DISSERTATION PRESENTED TO THE GRADUATE COUNCIL OF
THE UNIVERSITY OF FLORIDA
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE
DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1974

Dedicated to my wife Betty

ACKNOWLEDGEMENTS

I wish to thank Dr. S. H. West and Dr. G. C. Horn for serving as Chairmen of my Supervisory Committee. A special and sincere thanks is extended to Dr. J. N. Joiner for his guidance and patience during preparation of this manuscript.

I would also like to thank Dr. W. L. Currey, Dr. O. C. Ruelke, Dr. G. S. Smith and Dr. J. W. Strobel for their guidance and suggestions during the course of this research. Appreciation is extended to others at Ornamental Horticulture Greenhouses and Research Unit for their contribution.

And deepest appreciation is extended to my wife Betty for her support and understanding without which this degree would not have been accomplished.

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EFFECTS OF SOIL TEMPERATURE GRADIENT ON GROWTH AND CARBOHYDRATE AND NUTRIENT ELEMENT LEVELS IN THREE WARM-SEASON TURFGRASSES

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June, 1974

Chairman: Dr. S. H. West
Major Department: Agronomy

Effects of soil temperatures on growth of warm-season turfgrasses are important from a management standpoint, thus the objective of this work was to evaluate growth and tissue levels of carbohydrates and nutrient elements of 'Argentine' bahiagrass, Paspalum notatum Flugge, 'Floratine' St. Augustinegrass, Stenotaphrum secundatum (Walt.) Kuntz, and 'Tifgreen' bermudagrass, Cynodon dactylon (L.) Pers. X C. transvaalensis Davy as affected by a gradient of soil temperatures. An aluminum alloy plate was developed into a temperature gradient apparatus to maintain temperature of potted grass plugs or stolons at 10 to 46°C range. The three grasses were utilized in a six-day stolon study and grass plug studies of five to eight weeks duration. Growth was evaluated by terminal dry weight of clippings and plant parts and analyses of tissue for nutrient element levels and total nonstructural carbohydrates (TNC) on percent and total weight bases. Shoot growth decreased with decreasing soil temperatures, whereas rhizome growth increased. Higher soil temperatures were optimum for shoot than for rhizome and root growth. TNC levels in grass tissue responsed inversely or not at all to shoot growth but responded directly with rhizome and root growth. Root growth had higher optimum soil temperature on short term (6-day) than on long term bases. Carbohydrate reserves (TNC) were preferentially utilized for shoot growth with increasing soil temperatures but were translocated basipetally at cooler temperatures for growth and storage in rhizome and root tissue.

INTRODUCTION

Bahia, St. Augustine, and bermuda grass constitute the most important ornamental turfgrasses in Florida in terms of production, acreage, and value. However, little research is available on factors affecting growth of these warm-season turfgrasses.

Three major classes of factors affecting turfgrass growth are climatic, edaphic, and cultural practices. These interact to form the growing environment to which turfgrasses respond. Soil temperature, a climatic-edaphic factor, assumes major importance since it modifies and controls growth of almost half of the turfgrass plant tissue and has a significant indirect effect on the other half.

Limited investigations have been accomplished in which soil temperatures were monitored or evaluated on warm season turfgrass growth, and little consideration has been extended this factor when planning and undertaking cultural practices on such grasses. Top growth and aboveground environmental factors have been used primarily as the indicators for evaluation and cultural management of turfgrasses.

A better understanding of soil temperature effects on warm season turfgrasses can lead to cultural practices which improve factors detrimental to winter growth and survival of these grasses. This study was thus initiated to evaluate effects of soil temperature on total growth and chemical composition of 'Argentine' bahia, 'Floratine' St. Augustine, and 'Tifgreen' bermuda grass.

REVIEW OF LITERATURE

Temperature Effects on Turfgrasses

Shoot Growth

Plants have a range of three cardinal temperatures: Minimum temperature range is the lowest at which growth occurs, optimum is range at which growth is most active, and maximum is the highest range at which growth can occur (45, 60). Plant cardinal temperatures vary from species to species, within species and even between various plant parts on the same plant (6). Beard (6) pointed out the optimum temperature for maximum shoot growth may not be the same for maximum quality or desirability.

Numerous experiments have been reported which bracket air temperature range of 15.5 to 25°C (60 to 77°F) as optimum for maximum shoot growth of cool-season turfgrasses (6, 9, 15, 18, 28, 29, 34, 54, 60, 71). A few studies have reported a higher temperature range of 26 to 35°C (78 to 95°C) for maximum shoot growth of warm-season turfgrasses (6, 9, 29, 35, 49). Miller (34) reported that maximum photosynthetic rate of creeping bentgrass, a cool-season grass, occurred at 25°C (77°F) and maximum rate for bermudagrass, a warm-season grass, at 35°C (95°F).

Cooper and Tainton (9) divided forage grasses into temperate Festucoid grasses, having temperature optima between 20 to 25°C (68 to 77°F), and subtropical or tropical non-festucoid grasses (Panicoid and Chloridoid species), having an optimum range between 30 to 35°C (86 to 95°F). Beard (6), in a literature review, states that temperature above or below optimum range drastically reduced shoot growth.

Minimum and maximum temperature ranges are more difficult to delineate than temperature optima since nutrition, hydration, humidity, and temperature duration influence them markedly. Youngner (70) indicated that bermudagrass stopped top growth and proceeded into dormancy at approximately 10°C (50°F). Brown (7) observed that shoot growth of Kentucky and Canada bluegrass continued at 4.4°C (40°F). Ketellapper (21) concluded that soil temperature rather than air temperature was the determining factor for induction of summer dormancy in work with Reed Canarygrass.

Root Growth

Optimum temperatures for root growth of warm- and cool-season grasses are as disparate as for shoot growth, but ranges are lower for both. Beard (6), in a literature review, reported the optimum temperature range for root growth of most cool season turfgrasses was between 10 to 18.3°C (50 to 65°F), whereas, the optimum range for root growth of most warm season turfgrasses was 24 to 29.5°C (75 to 85°F). He added that information was limited concerning warm season turfgrasses.

Brown (7) used Cynodon dactylon and found the optimum temperature for maximum root weight was 37.8°C (100°F), and Lovvorn (28) observed similar results with the same species, although he gave the optimum for root growth as between 26.7 to 32.2°C (80 to 90°F). These early works did not consider the fact that entire plants were subjected to the reported temperatures and were maintained at low fertility with infrequent or no clipping of shoot growth.

Recently, Youngner (72) controlled air temperatures and varied root temperatures along a gradient and showed that a soil temperature of 23.3°C (74°F) provided maximum root weight and root length for Cynodon dactylon L.

West et al. (67) grew Digitaria decumbens Stent., a warm-season forage grass, on a gradient of soil temperatures for two weeks utilizing terminal stolon pieces and reported that maximum root weight and length occurred within a range of 31 to 34°C (88 to 93°F), but maximum root number occurred between 24 to 26°C (75 to 79°F). Schroder (50) grew 'Pensacola' bahiagrass, 'Coastal' bermudagrass, Pangolagrass and 'Slenderstem' digitgrass, warm-season grasses, over a range of soil temperatures and obtained maximum root weight between 26.7 to 30°C (80 to 86°F) under pasture management conditions.

Root morphology was influenced by soil temperatures, according to Beard (6), who stated, in a literature review, that optimum soil temperatures produced turfgrass roots that were multibranched, thick, and white, whereas, roots grown at temperatures below optimum were thicker, shorter, and less to non-branched (21, 58). Beard (6) also indicated that soil temperatures above optimum hastened maturity and senescence, resulting in brown, spindly roots.

Seasonal variation in root growth of temperate grasses has been documented with the findings that most growth occurred in early spring and, to a lesser extent, in late fall when soil temperatures were low (4, 7, 44, 56, 73).

Youngner (73) stated that little was known of seasonal root growth patterns for warm-season grasses, but he noted that growth of stolons and roots of such grasses occurred simultaneously throughout the summer, thus seasonal responses may not be as obvious as with cool-season grasses. In contrast, he felt that root initiation and subsequent growth might occur in winter and early spring when no active top growth was visible.

Water absorption and movement within plants might be reduced at low soil temperatures according to Richards et al. (45), Nielson and Humphries (41), Kramer (25), Kleinendorst and Brouwer (22), and Mongelard and Mimura (36). Kramer (25) reported this could be caused by factors, such as increased viscosity of water, increased viscosity of protoplasm, decreased permeability of cells, decreased rate of movement of water from soil to root, and retardation of root elongation. Reduced water absorption can restrict growth only if transpiration rate exceeds absorption causing wilting. Davis and Lingle (13) concluded from work with shoot responses to root temperature in tomato that control of shoot growth by soil temperatures was not based on mineral or water availability to the shoot.

Nielson and Humphries (41) indicated that soil temperature influenced soil aeration, more specifically soil oxygen concentration and carbon dioxide tension around roots. Reduced soil temperatures would decrease oxygen diffusion through the soil and decrease its concentration held in ground water, however, the importance of these factors on root growth could not be determined.

Nielson and Humphries (41) pointed out that relationships between root temperature and shoot growth probably were complex since optimum root growth temperatures were lower than optimum shoot growth temperatures. They further stated that critical experiments in controlled root and shoot environments will be necessary to analyze interactions of shoot and root growth as affected by soil temperatures.

Davidson (11) studied root shoot (R/S) ratios of twelve pasture grasses and clover in which he evaluated five soil temperatures from 5 to 35°C with constant ambient temperature maintained. He found that lowest R/S ratios occurred at optimum soil temperature for forage yield and the R/S ratio increased at temperatures above or below this optimum. Troughton (59) reported that root relative to shoot growth varied directly with temperatures within the range of 10 to 26.7°C (50 to 80°F) when *Lolium perenne* L. was grown in controlled-environment cabinets. The root to shoot ratio probably is affected by soil temperatures, depending on whether they are more favorable for top growth or root growth.

Carbohydrate Levels

Smith (51, 53) classified perennial grasses into two groups based on type of nonstructural polysaccharides accumulated in vegetative plant parts. Warm-season grasses accumulate primarily starches, while temperate or cool-season grasses accumulate mostly fructosans. McIlory (32) classified carbohydrates into those involved in structural framework cells and nonstructural components, such as free monosaccharides, oligosaccharides and 'reserve' polysaccharides. Smith (52) used 'total nonstructural carbohydrates' (TNC) as an estimate of carbohydrate energy readily available to plants.

Carbohydrate reserves were defined by Beard (6) as those that accumulated in permanent organs of plants in nonstructural forms and which were available for subsequent utilization in assimilatory processes. These reserves provide energy for periods of rapid growth, regrowth from adverse conditions and as an energy source for respiration (73).

Madison (29) indicated that as temperature rose above 35°C (95°F) carbohydrate storage stopped for temperate season grasses and reserves were used up by high respiration rate. There are differences in Q_{10} of respiration and photosynthesis at different temperatures. Went (66) proposed that the photosynthesis to respiration ratio was greater than 10 at low temperatures, but at high temperatures, respiration increased relatively more than photosynthesis and an imbalance of carbohydrate synthesis and utilization was attained.

Soil temperatures affect carbohydrate status of shoots of perennial ryegrass as shown by Sullivan and Sprague (57), who reported reduced carbohydrate content of tops as soil temperature increased from 10 to 32°C (50 to 90°F). Zanoni et al. (74) stated that seasonal fluctuations in carbohydrate levels of several cool-season turfgrasses were directly related to soil temperatures. Brown and Blaser (8) found that growth of tall fescue or orchardgrass, cool-season grasses, were reduced by low soil temperatures and reserve carbohydrates increased.

Schmidt and Blaser (49) reported that growth and carbohydrate reserves in stolons of 'Tifgreen' bermudagrass were generally larger and nitrogen content less with high than with low ambient temperatures.

Youngner (72) reported that maximum carbohydrate storage of bermudagrass and Kentucky bluegrass occurred at temperatures near minimum for measurable growth. High temperatures for only a few days rapidly depleted carbohydrate reserves.

Schmidt (47) discovered that increased air temperatures around bentgrass decreased carbohydrate reserves but increased respiration, shoot growth, and carbohydrate content of bermudagrass. According to McKell, et al. (33), results with Kentucky bluegrass and 'Coastal' bermudagrass conflicted with Schmidt's (47) in that they obtained highest concentration of carbohydrates at the coolest temperatures.

According to Nowakowski et al. (42) total soluble carbohydrate content of ryegrass dry matter was least at 19.5°C (67°F) soil temperature and largest at 11°C (52°F). Davidson (11) reported a decline in total soluble carbohydrates (TSC) in ryegrass roots with increasing soil temperatures.

Youngner (73) stated in summary that warm-season grasses accumulated reserve carbohydrates at higher temperatures than cool-season grasses and that seasonal fluctuations in carbohydrate reserves were largely results of changes in climatic conditions. Numerous authors agree that temperature is a major factor dictating carbohydrate accumulation and utilization (7, 34, 57, 61). Youngner (73) also stated that the maximum rate of reserve carbohydrate accumulation in cool-season grasses occurred in late fall during periods of slow shoot growth and gradual decrease occurred during winter with slight increase prior to the drastic reduction due to spring regrowth after which reserves may increase slowly into the autumn. He further stated that warm-season grasses show a similar trend with maximum accumulation in the fall and gradual depletion during winter dormancy. The only difference was a marked increase of reserves during the summer in contrast to a decrease in cool-season grasses. Schmidt (47) reported that carbohydrates in bermudagrass stolons decreased during the winter and spring, increased during summer, and reached a maximum by late fall.

Apparently carbohydrate storage capabilities of rhizomes are several fold greater than that of roots in the warm-season grasses. Reserve carbohydrates of cool-season grasses appear to fluctuate more widely than that in warm-season grass species.

Elemental Nutrition

Nielson and Humphries (41) indicated that soil temperature influenced plant nutrition by changing effective concentrations of soluble nutrients in the soil or by affecting ability of plants to absorb and utilize them. Extremes of temperature in field situations indirectly alter mineral availability due to affects on microbial decomposition of organic materials. They further stated that size and activity of plant root systems determined their ability to obtain many nutrients, especially those of low soil mobility. Therefore, if temperature restricted root growth, nutrient absorption also would be restricted, especially if any of these non-mobile nutrients were scarce. Kramer (25) indicated that ion concentration in soil nutrient solution is temperature dependent and low soil temperatures reduced ion availability and concentration.

Harrison (18) studied responses of Kentucky bluegrass to temperature and nitrogen fertility, and his results indicated that maximum root weights were obtained at lowest temperature 16.1°C (60°F) and no added nitrogen.

Nowakowski et al. (42) reported that increased soil temperature increased total soluble-nitrogen in Italian ryegrass and decreased protein-nitrogen whether NO_3^- or NH_4^+ forms were applied.

