

SOME PHYSIOLOGICAL RESPONSES OF TWO GRASSES  
AS INFLUENCED  
BY TEMPERATURE, LIGHT, AND NITROGEN FERTILIZATION

by

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## TABLE OF CONTENTS

|                                                                                                                                                                                                           | page |
|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------|
| I. ACKNOWLEDGMENTS . . . . .                                                                                                                                                                              | 2    |
| II. INTRODUCTION . . . . .                                                                                                                                                                                | 11   |
| III. REVIEW OF LITERATURE . . . . .                                                                                                                                                                       | 12   |
| Responses of Grass to Temperature . . . . .                                                                                                                                                               | 12   |
| Responses of Grass to Nitrogen . . . . .                                                                                                                                                                  | 17   |
| Responses of Grass to Light . . . . .                                                                                                                                                                     | 20   |
| IV. EXPERIMENT I. The Effect of Temperature and Nitrogen<br>on Growth and Composition of Bentgrass and Bermuda-<br>grass . . . . .                                                                        | 24   |
| PROCEDURE . . . . .                                                                                                                                                                                       | 24   |
| RESULTS . . . . .                                                                                                                                                                                         | 27   |
| Bentgrass, Experiment IA . . . . .                                                                                                                                                                        | 27   |
| Bentgrass, Experiment IB . . . . .                                                                                                                                                                        | 34   |
| Bermudagrass, Experiment IA , . . . . .                                                                                                                                                                   | 43   |
| Bermudagrass, Experiment IB . . . . .                                                                                                                                                                     | 47   |
| DISCUSSION . . . . .                                                                                                                                                                                      | 54   |
| Bentgrass . . . . .                                                                                                                                                                                       | 54   |
| Bermudagrass . . . . .                                                                                                                                                                                    | 56   |
| V. EXPERIMENT II. The Effect of Light Intensity, Night<br>Temperature, and Nitrogen on Bentgrass and Bermuda-<br>grass Growth, NAR, Respiration, Nitrogen Content,<br>and Carbohydrate Reserves . . . . . | 59   |
| PROCEDURE . . . . .                                                                                                                                                                                       | 59   |
| RESULTS . . . . .                                                                                                                                                                                         | 61   |
| Bentgrass, Experiment II . . . . .                                                                                                                                                                        | 61   |
| Bermudagrass, Experiment II . . . . .                                                                                                                                                                     | 72   |
| DISCUSSION . . . . .                                                                                                                                                                                      | 82   |
| Bentgrass . . . . .                                                                                                                                                                                       | 82   |
| Bermudagrass . . . . .                                                                                                                                                                                    | 84   |

|                                                                                                                                              | page |
|----------------------------------------------------------------------------------------------------------------------------------------------|------|
| VI. EXPERIMENT III. The Influence of Nitrogen and Season<br>on the Carbohydrate Content of Bentgrass and Bermuda-<br>grass Stolons . . . . . | 86   |
| PROCEDURE . . . . .                                                                                                                          | 86   |
| RESULTS . . . . .                                                                                                                            | 88   |
| Bentgrass, Experiment III . . . . .                                                                                                          | 88   |
| Bermudagrass, Experiment III . . . . .                                                                                                       | 93   |
| DISCUSSION . . . . .                                                                                                                         | 95   |
| Bentgrass . . . . .                                                                                                                          | 95   |
| Bermudagrass . . . . .                                                                                                                       | 99   |
| VII. GENERAL DISCUSSION . . . . .                                                                                                            | 101  |
| VIII. SUMMARY . . . . .                                                                                                                      | 105  |
| IX. LITERATURE CITED . . . . .                                                                                                               | 108  |
| X. VITA . . . . .                                                                                                                            | 117  |

## TABLES

|                                                                                                                                                                                                                                                                         | page |
|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------|
| TABLE 1. Carbohydrates (% of dry matter) in bentgrass leaves and stolons with two nitrogen rates and each of three temperatures. . . . .                                                                                                                                | 28   |
| TABLE 2. Nitrogen fractions (% of dry matter) in bentgrass leaves and stolons with two nitrogen rates and each of three temperatures. . . . .                                                                                                                           | 29   |
| TABLE 3. Effect of nitrogen rates and temperatures on bentgrass and bermudagrass clippings (average dry weight in grams per pot for 7 clippings) during 45 days. . . . .                                                                                                | 30   |
| TABLE 4. Effect of nitrogen rates and temperatures on bentgrass and bermudagrass roots during 45 days. . . . .                                                                                                                                                          | 31   |
| TABLE 5. Carbohydrates (% dry weight) in bentgrass stolons with two nitrogen rates with each of three temperatures for 45 days plus 10 subsequent days with the original and two other temperatures. . . . .                                                            | 35   |
| TABLE 6. Carbohydrate (% dry weight) in bentgrass leaves with two nitrogen rates with each of three temperatures for 45 days plus 10 subsequent days with the original and two other temperatures. . . . .                                                              | 36   |
| TABLE 7. Ten-day clipping yields (average dry weight in grams per pot for last 10 days) of bentgrass and bermudagrass from two nitrogen rates with each of three temperatures for 45 days plus 10 subsequent days with the original and two other temperatures. . . . . | 40   |
| TABLE 8. Root weights (average dry weight in grams per pot) of bentgrass and bermudagrass from two nitrogen rates with each of three temperatures during 45 days plus 10 subsequent days with the original and two other temperatures. . . . .                          | 42   |
| TABLE 9. Carbohydrates (% dry matter) in bermudagrass leaves, stolons, and rhizomes with two nitrogen rates with each of three temperatures. . . . .                                                                                                                    | 44   |