A review presented by Richards et al. (45) reported that low soil temperatures did not seriously retard absorption of N but possibly affected the capacity of roots to reduce absorbed nitrates and convert or assimilate them into organic nitrogenous components. Brown (7) worked with four pasture grasses and confirmed the finding that retarded growth from low temperatures was due to reduced rates of N assimilation rather than restricted N absorption.

Ryegrass was grown by Parks and Fisher (43) at three soil temperatures (10, 20, and 30°C), and they reported increased soil temperatures affected absorption of such divalent cations as Mg and Ca. They further reported that K, Ca, Mg, and P contents were retarded at 10°C (50°F) with largest yield of forage occurring at 20°C (68°F). Ehrler and Bernstein (16), however, reported contradictory results with rice which showed no interactions between root temperature and cation concentration or cation ratio. They stated that low root temperature affected only K concentration and absorption sufficiently to decrease yields.

Nielson and Cunningham (40) reported increased soil temperatures increased % Ca and % Mg in ryegrass and had little influence on concentration of N, P, S, Na, and K. the lowest soil temperature (11°C) grew ryegrass with the highest Cl content. Knoll et al. (23) studied soil temperature effects on growth of corn and concluded that P uptake increased as soil temperatures were raised from 15 to 25°C (59 to 77°F).

Davis and Lingle (13) concluded after studying shoot response to root temperature in tomato that control of shoot growth by root temperature does not reside primarily in rates of minerals or water supply to the shoots.

Cultural Practices

Soil temperature plays an important role in turfgrass growth and quality, therefore, it should be considered in turfgrass management decisions. Schmidt and Blaser (48) concluded that seasonal temperature must be considered in timing N fertilization for bentgrass development. Fertilizer timing and fertilizer rates and ratios must be governed to promote such growth and quality necessary without excesses.

Close mowing height and frequency, if performed too severely, restrict root growth for extended periods of time depending on the damage done, according to Madison (29). When soil temperatures are above or below optimum, root regrowth from such damage will be restricted significantly. Should soil temperatures be optimum for maximum root growth, mowing practices should be geared to remove the least amount of foliage as infrequently as possible. Beard (6) indicated that cutting height of greens can be raised to provide a measure of insulation against extremes in high soil temperature by increasing depth of turfgrass canopy.

Irrigation can be used to reduce soil temperatures if sufficient water is applied. Beard (5) utilized syringing (i.e., light application of water) as a method of moderating midday heat build up in turf situations and reported that an application of 0.25 inches of water to bentgrass turf at noon reduced the soil temperature at the 2 inch depth by 1.6°C (3°F). He also stated that a cool intense rain or frequent irrigations of 0.75 inches or more resulted in soil cooling.

Other cultural practices, such as covers and mulches, have proved effective in altering micro-climate of close-clipped grasses (62). Covers have been used to buffer against such extremes in cold temperature, and treated areas are usually the first to turn green in early spring. Watson (62) also mentioned the use of lamp black and other dark substances as a cover over turfgrass areas to absorb radiant heat. The common practice of topdressing greens to improve putting trueness should be avoided during warm periods as the dark topdressing material will act much like the lamp black and increase soil temperatures.

Electric heating cables recently have been installed below the soil surface to raise soil temperatures sufficiently for year-round turfgrass growth and/or prevention of soil freezing on athletic fields in winter (1, 10, 17, 26, 30, 31). According to Beard (6) the primary objective of soil warming is to protect against frost damage and to maintain green color throughout winter. Soil temperature ranges of 1.7 to 7.2°C (35 to 45°F) are sufficient to accomplish this with cool-season grasses, but a warmer soil temperature range of 15.6 to 18.3°C (60 to 65°F) is necessary for warm-season grasses to retain green color (1, 30, 31).

Recent work has been reported which utilized growth regulators such as gibberellic acid applications to grasses in order to maintain green growing tissue at or below minimum temperatures (14, 20, 37, 46, 68, 69). Other recent developments in cool temperature effects on turfgrass growth involved the use of foams as temporary blankets for cold protection (3).

METHODS AND MATERIALS

Temperature Gradient Plate Experiments

Three experiments consisting of nine treatments each placed in randomized block design were initiated to test effects of soil temperatures on growth of 'Argentine' bahiagrass, *Paspalum notatum* Flugge, 'Floratine' St. Augustinegrass, *Stenotaphrum secundatum* (Walt.) Kuntz, and 'Tifgreen' bermudagrass, *Cynodon dactylon* (L.) Pers. X *C. transvaalensis* Davy. Treatments were replicated four times with one pot containing a grass plug as the experimental unit.

A temperature plate was constructed based on apparatus by Barbour and Racine (2) and West *et al.* (67) to obtain a gradient of soil temperatures from 10 to 46°C (48 to 115°F). The apparatus consisted of an aluminum alloy plate 75 cm x 293 cm x 1.9 cm, with 28 cm of each end immersed in a sealed temperature controlled water bath. One bath was maintained at 62.8°C (145°F) and the other at 3.3°C (38°F), which created a gradient of temperatures along the plate length. Intervening plate sections were partitioned into nine compartments by 1.9 cm wood partitions at intervals of 21.6 to 29.9 cm (Figs. 1 and 2). Water filled each compartment to a level of 11.1 cm to facilitate heat transfer from plate upward, and air was bubbled for 15 seconds at intervals of 30 seconds from two locations in each compartment to prevent vertical or horizontal temperature gradients.

Four pots of grass were immersed in each compartment, and each pot provided with tubes draining outside the apparatus. Drain tubes were connected to an aquarium air stone placed at the bottom of each pot to prevent sand loss (Fig. 3).

Outsides of the apparatus were insulated with 2.54 cm thick sheets of styrofoam, and pieces of styrofoam covered water surfaces of compartments to prevent ambient temperature influence on soil temperatures.

Soil temperatures were monitored with a twenty-four-point Honeywell recorder utilizing copper constantan thermocouples placed 7 cm below soil surface in selected pots. Temperatures were recorded twice per hour with reported temperatures being the mean daily temperature and maximum diurnal flux of 2°C±. Mean soil temperatures were slightly different for the three grass experiments as shown in Table 1.

A golf course cup cutter (plugger), 10.5 cm dia., was used to obtain grass plugs, and attached soil was trimmed to 2.54 cm thickness. The three grasses were cut and moved into the greenhouse at least two weeks prior to placement on the temperature apparatus. Grass plugs were potted in sterilized fine-grade builders sand, with bahiagrass in 14 cm diameter pots and St. Augustine and bermuda grass plugs in 11 cm diameter pots (1000 ml plastic beakers). Upper external surface of pot was spray painted or covered with opaque tape to prevent sunlight reaching below soil surface. Sod of the three grasses was obtained from Pursley Grass Co. of Palmetto, Florida.

Grass plugs were fertilized before and after placement on apparatus with modified Knoop's (24) nutrient solution every two days with enough water to assure slight drainage within one minute after application. Bahia and St. Augustine grass were fertilized with this solution at the rate of 0.5 lb of N/1000 sq. ft./month and bermuda at twice this rate.

Figure 1. Experimental, compartmentalized temperature gradient plate apparatus containing four pots of grass per temperature treatment.

Figure 2. Pots of grass in one temperature compartment showing surface insulation used to maintain temperature levels.

Figure 3. Sample of pots used in the experiments, with aquarium air stone in bottom to facilitate drainage and prevent sand media loss.

Table 1. Mean soil temperatures in three experiments utilizing temperature gradient plate apparatus.

Soil Temperature (°C)	Treatment Number	Experiments		
		Bahiagrass	St. Augustinegrass	Bermudagrass
10-11	9	10°C*	11	10
15-17	8	17	17	15
19-21	7	21	21	19
21-24	6	24	23	21
25-27	5	27	26	25
27-30	4	30	29	27
31-34	3	24	33	31
37	2	37	37	37
45-46	1	45	45	46

* Temperatures were monitored 7.6 cm below soil surface.

Shoot growth measurements were accomplished with periodic clipping at 7 or 4 day intervals by hand scissors fitted with foam rubber guards to trap and hold cut grass blades. Clipping heights were 6.4 cm (2.5 in.), 5.1 cm (2 in.) and 1.9 cm (.75 in.) for bahia, St. Augustine and bermuda grass, respectively. Cutting height was established using a clear rigid fiberglass template resting on pot edges and scissors were pressed against this plate, or pot edge in the case of bermudagrass, to maintain reference heights (Fig. 4).

Clippings were immediately placed in a 70°C oven and held for at least 72 hours, at which time dry weights were taken and samples ground twice in Wiley mill fitted with 20 mesh screen.

Termination of each experiment was accomplished by removing grasses from the pots and the sand separated from the roots by repeated dips in water baths. Roots were cut from the plugs with dissecting scissors. The sod plug was then washed with a stream of water to remove remaining soil, and rhizomes (bahia and bermuda grass) were cut from shoot tissue for the various plant fractions for analysis. Tissue was then held in 70°C oven for at least 96 hours before dry weights and subsequent grinding was initiated as for clipping tissue.

Various methods have been presented, revised and modified for quantitatively extracting available carbohydrate energy source (reserves) from plant tissue (27, 38, 52, 63). The procedure of removing and analyzing Total Nonstructural Carbohydrates (TNC) from plant tissue by Smith (52) has been accepted and extensively used for temperate and tropical forage grasses and was used in this study. Oven dry plant tissue was extracted with enzymes, and the resulting reduced sugars calculated with final determination reported as % TNC of dry weight.

Figure 4. Fiberglass template and scissors used in harvesting clippings at a specific cutting height.

Plant tissue was analyzed for N, P, K, Ca, Mg, Cu, Fe, Mn, and Zn contents utilizing micro-Kjeldahl for N determination, Beckman Model DU Flame Spectrometer for K, Ca, and Mg determinations, Bausch and Lomb Spectronic 20 for P determinations, and Perkin-Elmer Model 290-B Atomic Absorption Spectrophotometer for Cu, Fe, Mn, and Zn determinations (19).

No other cultural treatments were applied to grasses once on the temperature apparatus other than application of insecticide or fungicide for sod webworm and fungal disease control as needed.

The temperature gradient plate apparatus was located in a heated and air-conditioned greenhouse, however, diurnal ambient temperatures fluctuated between 15.6 and 46.1°C (60 to 115°F) due to radiant energy. During the St. Augustine and bermuda grass experiments, ambient night temperatures were slightly lower than 15.6°C due to loss of normal heat source and inadequacy of supplemental heating units. No control of photoperiod or supplemental light was undertaken, and three grass experiments were initiated in late fall and winter under short day conditions. Respective initiation and termination dates for bahia, St. Augustine and bermuda grass experiments were September 21 - November 16, 1972, October 9 - November 20, 1973, and December 10, 1973 - January 12, 1974.

Stolon Experiment

A short-term experiment utilizing stolon cuttings was initiated on the temperature apparatus to observe effects of soil temperature on root length and root weight for six days. A randomized block design was used with replications initiated six days apart and four samples taken per replication.

Terminal stolons were obtained from potted plugs of each grass which had been held and fertilized weekly in the greenhouse for at least one month prior to cutting. Stolons of bahiagrass were cut to provide approximately 0.6 cm rhizome and approximately 5.0 cm of shoot growth. St. Augustine and bermuda grass stolons were cut so that each had two nodes with the non-terminal node being stripped of its leaves (Fig. 5). St. Augustine, bahia, and bermuda grass stolons were placed in well-aerated, distilled water containers for 4, 3 and 1 days, respectively, prior to initiation of experiment. Timing of duration of stolon nodes in aerated container was determined by preliminary observation to allow formation of root initials before placement on temperature apparatus.

At initiation of the experiment each stolon was placed in a plastic centrifuge tube 18.7 x 111 cm filled with deionized water, and stolons suspended by expansion of foliage (Fig. 6). Stolon tubes were immersed in temperature compartments for six days with daily syringing and refilling of tubes as necessary to prevent wilting. The first stolon replication was started December 27, 1973 and fourth replication terminated January 19, 1974 with no interruption between replications. After six days on temperature apparatus, stolons were removed, root length measured, and dry weights of those roots recorded. Root number was not recorded due to variability observed in preliminary experiments.

Field Study

A completely randomized block experiment with split plot design was initiated in which winter fertilization and fertilizer ratios were evaluated as to their effect on winter root growth of the aforementioned grasses. Main plots were grasses and subplots fertilizer treatments with four replications.

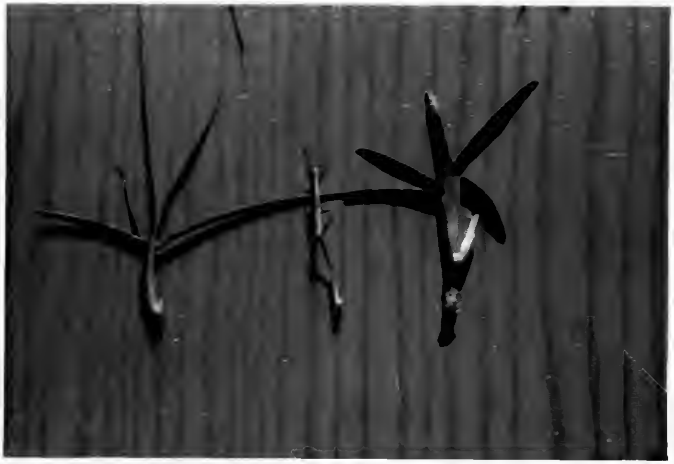

Figure 5. Initial rhizome and stolon pieces of bahia, bermuda, and St. Augustine grass (left to right) utilized in stolon experiment.

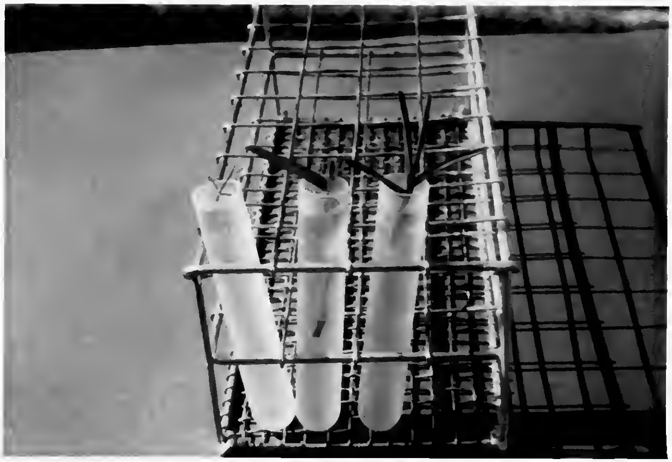

Figure 6. Rhizome and stolon pieces suspended in water filled tube used in stolon experiment. Racks with tubes were placed on temperature gradient apparatus.

The experimental area located at Oranmental Horticulture greenhouses was fumigated with methyl bromide September 1, 1972 and sod from Pursley's Grass Co., Palmetto, Florida, laid two weeks later (Fig. 7). Fertilizer treatments were begun October 24, 1972 and applied every two weeks until May 3, 1973. Fertilizer treatment ratios (N-P-K) were 1-0-1, 1-0-0, 0-0-2, 1-0-4, and Milorganite at equivalent rates of nitrogen. The N was derived from ammonium sulfate $(NH_4)_2SO_4$ and K from sulfate of potash magnesia K_2SO_4 - 2 Mg SO_4. Rates of N were 1 lb/1000 sq. ft./month on bermudagrass and half that for St. Augustine and bahia grasses. Rate of 0-0-2 treatment was 2 lbs/1000 sq. ft./month K for bermuda and half that for St. Augustine and bahia grass.

Grass plugs were extracted monthly using a golf course cup cutter and as much soil as possible washed from root systems below sod piece. Due to inability to remove all soil particles from root systems, a determination of combustionable organic matter was recorded by taking the difference between non-ashed weight and ashed weight.

Samples of shoot tissue were taken one month after termination of fertilizer treatments and elemental analysis performed on this tissue as per previous description.

Figure 7. Plots of bahia, St. Augustine, and bermuda grass utilized in outside winter fertilizer rate and ratio experiment.

RESULTS

Temperature Gradient Plate Experiments

Responses of clipping yields to soil temperature treatments are given in Tables 2, 3, and 4 for bahia, St. Augustine, and bermuda grass, respectively. Generally, highest yields occurred at warmer temperatures and lowest yields at coolest temperatures. Bermudagrass clipping yields showed a decrease of optimum temperature from December 11 to January 11 harvest date.

Total weight of top growth for each experiment showed the overall long-term effects of soil temperature in which maximum dry weights were attained within range of 25 to 46°C (Table 5). Bahiagrass shoot weights were much larger than St. Augustine and bermuda grass due to difference in duration of each experiment, being 8, 7, and 5 weeks, respectively, and differences in inherent growth rates (Fig. 8). Optimum long-term soil temperature for top growth of bahia and St. Augustine occurred within ranges of 34 to 45°C, 26 to 37°C, respectively, however, bermudagrass did not show a clear cut optimum temperature (Table 5).

Dry weights of various plant parts, other than top growth, determined at termination of experiment are presented in Tables 5 and 6. Verdure tissue comprised top growth above rhizomes or stolons, but below clipping height, and was mainly composed of older leaf blades and sheaths. Cardinal temperatures for growth of such tissue were difficult to characterize because bahiagrass responded to a wide range 21 to 45°C, St. Augustinegrass had an optimum at 26 to 37°C, and bermudagrass, a lower

Table 2. Mean clipping dry weights (gms) of bahiagrass as affected by a gradient of soil temperatures.

Soil Temperature (°C)	Harvest Dates (1972)						
	Oct. 5	Oct. 12	Oct. 19	Oct. 26	Nov. 3	Nov. 9	Nov. 16
10-11	.203 g*	.083 g	.150 f	.099 g	0.164 f	.138 f	0.140
15-17	.454 f	.235 f	.398 e	.252 f	0.453 e	.330 e	0.395
19-21	.505 ef	.291 ef	.420 e	.353 e	0.605 d	.464 d	0.622
21-24	.591 de	.345 de	.517 de	.417 de	0.762 d	.622 c	0.674
25-27	.624 cd	.387 cd	.594 b-d	.489 cd	0.983 c	.712 bc	0.866
27-30	.712 bc	.465 bc	.663 a-c	.562 c	1.001 bc	.754 b	0.785
31-34	.851 a	.499 b	.706 ab	.736 b	1.165 ab	.788 ab	0.915
37	.654 cd	.523 ab	.754 a	.805 ab	1.293 a	.898 a	1.002
45-46	.780 ab	.589 a	.559 cd	.897 a	1.166 ab	.829 ab	0.970
							NS

* Means in a column followed by the same letter are not significantly different as determined by Duncan's Multiple Range Test (5% level).

Table 3. Mean clipping dry weights (gms) of St. Augustinegrass as affected by a gradient of soil temperatures.

Soil Temperature (°C)	Harvest Dates (1973)							
	Oct. 15	Oct. 25	Oct. 30	Nov. 3	Nov. 7	Nov. 11	Nov. 17	Nov. 19
10-11	.0813 d*	.0505 f	.0530 e	.0330 e	.0500 e	.0353 e	.0863 e	.0868 e
15-17	.1083 d	.1460 ef	.1378 de	.1185 d	.1408 d	.1718 d	.2720 d	.1663 d
19-21	.1760 cd	.2635 de	.2303 cd	.1908 c	.2420 c	.2405 c	.3725 c	.2305 c
21-24	.1320 d	.2988 d	.2695 bc	.2380 bc	.2650 bc	.2838 bc	.4103 bc	.2528 bc
25-27	.2740 bc	.4333 bc	.3558 ab	.2828 ab	.3555 a	.3445 ab	.4633 ab	.3125 a
27-30	.2943 a-c	.5095 ab	.3775 a	.3470 a	.3893 a	.3583 a	.5210 a	.3158 a
31-34	.3085 ab	.5380 ab	.4275 a	.3048 ab	.3445 a	.3218 ab	.4260 bc	.3465 a
37	.4138 a	.6078 a	.3398 ab	.2823 ab	.3228 ab	.3383 ab	.3908 bc	.3003 ab
45-46	.2615 bc	.3563 cd	.2570 bc	.2040 c	.2543 bc	.2490 c	.2330 d	.2127 cd

* Means in a column followed by the same letter are not significantly different as determined by Duncan's Multiple Range Test (5% level).

Table 4. Mean clipping dry weights (gms) of bermudagrass as affected by a gradient of soil temperatures.

Soil Temperature (°C)	Harvest Dates (1973-1974)								
	Dec. 11	Dec. 15	Dec. 19	Dec. 23	Dec. 27	Dec. 30	Jan. 3	Jan. 7	Jan. 11
10-11	.0306 e*	.0516 g	.0313 g	.0256 f	.0714 e	.0547 d	.1307 d	.1190 d	.1310 d
15-17	.0453 de	.0878 f	.0849 f	.0811 e	.1515 d	.1003 c	.2195 a-c	.2041 a-c	.1988 ab
19-21	.0585 cd	.1239 e	.1285 e	.1123 d	.1600 b-d	.1253 b	.2619 a	.2389 a	.2152 a
21-24	.0628 b-d	.1714 d	.1761 d	.1339 cd	.1678 b-d	.1255 b	.2327 ab	.2025 a-c	.1924 ab
25-27	.0864 a	.2065 c	.2097 c	.1566 c	.1579 cd	.1300 b	.1968 bc	.1949 bc	.1800 a-c
27-30	.0915 a	.2343 bc	.2403 bc	.1939 b	.1945 a-c	.1525 a	.2426 a	.2073 ab	.1896 ab
31-34	.0603 cd	.2427 b	.2149 c	.1638 c	.1594 b-d	.1216 b	.1912 bc	.1646 c	.1505 cd
37	.0852 ab	.3086 a	.2767 b	.2016 b	.1990 ab	.1406 ab	.1848 c	.1719 bc	.1704 bc
45-46	.0752 a-c	.3131 a	.3092 a	.2313 a	.2211 a	.1229 b	.1329 d	.1236 d	.1250 d

* Means in a column followed by the same letter are not significantly different as determined by Duncan's Multiple Range Test (5% level).

Table 5. Total clipping and mean verdure dry weights of bahia, St. Augustine and bermuda grass as affected by a gradient of soil temperatures.

Soil Temperature (°C)	Total Clipping Dry Weight (gms)			Verdure Dry Weights (gms)		
	Bahia	St. Augustine	Bermuda	Bahia	St. Augustine	Bermuda
10-11	0.977 f*	0.476 d	0.646 d	.39 c	1.3745 e	2.1179 a
15-17	2.517 e	1.261 c	1.173 c	6.8 b	1.9898 d	1.7001 a-c
19-21	3.260 d	1.946 b	1.425 b	7.6 ab	2.3693 cd	1.8654 ab
21-24	3.939 c	2.150 b	1.465 b	8.0 ab	2.5970 bc	1.6779 a-c
25-27	4.655 b	2.822 a	1.519 ab	8.5 a	3.1763 a	1.4702 b-d
27-30	4.942 b	3.113 a	1.746 a	7.7 ab	3.1265 ab	1.3614 b-d
31-34	5.660 a	3.018 a	1.469 b	7.8 ab	2.5035 cd	1.1667 cd
37	5.929 a	2.996 a	1.739 a	7.7 ab	2.7213 a-c	1.0990 d
45-46	5.790 a	2.028 b	1.654 ab	7.4 ab	2.3498 cd	0.9126 d

* Means in a column followed by the same letter are not significantly different as determined by Duncan's Multiple Range Test (5% level).

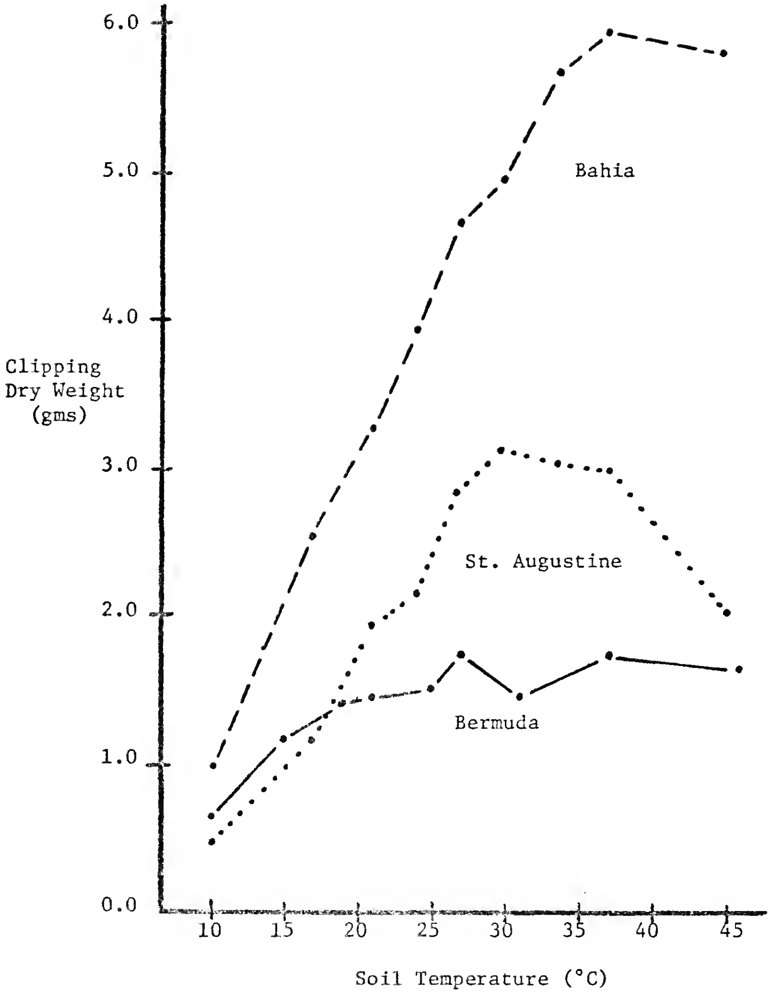

Figure 8. Total clipping dry weight of bahia, St. Augustine, and bermuda grass as affected by a gradient of soil temperatures.

Table 6. Mean rhizome, stolon and root dry weights of bahia, St. Augustine and bermuda grass as affected by a gradient of soil temperatures.

Soil Temperature (°C)	(gms)			Root Weight (gms)		
	Bahia Rhizomes	St. Augustine Stolons	Bermuda Rhizomes	Bahia	St. Augustine	Bermuda
10-11	10.2 ab*	1.8873	7.2477 a	0.511 f	.0807 e	.1537 a-c
15-17	12.1 ab	1.9770	5.5000 bc	1.581 cd	.3306 cd	.1886 a
19-21	10.8 ab	2.2175	5.9316 ab	2.166 a	.3450 b-d	.1884 a
21-24	10.2 abc	1.9880	4.7305 b-d	1.754 bc	.3942 a-c	.1456 a-c
25-27	9.0 bc	2.1070	4.0971 cd	1.807 b	.4250 a	.1676 ab
27-30	9.5 bc	1.9445	5.8840 ab	1.688 b-d	.4224 ab	.1664 ab
31-34	9.2 bc	1.8053	3.8899 d	1.502 de	.3833 a-c	.1092 cd
37	8.3 c	1.6168	4.0007 cd	1.343 e	.2807 d	.0905 d
45-46	8.8 bc	1.7083	3.6653 d	0.299 g	.0196 e	.1266 b-d
		NS				

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* Means in a column followed by the same letter are not significantly different as determined by Duncan's Multiple Range Test (5% level).

optimum of 10 to 21°C (Table 5, Fig. 9). Dry weight of verdure tissue was positively correlated to soil temperature for bahia and St. Augustine grass, and negatively correlated for bermudagrass.

Rhizome growth of bahia and bermuda grass generally responded with decreased weights as temperature decreased, whereas St. Augustinegrass stolon weight showed no response to soil temperature gradient (Table 6). Fluctuations can be seen in rhizome weights of bahia and bermuda grass between soil temperature extremes (Fig. 10).

Cardinal temperatures for root growth of bahiagrass were clearly delineated, but this was not true for St. Augustine and bermuda grass, since they exhibited wide ranges for these critical temperatures (Table 6, Fig. 11). Optimum soil temperature for bahiagrass root growth was 21°C, whereas maximum root growth of St. Augustinegrass occurred within a range of 23 to 34°C. Temperatures used in these studies were sufficiently extreme to have attained cardinal minimum and maximum temperatures for root growth of bahia and St. Augustine grass, however, bermudagrass did not show drastic reduction in root weight at coldest temperature (10°C) to demonstrate minimum growth level (Fig. 11). Affects of soil temperature on root morphology are visible in Fig. 12.

Total dry weight of all plant parts, less clippings, showed additive effects of soil temperature on entire grass plug or plant (Table 7). Optimum soil temperatures for bahia and St. Augustine grass occurred between the extreme high and low temperatures (10 to 45°C), whereas bermudagrass showed temperature optimum at the cooler temperatures from 10 to 19°C (Fig. 13). The entire grass plug with attached root system of each grass at termination can be seen in Figs. 14, 15, and 16.