|                                                                                                                                                                                                                                                                                                    | page |
|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------|
| TABLE 10. Nitrogen fractions (% of dry matter) in bermudagrass leaves, stolons, and rhizomes with two nitrogen rates with each of three temperatures. . . . .                                                                                                                                      | 45   |
| TABLE 11. Carbohydrates (% dry weight) in bermudagrass stolons with two nitrogen rates with each of three temperatures for 45 days plus 10 subsequent days with the original and two other temperatures. . . . .                                                                                   | 48   |
| TABLE 12. Carbohydrate (% dry weight) in bermudagrass leaves and rhizomes with two nitrogen rates with each of three temperatures for 45 days plus 10 subsequent days to the original and two other temperatures. . . . .                                                                          | 49   |
| TABLE 13. Significant (*) and highly significant (**) differences for carbohydrate data in Figures 6 and 7. . . . .                                                                                                                                                                                | 64   |
| TABLE 14. Top growth (mg dry matter) of bentgrass grown at L-1 and L-0.5 with two nitrogen rates at each of three night temperatures for three 10-day periods and also for switching the high-low temperatures for the last 10 days. (Temperature during 14 hrs. light was 95 F.) . . . . .        | 67   |
| TABLE 15. Root weights (mg dry matter per pot) of bentgrass grown at two light intensities with two nitrogen rates at each of three night temperatures after 30 days and also for switching the high-low temperatures for the last 10 days. (Temperature during 14 hrs. light was 95 F.) . . . . . | 69   |
| TABLE 16. Significant (*) and highly significant (**) differences for carbohydrate data in Figures 10 and 11. . . . .                                                                                                                                                                              | 75   |
| TABLE 17. Top growth (mg dry matter) of bermudagrass grown at L-1 and L-0.5 with two nitrogen rates at each of three night temperatures for three 10-day periods and also for switching the high-low temperatures for the last 10 days. (Temperature during 14 hrs. light was 95 F.) . . . . .     | 78   |

|           |                                                                                                                                                                                                                                                                                         |    |
|-----------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----|
| TABLE 18. | Root weights (mg dry matter per pot) of bermudagrass grown at two light intensities with two nitrogen rates at each of three night temperatures after 30 days and also for switching the high-low temperatures for the last 10 days. (Temperature during 14 hrs. light was 95 F.) . . . | 79 |
| TABLE 19. | Carbohydrate (% dry weight) in stolons of Cohansey bentgrass grown for two seasons at Blacksburg and Tifgreen bermudagrass grown for one season at Richmond with three nitrogen rates. . . . .                                                                                          | 92 |

## FIGURES

|                                                                                                                                                                                                                                                                                                   | page |
|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------|
| FIG. 1. Effect of temperature and nitrogen rates on net assimilation (NAR) and respiration of bentgrass and bermudagrass. . . . .                                                                                                                                                                 | 33   |
| FIG. 2. Total nitrogen content of bentgrass stolons and leaves with two nitrogen rates with each of three temperatures for 45 days plus 10 subsequent days with the original and two other temperatures. . . . .                                                                                  | 38   |
| FIG. 3. Protein nitrogen content of bentgrass leaves and stolons with two nitrogen rates with each of three temperatures for 45 days plus 10 subsequent days with the original and two other temperatures. . . . .                                                                                | 39   |
| FIG. 4. Total nitrogen content of bermudagrass leaves, stolons, and rhizomes with two nitrogen rates with each of three temperatures for 45 days plus 10 subsequent days with the original and two other temperatures. . . . .                                                                    | 51   |
| FIG. 5. Protein nitrogen of bermudagrass leaves, stolons, and rhizomes with two nitrogen rates with each of three temperatures for 45 days plus 10 subsequent days with the original and two other temperatures. . . . .                                                                          | 52   |
| FIG. 6. Carbohydrates (% dry weight) in stolons of bentgrass grown at 95 F for 14 hours at (3,000 ft-c) L-1 with two N rates at each of three night temperatures for three 10 day periods and also switching the high-low temperatures for the last 10 days. . . . .                              | 62   |
| FIG. 7. Carbohydrates (% dry weight) in stolons of bentgrass grown at 95 F for 14 hours at (1,500 ft-c) L-0.5 with two N rates at each of three night temperatures for three 10-day periods and also switching the high-low temperatures for the last 10 days. . . . .                            | 63   |
| FIG. 8. Total nitrogen content (% dry weight) in bentgrass stolons grown at 95 F for 14 hours at L-1 (3,000 ft-c) and L-0.5 (1,500 ft-c) with two N rates at each of three night temperatures for three 10-day periods also switching the high and low temperatures for the last 10 days. . . . . | 66   |