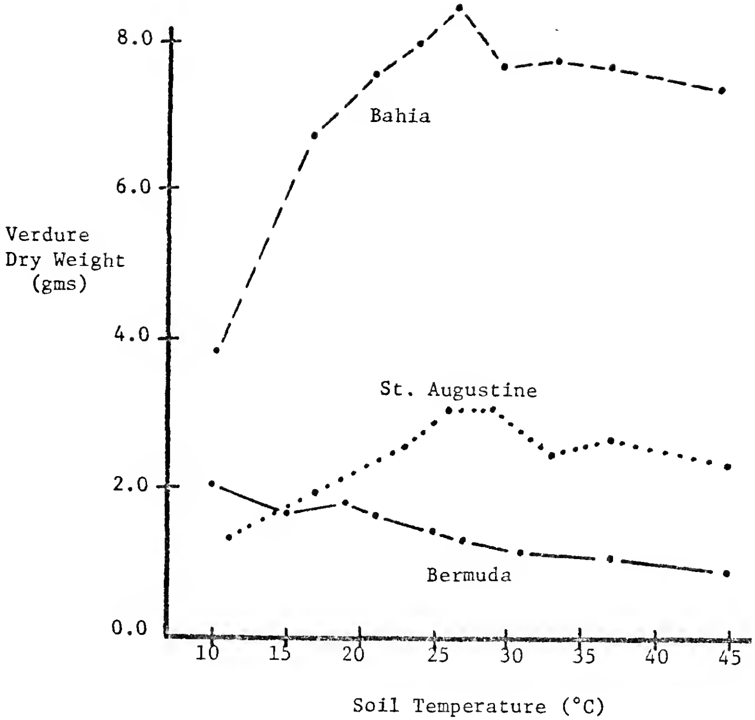

Figure 9. Mean verdure dry weight of bahia, St. Augustine, and bermuda grass as affected by a gradient of soil temperatures.

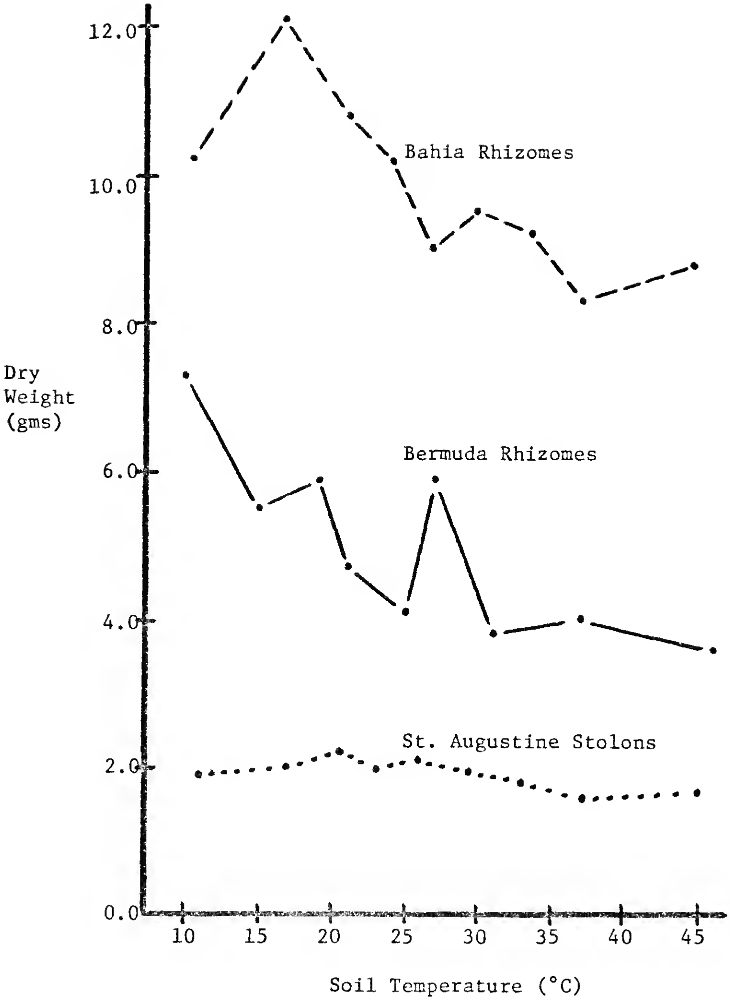

Figure 10. Mean dry weight of stolons or rhizomes of bahia, St. Augustine, and bermuda grass as affected by a gradient of soil temperatures.

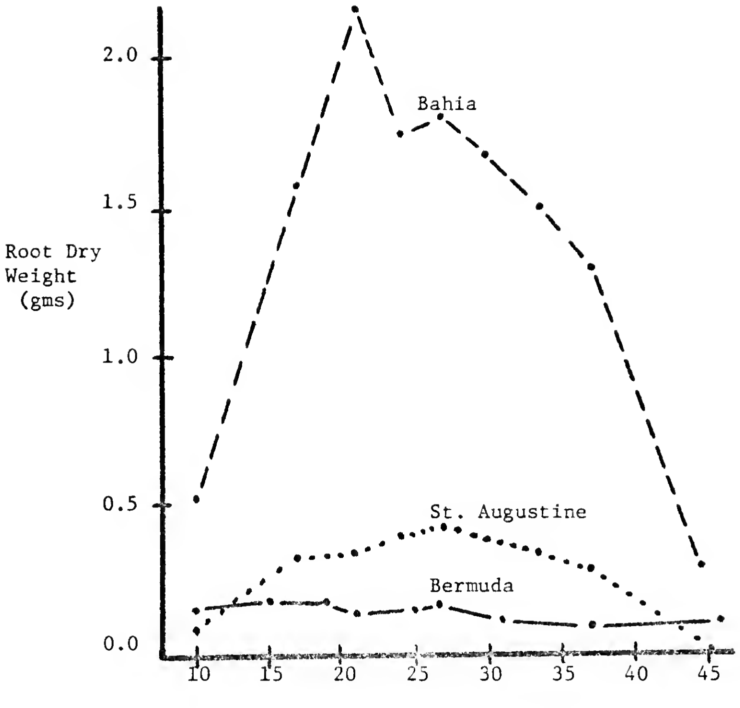

Figure 11. Mean root dry weight of bahia, St. Augustine, and bermuda grass as affected by a gradient of soil temperatures.

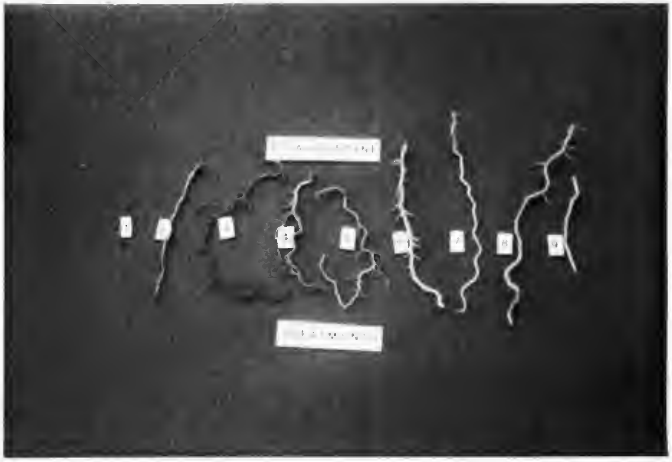

Figure 12. St. Augustinegrass root sections taken from grass plugs maintained on soil temperature gradient apparatus for seven weeks. Treatment 1 was 45°C, grading to 11°C at treatment 9.

Table 7. Total dry weight of plant tissue of bahia, St. Augustine and bermuda grass as affected by a gradient of soil temperatures.

Soil Temperature (°C)	Total Plant Weight (gms)		
	Bahia	St. Augustine	Bermuda
10-11	14.611 c*	3.872 d	9.634 a
15-17	20.481 a	4.994 b-d	7.427 a-c
19-21	20.566 a	5.613 a-c	8.008 ab
21-24	19.954 a	5.600 a-c	5.103 cd
25-27	19.307 ab	6.374 a	5.790 b-d
27-30	18.888 ab	6.080 ab	7.492 a-c
31-34	18.502 ab	5.174 a-d	5.188 cd
37	17.343 abc	5.154 a-d	5.214 cd
45-46	16.499 bc	4.621 cd	4.767 d

* Means in a column followed by the same letter are not significantly different as determined by Duncan's Multiple Range Test (5% level).

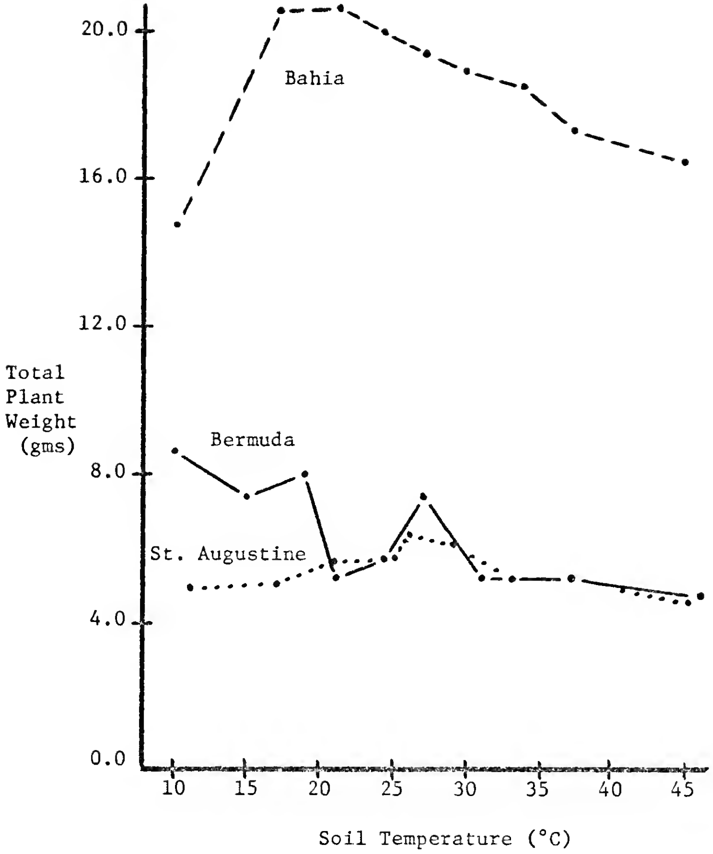

Figure 13. Total dry weight of plant tissue of bahia, St. Augustine, and bermuda grass as affected by a gradient of soil temperature.

Figure 14. Bahiagrass plugs and roots after eight weeks growth on soil temperature gradient apparatus. Treatment 1 was 45°C, grading to 11°C at treatment 9.

Figure 15. St. Augustinegrass plugs and roots after seven weeks growth on soil temperature gradient apparatus. Treatment was 45°C, grading to 11°C at treatment 9.

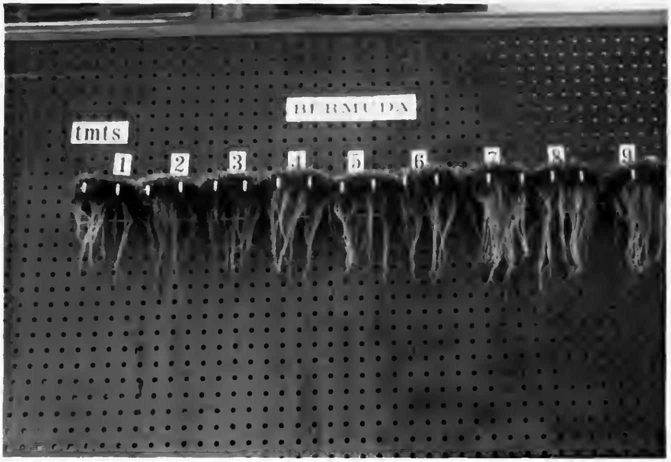

Figure 16. Bermudagrass plugs and roots after five weeks growth on soil temperature gradient apparatus. Treatment 1 was 46°C, grading to 11°C at treatment 9.

Carbohydrate storage levels and capacity were recorded as percent Total Nonstructural Carbohydrates (TNC) on dry weight basis and as total (mg) TNC per pot or experimental unit. Percent TNC evaluated the capacity of specific tissues in storing reserve carbohydrates.

Percent TNC of clippings averaged over the study period indicated that bahia and St. Augustine grass stored carbohydrates in tissue at similar levels, however bermudagrass TNC storage was consistently one or more percent lower (Table 8, Fig. 17). Bahia and St. Augustine grass clippings TNC levels were more responsive to soil temperatures than bermudagrass.

TNC levels in verdure tissue indicated that bahiagrass stored higher percentages than St. Augustine or bermuda grass (Table 8). Bermudagrass verdure tissue showed limited responsitivity to soil temperatures when evaluated by % TNC, however at lowest temperature (10°C) the level was highest (Fig. 18). St. Augustinegrass verdure tissue had increased % TNC as soil temperature increased, whereas bahiagrass stored the minimum TNC within range of 24 to 37°C and maximum at 10°C.

Carbohydrate storage organs, such as rhizomes, stolons and roots, exhibited sensitivity to soil temperatures by a large variation in % TNC levels (Figs. 8 and 9). Percent TNC decreased as soil temperature increased in the three plant tissues of the three grasses. Lowest levels of 3.09 to 4.08% TNC in rhizomes and stolons occurred at 37 to 46°C and maximum levels of 5.93 to 12.18% TNC at 10 to 11°C. St. Augustinegrass stolons stored less percent TNC than bahia or bermuda grass rhizomes, and root tissue stored less TNC than rhizome or stolon tissue (Table 9). Percent TNC of bahiagrass root tissue was lowest (1.10%) at 30°C, whereas

Table 8. Mean percent Total Nonstructural Carbohydrates (TNC) in clippings averaged for all harvest dates and mean percent TNC in verdure tissue of bahia, St. Augustine and bermuda grass as affected by a gradient of soil temperatures.

Soil Temperature (°C)	% TNC of Clippings			% TNC of Verdure		
	Bahia	St. Augustine	Bermuda	Bahia	St. Augustine	Bermuda
10-11	4.86	3.74	2.40	9.88 a*	1.40 d	4.70 a
15-17	4.63	3.81	2.34	8.07 b	1.76 cd	2.81 b
19-21	4.71	4.00	2.49	6.50 bc	2.69 bc	3.02 b
21-24	4.33	4.36	2.44	6.70 b-d	2.65 bc	3.05 b
25-27	4.36	4.28	2.40	6.79 b-d	2.47 bc	2.81 b
27-30	3.99	4.16	2.16	5.96 d	2.33 bc	2.88 b
31-34	4.16	3.82	2.29	6.40 cd	2.59 bc	2.56 b
37	4.06	3.45	2.49	6.95 b-d	3.13 b	2.89 b
45-46	3.71	4.14	2.39	7.66 bc	4.76 a	2.72 b

* Means in a column followed by the same letter are not significantly different as determined by Duncan's Multiple Range Test (5% level).

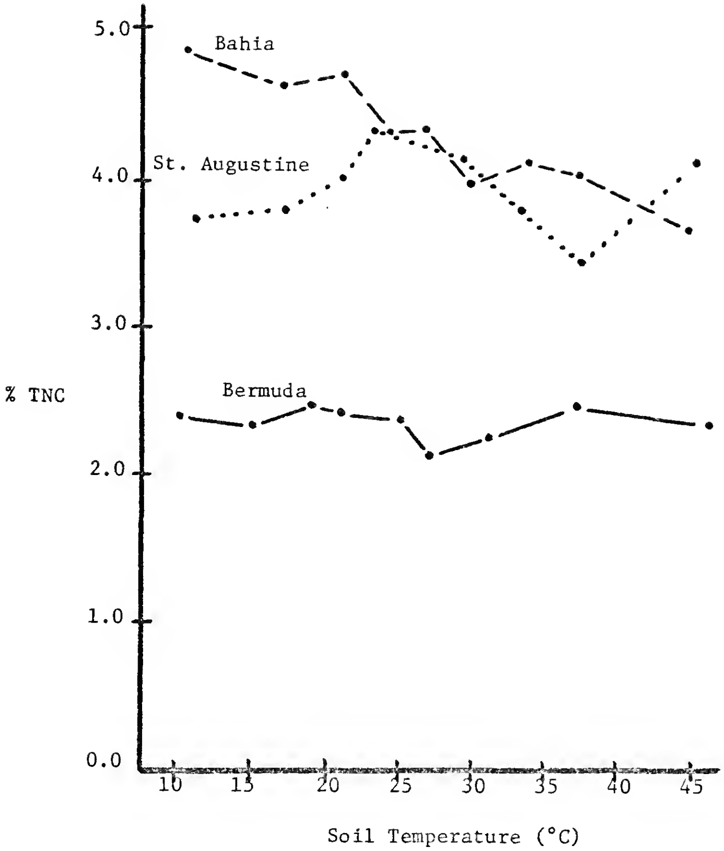

Figure 17. Percent TNC in clippings averaged over all harvest dates of bahia, St. Augustine, and bermuda grass as affected by a gradient of soil temperatures.

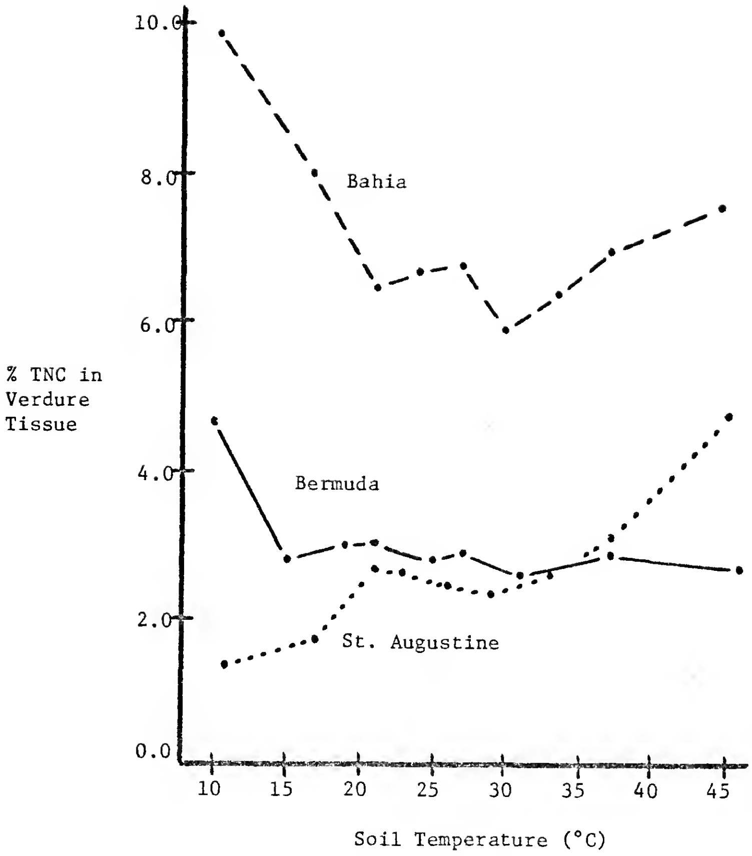

Figure 18. Percent TNC in verdure tissue of bahia, St. Augustine, and bermuda grass as affected by a gradient of soil temperatures.

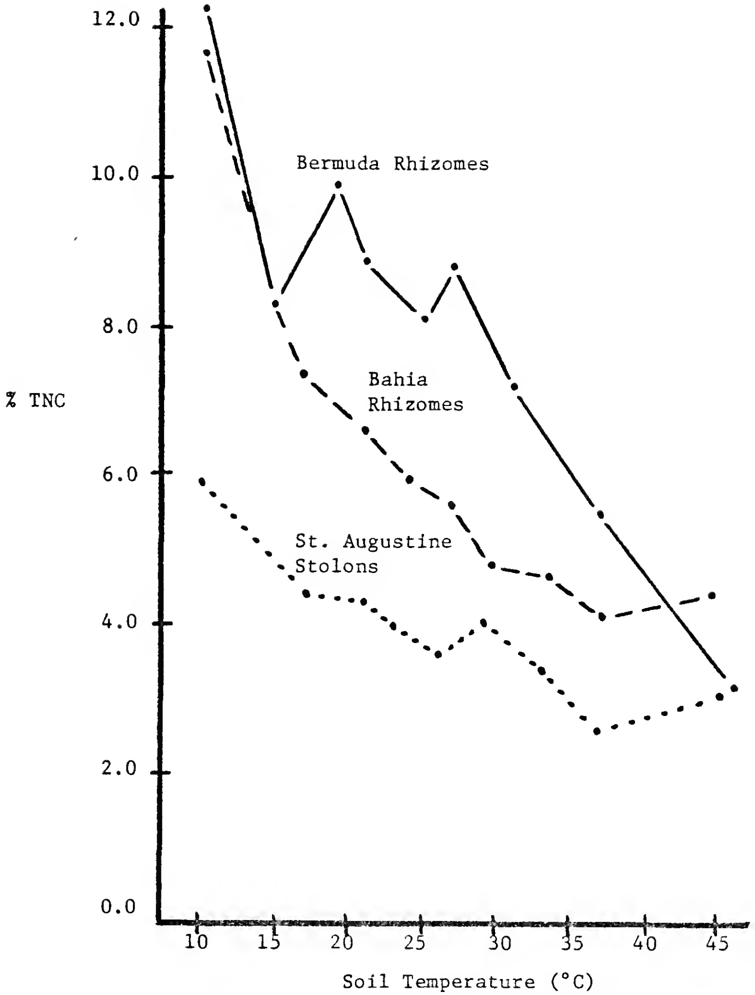

Figure 19. Percent TNC in rhizomes and stolons of bahia, bermuda, and St. Augustine grass as affected by a gradient of soil temperatures.

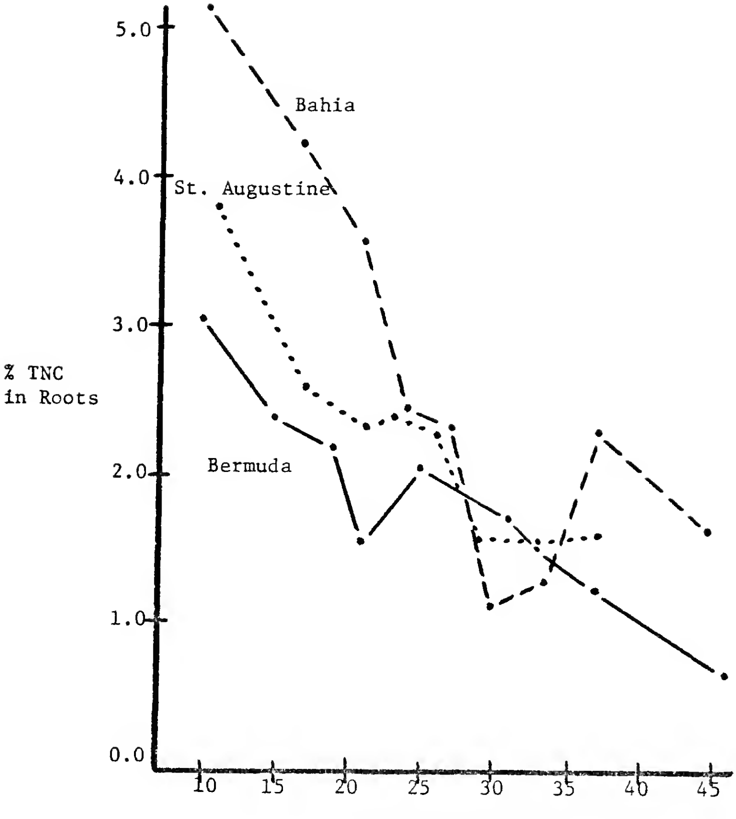

Figure 20. Percent TNC in roots of bahia, St. Augustine, and bermuda grass as affected by a gradient of soil temperatures.

Table 9. Mean percent Total Nonstructural Carbohydrates (TNC) in rhizomes, stolons and roots of bahia, St. Augustine and bermuda grass as affected by a gradient of soil temperatures.

Soil	% TNC			% TNC in Roots		
Temperature (°C)	Bahia Rhizomes	St. Augustine Stolons	Bermuda Rhizomes	Bahia	St. Augustine	Bermuda
10-11	11.59 a*	5.93 a	12.18 a	5.14 a	3.82 a	3.06 a
15-17	7.34 b	3.43 bc	8.25 bc	4.27 ab	2.64 b	2.39 b
19-21	6.61 bc	3.33 bc	9.57 b	3.60 b	2.32 bc	2.19 bc
21-24	5.96 cd	2.99 bc	8.85 bc	2.39 c	2.39 bc	1.53 f
25-27	5.60 c-e	3.59 bc	8.05 bc	2.31 c	2.27 bc	2.04 cd
27-30	4.76 d-f	4.02 b	8.79 bc	1.10 d	1.57 c	1.97 d
31-34	4.67 d-f	3.44 bc	7.23 cd	1.29 cd	1.54 c	1.70 e
37	4.08 f	2.59 c	5.50 d	2.31 c	1.60 c	1.22 g
45-46	4.40 ef	3.04 b	3.09 e	1.64 cd	---**	0.67 h

* Means in a column followed by the same letter are not significantly different as determined by Duncan's Multiple Range Test (5% level).

** Not sufficient tissue for TNC analysis.

in bermuda and St. Augustine grass, percent TNC was minimum at 45 to 46°C and 27 to 46°C, respectively (Fig. 20). Maximum % TNC storage in root tissue of the three grasses occurred at 10 to 11°C.

The total TNC per experimental unit (pot) was determined by multiplication of % TNC level within tissue by its dry weight to give values expressed as milligrams TNC per pot on tissue dry weight basis.

Average TNC content per pot for clipping yields collected during the study show maxima similar to dry weight results (Table 10, Fig. 21). No statistical analysis was performed on these data due to lack of clipping tissue.

Table 11 presents TNC content of verdure tissue, with bahiagrass having highest content compared with other grasses, although treatments did not significantly affect this measurement in bahiagrass. Bermuda and St. Augustine grass had comparable TNC content per pot within verdure tissue, although the relationship to soil temperature was contradictory, being negative and positive, respectively (Fig. 22).

The importance of rhizomes as carbohydrate storage organs is apparent from data in Table 11 in which TNC weight reached maximum of 118 mgs per pot in bahiagrass rhizomes at 10°C. St. Augustine stolons stored less than half as much TNC per pot as rhizomes of other two grasses. Weight of TNC per pot found in rhizomes and stolons of these grasses varied. As soil temperature decreased, TNC increased, and rhizomes and stolons were the largest reservoirs of TNC in the plant (Fig. 23).

TNC content in roots constituted a much smaller proportion of stored TNC than other tissues, especially with St. Augustine and bermuda grass in which less than one milligram per pot was stored at the highest

Table 10. Total Nonstructural Carbohydrates (TNC) content per pot of clippings averaged for all harvest dates as affected by a gradient of soil temperatures.

Soil Temperature (°C)	Milligrams TNC per pot in clippings		
	Bahia	St. Augustine	Bermuda
10-11	4.75	1.77	1.55
15-17	11.65	4.80	2.75
19-21	15.36	7.78	3.55
21-24	17.06	9.37	3.58
25-27	20.30	12.08	3.65
27-30	19.72	12.95	3.77
31-34	23.55	11.53	3.36
37	24.07	10.34	4.33
45-46	21.48	8.40	3.95

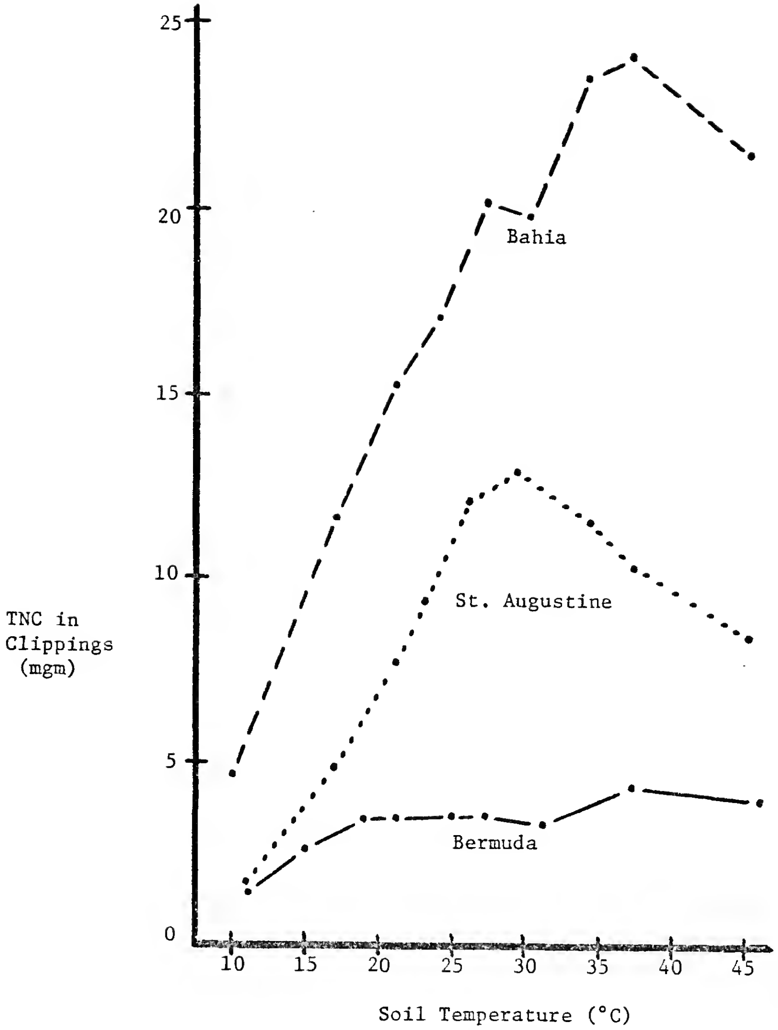

Figure 21. Mean TNC content (mgm) per pot in total clipping yields per pot of bahia, St. Augustine, and bermuda grass as affected by a gradient of soil temperatures.

Table 11. Mean Total Nonstructural Carbohydrate (TNC) content per pot in verdure, rhizome and stolon tissue of bahia, St. Augustine and bermuda grass as affected by a gradient of soil temperatures.

Soil Temperature (°C)	Milligrams TNC per pot in Vurdure			Milligrams TNC per pot		
	Bahia	St. Augustine	Bermuda	Bahia Rhizomes	St. Augustine Stolons	Bermuda Rhizomes
10-11	38.618	1.995 d*	9.937 a	118.100 a	11.107 a	88.830 a
15-17	55.085	3.625 cd	4.797 bc	88.975 b	6.757 b	46.383 b-d
19-21	56.603	6.504 bc	5.933 b	70.960 bc	7.637 ab	57.540 b
21-24	53.670	6.991 b	5.150 bc	60.895 cd	6.028 b	41.825 b-d
25-27	57.338	7.879 b	4.244 bc	49.880 de	6.494 b	32.995 c-e
27-30	46.885	7.287 b	3.924 bc	45.178 de	8.046 ab	51.800 bc
31-34	49.535	6.632 bc	3.044 c	42.575 de	6.204 b	28.043 d-f
37	53.938	8.611 ab	3.105 c	32.873 e	4.160 b	21.503 ef
45-46	56.463	11.171 a	2.504 c	37.965 e	5.318 b	11.303 f

* Means in a column followed by the same letter are not significantly different as determined by Duncan's Multiple Range Test (5% level).

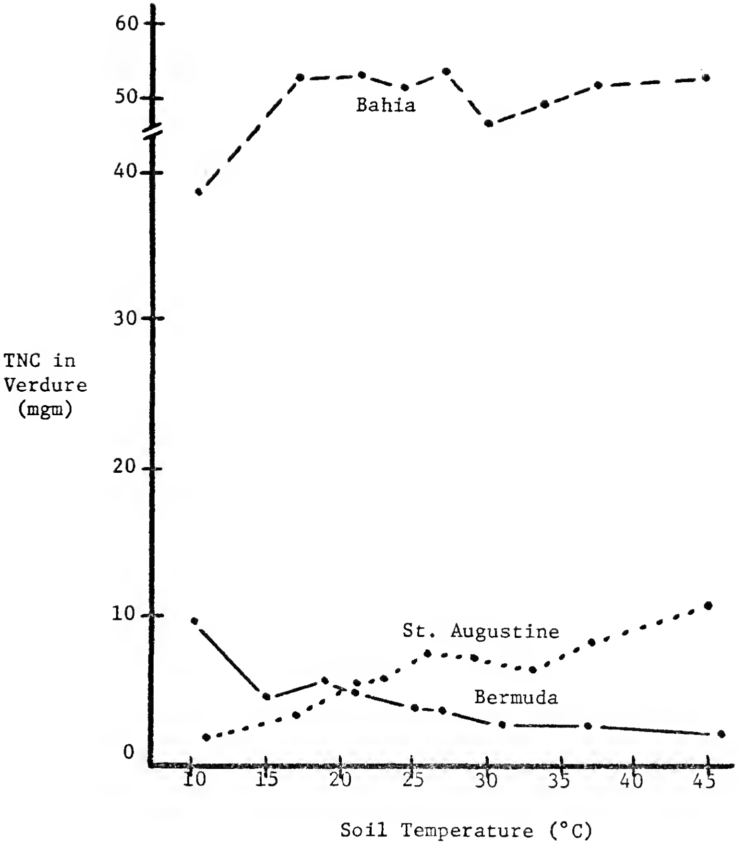

Figure 22. Mean TNC content (mgm) per pot in verdure tissue of bahia, St. Augustine, and bermuda grass as affected by a gradient of soil temperatures.

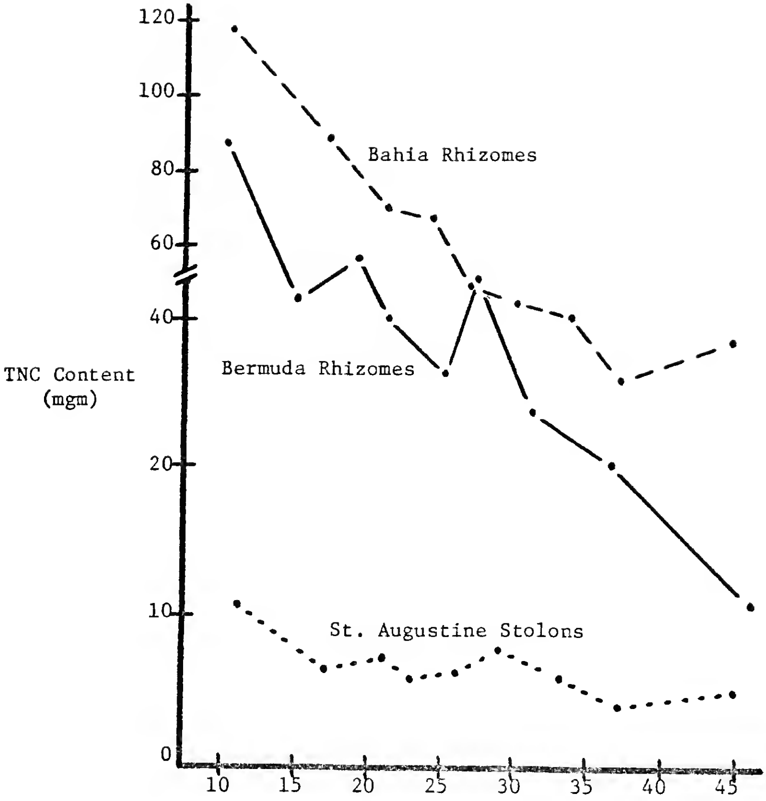

Figure 23. Mean TNC content (mgm) per pot in rhizomes and stolons of bahia, St. Augustine, and bermuda grass as affected by a gradient of soil temperatures.

Table 12. Mean Total Nonstructural Carbohydrate (TNC) content per pot in roots and overall total of tissues of bahia, St. Augustine and bermuda grass as affected by a gradient of soil temperatures.

Soil Temperature (°C)	Milligrams TNC in Roots			Total Milligrams TNC per pot		
	Bahia	St. Augustine	Bermuda	Bahia	St. Augustine	Bermuda
10-11	2.635 bc*	0.308 c	0.470 a	159.353 a	13.879	99.238 a
15-17	6.762 a	0.933 a	0.451 a	150.823 a	11.855	51.630 bc
19-21	7.765 a	0.786 ab	0.413 ab	135.328 ab	15.502	63.886 b
21-24	4.211 b	0.966 a	0.223 c	118.778 bc	14.266	47.197 b-d
25-27	4.157 b	0.958 a	0.342 b	111.375 bc	16.041	37.581 c-e
27-30	1.903 cd	0.667 a-c	0.328 b	93.965 c	16.676	56.052 bc
31-34	1.840 cd	0.604 bc	0.186 cd	93.950 c	14.027	31.272 d-f
37	3.047 bc	0.438 bc	0.110 de	89.858 c	13.689	24.718 ef
45-46	0.544 d	---**	0.085	94.973 c	17.022	13.891 f
					NS	

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* Means in a column followed by the same letter are not significantly different as determined by Duncan's Multiple Range Test (5% level).

** Not sufficient tissue for TNC analysis.

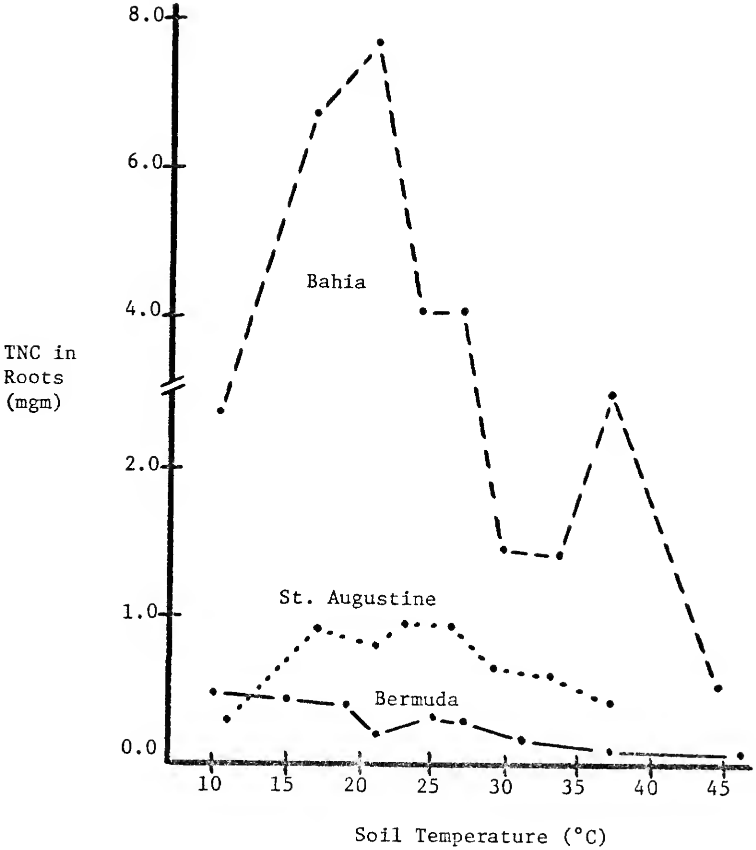

Figure 24. Mean TNC content (mgm) per pot in roots of bahia, St. Augustine, and bermuda grass as affected by a gradient of soil temperatures.

temperature (Table 12). Total stored TNC in roots of bermudagrass was negatively correlated with soil temperature, while bahia and St. Augustine grass stored maximum TNC in roots at 17 to 29°C (Fig. 24).

St. Augustinegrass did not respond to soil temperature in terms of total TNC per pot less clippings, and it stored less than bermuda or bahia grass, which increased in TNC content as soil temperatures decreased (Table 12). Bermudagrass had the widest range of TNC levels per pot with levels of 13.9 mg TNC at 46°C to 99.2 mg at 10°C. Several fluctuations in total TNC per pot occurred in bermudagrass tissues with these fluctuations traced to differences in rhizome dry weight and % TNC levels (Fig. 25).

Significant effects of soil temperature on levels of nutrient elements in tissues of the three grasses are given in Table 13. Macronutrient levels in tissues were more responsive to treatment effects than micronutrient levels with 21 out of 32 possible effects being nonsignificant at the 5% level of probability. Phosphorus and K levels were most frequently altered by soil temperature, with Ca and Mg second in frequency of significant variation.

Bahiagrass verdure, rhizome and root tissues, St. Augustinegrass verdure and stolon tissues, and bermudagrass verdure and rhizome tissues were analyzed for nutrient element content.

Bahiagrass verdure tissue had lower levels of P and K but increased levels of Ca, Mg, Fe, and Cu at highest soil temperatures (Table 14). N and K levels varied in rhizome tissue with N level highest at extreme temperatures and K highest at the lowest temperature (Table 15). Bahiagrass root tissue varied in N, P, K, Mg, and Cu levels, but no definite trend occurred. There was insufficient tissue at extreme temperature treatments for analysis (Table 15).

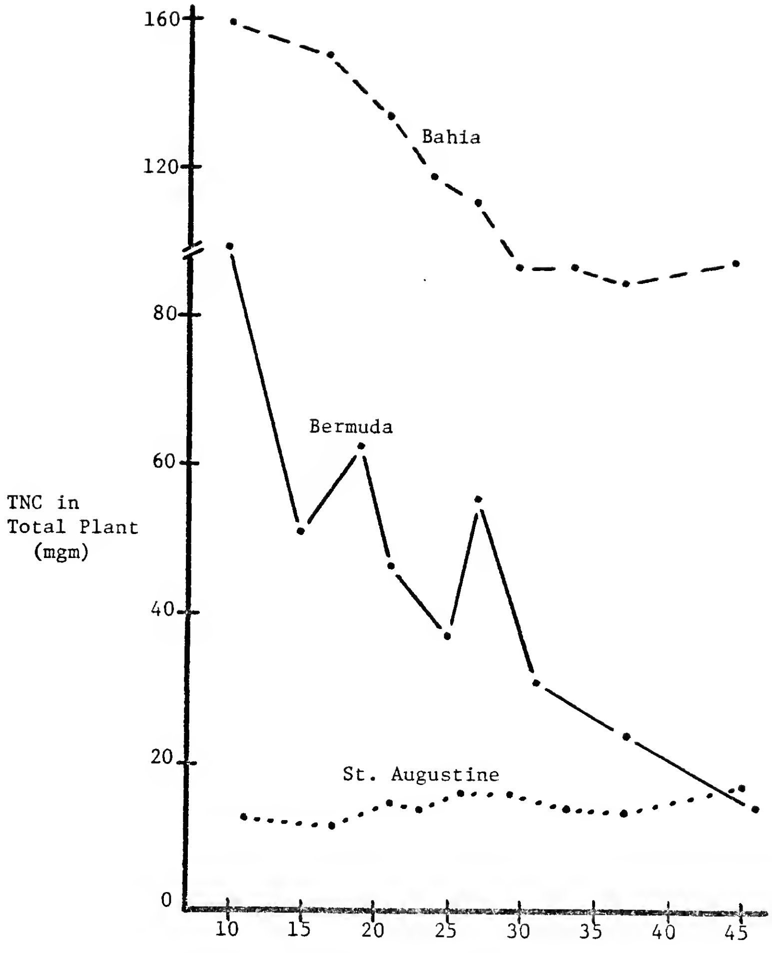

Figure 25. Mean TNC content (mgm) per pot in plant parts of bahia, St. Augustine, and bermuda grass as affected by a gradient of soil temperatures.

Table 13. Analysis of variance table for content of nutrient elements in bahia, St. Augustine and bermuda grass tissue.

		%					ppm			
Grass	Tissue	N	P	K	Ca	Mg	Cu	Zn	Fe	Mn
Bahiagrass	Verdure		+*	+	+	+	+		+	
	Rhizome	+		+						
	Roots	+	+	+		+	+			
St. Augustine	Verdure		+		+	+				+
	Stolons		+	+	+	+		+		+
Bermuda	Verdure	+						+		+
	Rhizome		+	+	+				+	

* + indicates significant F-test value (5% level).

Table 14. Content of nutrient elements in bahiagrass verdure tissue as affected by a gradient of soil temperatures.

Soil Temperature	%				ppm	
(°C)	P	K	Ca	Mg	Fe	Cu
10	0.36 ab*	2.15 a	0.27 d	0.79 d	183 e	29 c
17	0.41 a	1.88 a-c	0.26 d	1.10 c	293 b-d	39 bc
21	0.40 a	1.82 bc	0.26 d	1.26 a-c	190 de	34 bc
24	0.31 b-d	1.68 c	0.24 d	1.19 bc	308 a-c	40 bc
27	0.33 bc	1.82 bc	0.32 cd	1.37 a	213 c-e	40 bc
30	0.29 c-e	2.06 ab	0.44 ab	1.32 ab	383 ab	45 b
34	0.28 de	1.78 bc	0.41 bc	1.23 a-c	285 b-e	35 bc
37	0.24 e	1.73 e	0.49 ab	1.17 bc	395 a	38 bc
45	0.27 de	1.68 c	0.51 a	1.16 bc	265 de	58 a

* Means in a column followed by the same letter are not significantly different as determined by Duncan's Multiple Range Test (5% level).

Table 15. Content of nutrient elements in bahiagrass rhizomes and roots as affected by a gradient of soil temperatures.

Soil Temperature (°C)	Rhizome Tissue		Root Tissue				
	%		%				ppm
	N	K	N	P	K	Mg	Cu
10	1.60 a-c*	0.70 a	---	---	---	---	---
17	1.53 bc	0.53 b	1.73 a	0.23 a	2.38 a	0.50 bc	41 b
21	1.48 c	0.53 b	1.68 a	0.17 b	1.71 b	0.66 a	49 a
24	1.55 bc	0.58 b	1.48 ab	0.16 b	1.43 bc	0.67 a	30 c
27	1.48 c	0.54 b	1.33 bc	0.16 b	1.03 d	0.59 ab	41 b
30	1.83 ab	0.53 b	1.05 c	0.19 ab	0.89 d	0.47 bc	40 b
34	1.78 a-c	0.53 b	1.65 a	0.21 ab	1.04 d	0.45 c	40 b
37	1.85 a	0.52 b	1.58 ab	0.20 ab	1.19 cd	0.46 bc	46 ab
45	1.68 a-c	0.50 b	---	---	---	---	---

* Means in a column followed by the same letter are not significantly different as determined by Duncan's Multiple Range Test (5% level).

St. Augustinegrass verdure and stolon tissue had variations in levels of P, Ca, Mn, and Mg, with Ca, Mg, and Mn having generally a positive correlation and P a negative one with soil temperatures (Table 16). K and Zn content in St. Augustinegrass stolon tissue exhibited a positive correlation but little significance to soil temperature up to the maximum temperature attained (46°C).

Bermudagrass verdure and rhizome tissue had few elements which were significantly affected by soil temperature (Table 17). Soil temperature affected Zn and Mn in the verdure tissue with levels of these elements being maximum at highest soil temperature. Bermudagrass rhizome tissue varied in P, K, Ca, and Fe, with K and Ca generally lower as temperature decreased.

Stolon Experiment

Results of a short-term (6-day) study in which root dry weight and length were evaluated from stolon or rhizome pieces of bahia, St. Augustine, and bermuda grass are shown in Table 18 and Figs. 26, 27, and 28. Optimum root medium temperatures for maximum root weights were 31°C, 21 to 31°C, and 27 to 31°C for bahia, St. Augustine, and bermuda grass, respectively (Fig. 29). Maximum temperatures for root weight were reached at highest temperature 45°C, while minimum temperature ranged from 10 to 15°C for the three grasses (Table 18).

Optimum temperatures for root length extended the ranges into higher temperatures giving bahia, St. Augustine, and bermuda grass an optimum temperature range of 31 to 37°C, 21 to 27°C, and 27 to 31°C, respectively (Table 18). Only St. Augustinegrass root length reached its minimum and maximum temperature, however, bahia and bermuda grass were close to those cardinal points (Fig. 30).

Table 16. Content of nutrient elements in St. Augustinegrass verdure and stolon tissue as affected by a gradient of soil temperatures.

Soil Temperature (°C)	Verdure Tissue				Stolon Tissue					
	%				%				ppm	
	P	Ca	Mg	Mn ppm	P	K	Ca	Mg	Zn	Mn
11	0.31 d*	0.30 c	0.44 e	78 c	0.14 bc	3.31 ab	0.14 c	0.27 e	464 d	63 bc
17	0.36 b-d	0.34 bc	0.58 de	70 c	0.18 b	2.74 b	0.15 c	0.39 d	491 cd	40 c
21	0.46 a	0.45 ab	0.87 bc	80 bc	0.22 a	4.03 ab	0.18 c	0.46 cd	528 b-d	55 bc
23	0.40 ab	0.46 a	1.02 ab	78 c	0.17 b	3.42 ab	0.17 c	0.51 b-d	578 bc	80 ab
26	0.34 b-d	0.51 a	1.01 ab	83 bc	0.15 bc	3.44 ab	0.21 bc	0.51 b-d	573 bc	53 bc
29	0.33 cd	0.45 ab	1.13 a	90 bc	0.17 b	4.79 a	0.25 ab	0.63 ab	613 b	75 ab
33	0.38 bc	0.55 a	1.12 a	123 a	0.15 bc	4.40 a	0.29 a	0.65 a	770 a	95 a
37	0.34 b-d	0.51 a	0.95 ab	120 a	0.14 bc	4.74 a	0.28 a	0.54 a-c	627 b	78 ab
45	0.31 cd	0.52 a	0.71 cd	108 ab	0.12 c	4.69 a	0.31 a	0.46 cd	500 cd	65 bc

* Means in a column followed by the same letter are not significantly different as determined by Duncan's Multiple Range Test (5% level).

Table 17. Content of nutrient elements in bermudagrass verdure and rhizome tissue as affected by a gradient of soil temperatures.

Soil Temperature (°C)	Verdure Tissue			Rhizome Tissue			
				%			ppm
	% N	Zn ppm	Mn ppm	P	K	Ca	Fe
10	2.50 ab*	445 e	130 b	0.17 a-c	1.08 e	0.11 b	293 a-c
15	2.50 ab	540 d	180 b	0.15 a-c	1.24 de	0.14 b	370 ab
19	2.63 a	581 cd	180 b	0.15 a-c	1.45 cd	0.15 b	283 bc
21	2.38 ab	656 bc	233 b	0.15 a-c	1.48 cd	0.16 b	213 c
25	2.23 bc	610 b-d	258 b	0.11 c	1.54 b-d	0.16 b	295 a-c
27	2.40 ab	624 b-d	250 b	0.13 bc	1.90 a	0.15 b	258 bc
31	2.40 ab	644 bc	263 b	0.12 c	1.79 ab	0.14 b	313 a-c
37	2.45 ab	691 ab	280 b	0.21 ab	1.81 ab	0.15 b	308 a-c
46	2.03 c	770 a	483 a	0.23 a	1.63 a-c	0.27 a	413 a

* Means in a column followed by the same letter are not significantly different as determined by Duncan's Multiple Range Test (5% level).

Table 18. Mean root length and dry weight of bahia, St. Augustine and bermuda grass initiated on stolons or rhizomes and affected by a gradient of soil temperatures for six days.

Soil Temperature (°C)	Root Length (mm)			Root dry weight (mgm)		
	Bahia	St. Augustine	Bermuda	Bahia	St. Augustine	Bermuda
10	2.5 d*	0.0 c	7.3 g	2.0 d	0.0 d	1.5 ef
15	11.5 d	12.3 bc	19.0 f	7.1 d	13.7 c	2.8 de
19	35.8 c	25.5 b	34.8 e	22.5 c	15.6 c	4.1 cd
21	35.0 c	48.5 a	50.3 d	22.7 c	26.9 ab	5.0 bc
25	43.5 c	51.5 a	59.8 cd	25.7 c	29.6 a	5.2 bc
27	66.0 b	64.3 a	71.8 ab	36.2 b	34.7 a	7.1 ab
31	104.0 a	60.8 a	77.3 a	45.8 a	28.2 a	7.5 a
37	98.0 a	52.8 a	66.0 bc	34.6 b	16.9 bc	6.0 a-c
46	5.8 d	0.0 c	5.5 g	5.1 d	0.0 d	0.0 f

* Means in a column followed by the same letter are not significantly different as determined by Duncan's Multiple Range Test (5% level).

Figure 26. Bahiagrass rhizome pieces after six days growth on soil temperature gradient apparatus. Treatment 1 was 46°C, grading to 10°C at treatment 9.

Figure 27. St. Augustinegrass stolon pieces after six days growth on soil temperature gradient apparatus. Treatment 1 was 46°C, grading to 10°C at treatment 9.

Figure 28. Bermudagrass stolon pieces after six days growth on soil temperature gradient apparatus. Treatment 1 was 46°C, grading to 10°C at treatment 9.

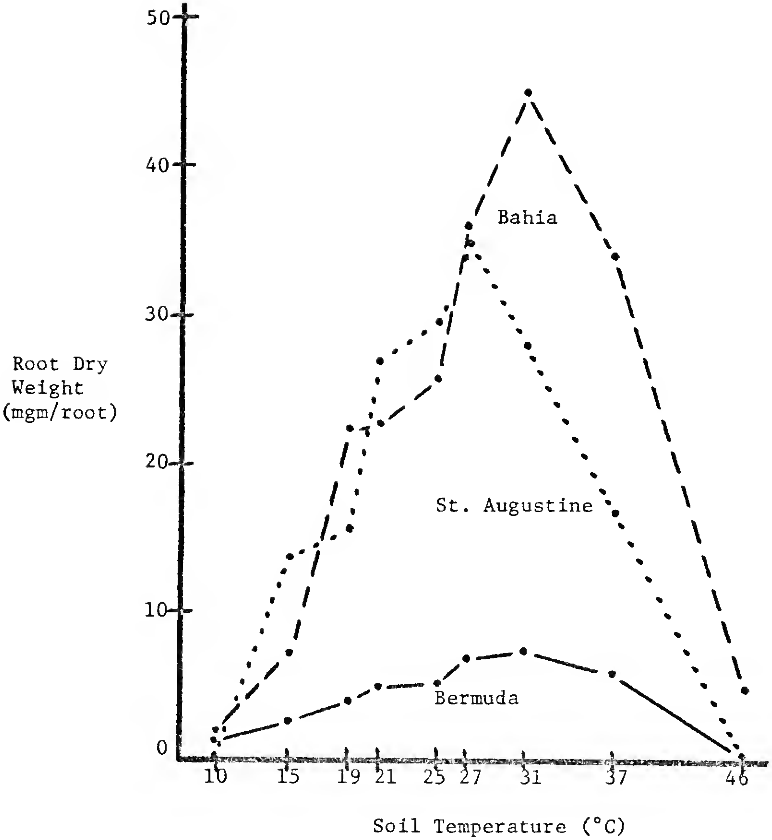

Figure 29. Mean root dry weight (mgm) initiated on bahia, St. Augustine, and bermuda grass rhizomes or stolons as affected by a gradient of root media temperatures.

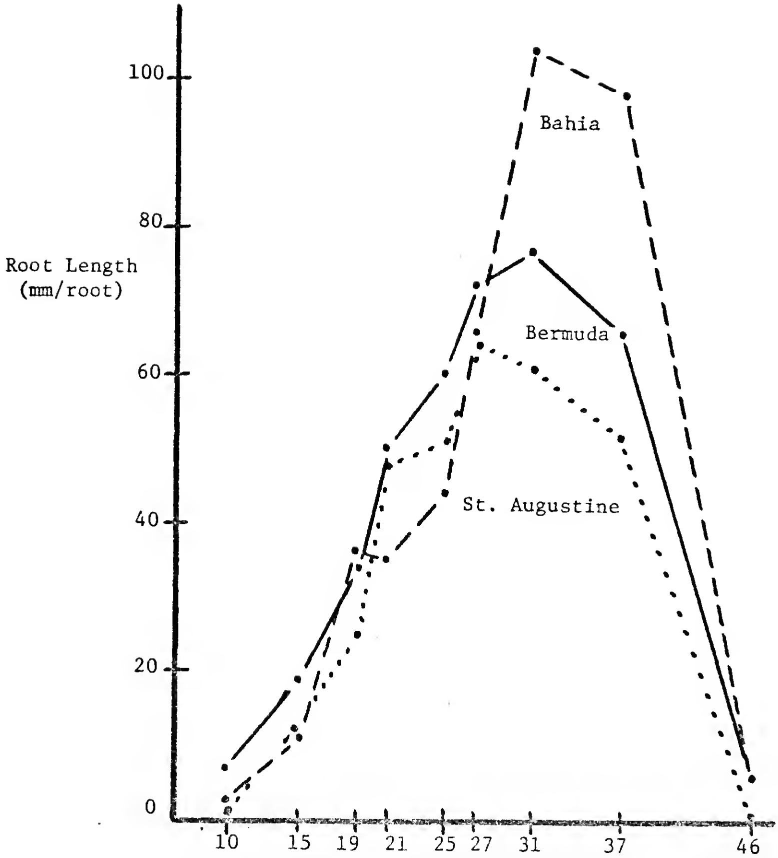

Figure 30. Mean root length (mm) initiated on bahia, St. Augustine, and bermuda grass stolons or rhizomes as affected by a gradient of root media temperatures.

Bahiagrass had the highest optimum root media temperature for root growth (weight and length) with bermuda and St. Augustine grass next.

Field Study

No significant responses occurred with bahia, St. Augustine, and bermuda grass to five fertilizer treatments during winter months of 1972-73 as to combustionable carbon weight of root tissue. The only differences in winter root growth were between grasses on the last four out of five harvest dates (Table 19). Bahiagrass had highest root weights with St. Augustinegrass second and bermudagrass third (Fig. 31).

Nutrient element analysis of leaf tissue taken one month after termination of fertilizer treatments indicated some differences due to fertilizer treatments and between grasses (Tables 20 and 21). Fertilizer treatments affected N, P, Ca, and Mn levels in the three grasses, and grasses contained different levels of N, P, K, Ca, Mg, Mn, and Cu.

Table 19. Mean monthly combustionable carbon root weight for bahia, St. Augustine and bermuda grass from fertilizer field study (averaged over five fertilizer treatments and four replications).

Grasses	Dec. 19	Jan. 20	Feb. 23	March 28
Bermuda	0.4844 b*	0.4713 c	0.4698 c	0.6550 b
Bahia	0.7918 a	0.9345 a	0.8360 a	0.9688 a
St. Augustine	0.6975 a	0.7528 b	0.7072 b	0.9262 a

Table 20. Mean content of nutrient elements in leaf tissue taken from bahia, St. Augustine and bermuda grass four weeks after termination of fertilizer field study.

Fertilizer Ratio	% Dry Weight			ppm
	N	P	Ca	Mn
1-0-1	2.78 ab*	0.29 b	0.45 b	110 a
1-0-0	2.92 a	0.29 b	0.52 a	115 a
0-0-2	2.37 c	0.30 ab	0.50 ab	43 b
1-0-4	2.78 ab	0.31 ab	0.31 c	103 a
Milorganite	2.65 b	0.34 a	0.44 b	53 b

Table 21. Mean content of nutrient elements in bahia, St. Augustine and bermuda grass top tissue taken three weeks after termination of fertilizer field study.

Grasses	%					ppm	
	N	P	K	Ca	Mg	Mn	Cu
Bermuda	3.02 a*	0.27 b	1.82 b	0.71 a	0.33 b	115 a	24 b
Bahia	2.65 b	0.25 b	1.97 b	0.40 b	0.45 a	111 a	33 a
St. Augustine	2.43 c	0.39 a	2.54 a	0.22 c	0.28 c	29 b	19 b

* Means in a column followed by the same letter are not significantly different as determined by Duncan's Multiple Range Test (5% level).

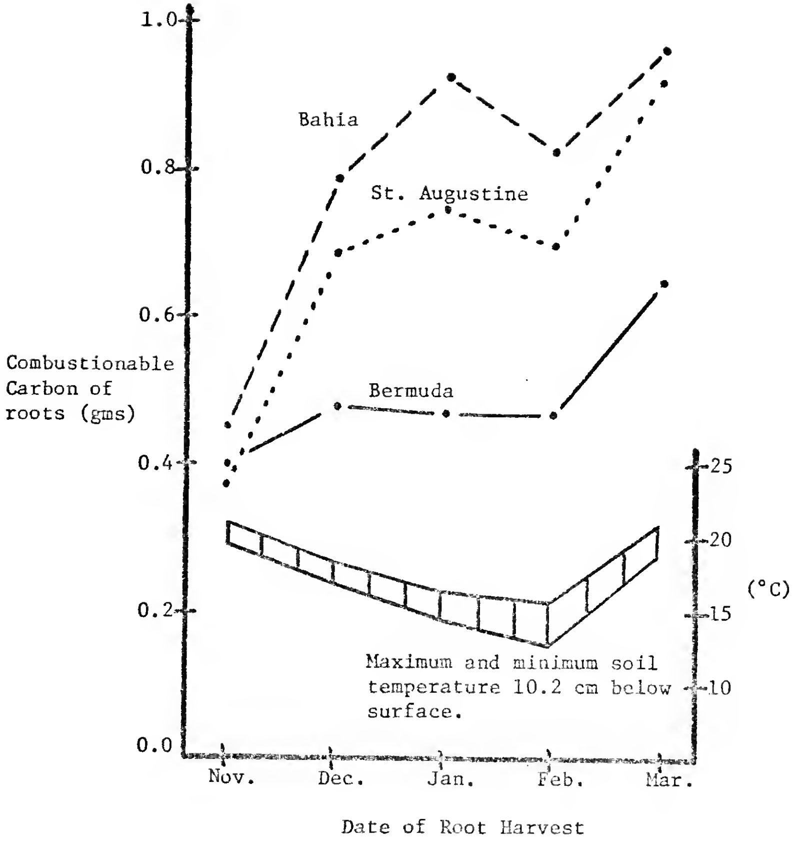

Figure 31. Mean monthly combustionable carbon root weight for bahia, St. Augustine, and bermuda grass averaged from five fertilizer treatments in field study.

DISCUSSION

Effects of Soil Temperature Gradient

Shoot Growth

Results from these experiments indicated that shoot growth was indirectly affected by soil temperature effects on below-ground plant parts. Total dry weight of clippings increased with increasing soil temperatures. Bahiagrass showed highest optimum temperature, followed by St. Augustine and bermuda grass. These results agreed with soil temperature ranges reported by Schroder (50) for maximum shoot growth of 'Pensacola' bahiagrass and 'Coastal' bermudagrass at 36.6 and 40.6°C, respectively, when controlled independently of ambient temperatures. Street (55) postulated two factors about root systems which control shoot growth: (1) Roots served as carbohydrate "sinks" or storage organs and as assimilators for amino acid and protein synthesis since N is absorbed by roots and translocated to shoots in organic combinations. Therefore, roots regulate shoot growth by intensity or direction of carbohydrate gradient. (2) Roots supplied hormonal substances to shoots which had growth regulating effects, thus, factors which affect root growth or function indirectly alter shoot growth.

Percent TNC of clippings showed little response to gradient of soil temperatures, as indicated by TNC weight per pot in clipping yields curve which closely paralleled dry weight results (Figs. 8 and 21). Nielsen and Humphries (41) explained that temperature effects on plant growth and carbohydrate levels were manifest in preferential utilization of available carbohydrates for shoot growth with excesses translocated to rhizomes and roots. Results herein showed no TNC accumulated in clippings, except that utilized for growth, and excess TNC was translocated basipetally as evidenced in accumulation of TNC in rhizomes, stolons, and roots (Figs. 19, 20, 23, and 24).

Effects of soil temperature on clipping yields appeared to be reduction of growth at cooler temperatures and translocation of carbohydrates from continued photosynthetic rates to other plant parts at these cool temperatures. At warm, near optimum temperatures for growth, available carbohydrates were incorporated in growth with increased respiration, and no translocation and subsequent accumulation in other plant parts occurred.

Verdure Growth

Verdure tissue in this study included shoot growth below clipping height, but excluded stolons, rhizomes, and roots. Initial grass plugs in each experiment contained a large volume of verdure tissue, thus to obtain significant differences required large changes from initial to final weights and TNC levels.

Maximum weights of bahia and St. Augustine grass verdure tissue occurred within a range of 25 to 30°C soil temperature, whereas bermudagrass verdure dry weight decreased with increased soil temperatures from 10 to 46°C (Fig. 9). Lowest dry weights of bahia and St. Augustine grass verdure tissue occurred at 10 to 11°C soil temperature. Reduction in growth of bahia and St. Augustine grass verdure at coldest temperature was due to root effects on shoot growth similar to clipping yield results. Slight decreased growth of verdure tissue of these two grasses at highest temperature was due possibly to lack of adequate root system for regulation and assimilation of substances for further shoot growth (Figs. 9 and 11). Possibly available carbohydrates also were utilized for growth of clippings which had higher optimum temperature for growth.

Negative relationship of bermudagrass verdure growth and TNC weight per pot to soil temperature was opposite or contrasted with clipping responses, therefore, some available carbohydrates must have been utilized for growth of verdure tissue at cooler temperatures instead of translocation to rhizomes and roots. The constant level of % TNC in verdure tissue, except at 10°C, could substantiate the previous explanation of growth responses, since carbohydrates were not accumulated in clippings or verdure, except at 10°C. Thus, excess carbohydrates not utilized for shoot growth of bermudagrass were translocated basipetally (Figs. 23 and 24). The reason for high % TNC and TNC total weight in bermudagrass verdure at 10°C could have resulted from reduced basipetal translocation, since carbohydrates were also high in rhizomes and roots at this temperature. Increased TNC synthesis accompanied by reduced respiration at this temperature also would explain such accumulation at the cold temperature.

Percent and total TNC of bahia and St. Augustine grass verdure tissue differed from each other in response to gradient of soil temperatures. Bahiagrass had maximum % TNC at 10°C, which decreased to lowest point at 30°C, then increased (Fig. 18). Lowest % TNC corresponded to greatest amount of growth, thus TNC was consumed in growth at this point. Increased TNC level at warmer and cooler temperatures indicated increased TNC synthesis or reduced translocation (Fig. 18). TNC weight per pot in bahia verdure varied across the soil temperature gradient but did not change sufficiently to provide a significant response.

TNC percent and total weight in St. Augustinegrass verdure generally increased with increasing temperatures (Figs. 18 and 22). At higher temperatures there appeared a higher rate of synthesis and accumulation of TNC, however, as soil temperature was reduced past the point at which maximum growth occurred, storage was reduced. This indicated that St. Augustinegrass verdure translocated excess TNC to stolons or roots similar to what happened in clipping tissue.

No nutrient elemental levels in any tissue of the three grasses correlated with growth responses or to soil temperatures, although there were significant differences in some elemental levels (Tables 13 to 17). Lack of correlation or relationship to growth responses was probably due to the frequency of liquid nutrient application (every two days) and to readily soluble source of elements and the fact that none apparently were deficient or in excess. Grass plugs were grown on pure builders sand media, thus nutrient availability was optimum for absorption and assimilation.

Stolon and Rhizome Growth

St. Augustinegrass stolon growth did not respond to soil temperature gradient, although % TNC and TNC total weight did vary similarly with a general decrease from low to high soil temperatures (Tables 6, 9, 11 and Figs. 10, 19, and 23). TNC weight and % TNC showed similar responses probably because most TNC was incorporated into growth of this tissue with some accumulation at 11°C.

Bahia and bermuda grass rhizome dry weights fluctuated across the soil temperature gradient, but generally there was an inverse relationship with growth decreasing as soil temperatures increased. When % TNC and weight were evaluated, a more definite inverse relationship was observed, thus showing a positive relationship of tissue growth with TNC status of the tissue (Figs. 10, 19, and 23). This can be explained by Wardlaw's (61) statement that carbohydrate distribution was associated with growth rather than translocation and as temperatures were decreased there was a shift in carbohydrate distribution from shoots to roots. At warmer soil temperatures, shoot growth of bahia and bermuda grass was maximum, and available TNC was incorporated into those tissues. However, as soil temperatures were reduced rhizome growth was increased, and available carbohydrates were translocated basipetally at expense of shoot growth. Carbohydrate translocation thus occurred, as described by Nielsen and Humphries (41) earlier. At cooler soil temperatures, photosynthesis appeared to continue in shoot growth, but carbohydrate translocation was basipetal to rhizomes and roots with little subsequent acropetal movement.

Root Growth

Root growth of bahia and St. Augustine grass was maximum at 19 to 21°C and 25 to 30°C, respectively, whereas bermudagrass root growth was not statistically delineated but approached a maximum at 15 to 21°C (Table 6). Youngner (72) reported optimum soil temperature for bermudagrass root growth as 23.3°C, whereas Schroder (50) found maximum root weight of 'Coastal' bermudagrass at 26.9°C and maximum for 'Pensacola' bahiagrass at 30°C. Minimum and maximum root growth temperatures were attained with bahia and St. Augustine grass since very little root tissue developed at temperature extremes (Fig. 11).

Bermudagrass root growth did not show minimum-maximum temperature response possibly due to the fact that bermudagrass plugs were allowed one week of root growth before being placed on temperature apparatus, thus some root growth occurred before treatments were applied. Nevertheless, root growth of bermudagrass did appear to have a lower optimum soil temperature than bahia or St. Augustine grass. No clear explanation can be given for this observation except that bermudagrass verdure and rhizome tissue also had lower optima soil temperatures than the other grasses, indicating its genetic origin permitted cooler adaptation than bahia or St. Augustine grass.

Percent TNC found in root systems of the three grasses indicated general decrease as temperature increased with the highest level at 10 to 11°C and lowest at 45 to 46°C (Table 9). These results agree with reports by Davidson (11) and Weinmann (64), showing high concentrations of soluble carbohydrates at low soil temperatures. Davies (12) reported carbohydrate levels in ryegrass to be positively correlated with growth rate of root systems. Weight of TNC in roots of these three grasses agreed with Davies' (12) results since there was decrease in TNC weight as temperature was decreased or increased from optimum (Fig. 24). Explanation for carbohydrate status of root systems was based on growth curves of shoots and roots, showing a preferential translocation of carbohydrates to growth centers. Excess TNC from shoots at cooler temperatures was translocated to root and rhizome tissue where it was utilized for growth and excesses stored.

Length and dry weight of roots initiated from rhizome and stolon pieces as affected by root media temperature were evaluated over a six-day period. Maximum root length and dry weights occurred within ranges of 31, 21, and 27 to 37°C for bahia, St. Augustine, and bermuda grass, respectively (Table 18). Such results indicated a slightly higher optimum soil temperature for short-term root growth than reported in long-term grass plug experiments conducted on the same apparatus.

Beard (6) observed a similar response with bentgrass root growth in which he reported root elongation was more rapid at high temperatures on short-term bases of one to two weeks. West et al. (67) studied root growth from Pangolagrass stem sections as affected by gradient of root media temperatures for two weeks, and their results indicated maximum root weight and length occurred at 31 to 34°C, which is within the range reported here.

An explanation for observed increases in optimum temperature for growth in this short-term study was due probably to increased respiration and subsequent growth, however, the study was too short to deplete reserve carbohydrates of stolon or rhizome pieces.

Effects of long-term soil temperatures on root morphology were identical to those reported by several authors (6, 21, and 39). Roots were shorter, thicker, less branched and whiter at temperatures below optimum, whereas roots were brown, spindly, and multibranched at temperatures above optimum up to the maximum temperature. Minimum and maximum cardinal temperatures for root growth appeared within the range (10 to 46°C) of these studies for the three grasses. Beard (6) explained morphological responses were caused by degree of tissue maturity. Root maturation was accelerated by high soil temperatures which caused subsequent brown color and increased branching.

Winter Root Growth in Field

The field study was conducted to evaluate winter root growth of the three warm-season grasses and to observe effects of winter fertilization on such growth. Root growth did not respond to fertilizer rates or ratios. There were only differences between grasses. Apparently, the soil had a high inherent fertility level, and fertilizer treatments did not influence growth significantly during this time of year. Grass shoots were dormant part of the study duration, therefore, carbohydrates came from reserves and growth was at expense of these reserves. Root growth, therefore, responded to temperature and carbohydrate levels rather than fertilizer treatments. Winter root growth occurred within soil temperature range of 12.8 to 21.1°C when shoot growth was reduced (Fig. 31).

Seasonal Grass Growth

There were seasonal growth responses of warm-season grasses divided into shoot and below-ground tissue responses. Seasonal shoot growth response agreed with findings by many authors which showed positive correlations to temperatures (ambient and soil) (6, 21, and 39). Seasonal growth responses of rhizomes and roots are not well documented, but Youngner (72) reported root and shoot growth of bermudagrass occurred simultaneously throughout warm season. He further stated that opposing root-shoot growth responses did not exist to the same degree as noted in cool-season grasses. These studies indicated that root and rhizome growth was seasonal and opposite to that of shoot growth. Weinmann (65) reported seasonal TAC (Total Available Carbohydrate) flux in which plant parts of various warm-season grasses contained lowest TAC levels (8.4%) in summer and highest (18 to 19%) TAC content in winter. Results from these studies concurred with Weinmann's (65) observations.

Cultural Practices

Cultural practices need be initiated with ambient and soil temperatures considered so as to minimize damage and/or maximize regrowth potential of turfed areas. Soil aerification which injures roots and rhizomes should be initiated in early spring or fall when soil temperatures are low enough to attain maximum root and rhizome regrowth. Vertical mowing should be done in warm periods when shoot growth is maximum. Corrections for extremely high soil temperatures can be accomplished by periodic syringing, regardless of evidence of wilt.

More timely fertilizing, such as late fall and possibly winter fertilization, is needed to insure adequate nutrient status for early spring root growth. Protective covers against extremes in soil temperatures could be effectively used during cool portions of the year.

SUMMARY

Results from these experiments indicated that soil temperatures played important roles in growth of roots and shoots. Roots appeared to have growth regulatory effects on shoots since ambient temperatures were not altered but soil temperatures were. Regulatory effects were manifested in contradictory dry weight curves of roots, rhizomes, and shoots across the soil temperature gradient. Maximum shoot dry weight occurred when root and rhizome dry weight was lowest and was minimum when root and rhizome dry weight was maximum. Root dry weight did not necessarily reflect extensiveness and activity of the root system. Carbohydrate translocation occurred between shoots, rhizomes, and roots with shoots and rhizomes apparently utilizing and storing carbohydrates in higher quantities than roots. Bahia, St. Augustine, and bermuda grass responded similarly to a gradient of soil temperatures, although soil temperature optima for overall growth was highest for bahiagrass followed by St. Augustine and bermuda grass. Overall, bahiagrass stored higher % TNC in plant parts than St. Augustine or bermuda grass.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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