|          |                                                                                                                                                                                                                                                                                          |    |
|----------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----|
| FIG. 9.  | NAR and respiration rates of bentgrass grown at L-1 (3,000 ft-c) and L-0.5 (1,500 ft-c) with two N rates at each of three night temperatures for 30 days and also for switching the high-low temperatures for the last 10-day period. . . . .                                            | 70 |
| FIG. 10. | Carbohydrates (% dry weight) in stolons of bermudagrass grown at 95 F for 14 hours at L-1 (3,000 ft-c) with two N rates at each of three night temperatures for three 10-day periods and also switching the high and low temperatures for the last 10 days. . . . .                      | 73 |
| FIG. 11. | Carbohydrates (% dry weight) in stolons of bermudagrass grown at 95 F for 14 hours at L-0.5 (1,500 ft-c) with two N rates at each of three night temperatures for three 10-day periods and also switching the high and low temperatures for the last 10 days. . . . .                    | 74 |
| FIG. 12. | Total nitrogen content (% dry weight) in bermudagrass grown at 95 F for 14 hours at L-1 (3,000 ft-c) and L-0.5 (1,500 ft-c) with two N rates at each of three night temperatures for three 10-day periods and also switching the high and low temperatures for the last 10 days. . . . . | 76 |
| FIG. 13. | NAR and respiration rates of bermudagrass grown at 95 F for 14 hours at L-1 (3,000 ft-c) and L-0.5 (1,500 ft-c) with two N rates at each of three night temperatures for 30 days and also for switching the high-low temperatures for the last 10 days. . . . .                          | 81 |
| FIG. 14. | Seasonal influence (1962-1963) on carbohydrates in stolons of creeping bentgrass (mean of three N rates). . . . .                                                                                                                                                                        | 89 |
| FIG. 15. | Seasonal influence on carbohydrates in stolons of creeping bentgrass fertilized with high and low nitrogen rates. . . . .                                                                                                                                                                | 90 |
| FIG. 16. | Seasonal influence (1964-1965) on carbohydrates in stolons of creeping bentgrass (mean of three N rates). . . . .                                                                                                                                                                        | 91 |
| FIG. 17. | Seasonal influence (1963-1964) on carbohydrates in stolons of bermudagrass (mean of three N rates). . . . .                                                                                                                                                                              | 94 |

|                                                                                                                                 |      |
|---------------------------------------------------------------------------------------------------------------------------------|------|
|                                                                                                                                 | page |
| FIG. 18. Seasonal temperatures (14-day means of minimum<br>and maximum) taken five feet above the sod at<br>Blacksburg. . . . . | 97   |
| FIG. 19. Seasonal temperatures (14-day means of minimum<br>and maximum) taken five feet above the sod at<br>Blacksburg. . . . . | 98   |
| FIG. 20. Seasonal temperatures (14-day means of minimum<br>and maximum) taken five feet above the sod at<br>Richmond. . . . .   | 100  |

## INTRODUCTION

Bentgrass (Agrostis palustris Huds.) and bermudagrass (Cynodon dactylon (L.) Pers.) are widely used for specialized turf, such as golf putting greens. Although the former grass is adapted to cool climates and the latter is a native of the semi-tropics, both are used extensively in Virginia, a climatic transition zone. These grasses are often injured during periods of stress because they are grown out of their adapted ecological environment. Close mowing and high nitrogen fertility to maintain the desired turf density and color often aggravate injury during unfavorable conditions.

Considerable research on forage grasses shows that stored carbohydrates influence regrowth and survival during conditions of stress. Little work, however, has been reported on the effects of temperature and nitrogen fertilization on carbohydrate reserves of turfgrasses that are maintained in the vegetative stage by frequent close clipping. Information of the carbohydrate status of turf grasses, as influenced by natural and imposed variables, may be useful in diagnosing and predicting turfgrass behavior.

The laboratory research reported here was conducted to study the growth behavior and some physiological effects of a warm season (Tifgreen bermudagrass), and a cool season (Cohansey bentgrass) turfgrass with nitrogen, temperature, and light variables in factorial combinations. The influence of nitrogen and season on carbohydrate reserves of the two grasses was studied in the field.

## REVIEW OF LITERATURE

## Responses of Grass to Temperature

Growth:

Many investigators have reported on the influence of temperature on growth and the morphological changes of species. Bermudagrass (Cynodon dactylon) made no growth at 40 F and Kentucky bluegrass (Poa pratensis), Canada bluegrass (Poa compressa), and orchardgrass (Dactylis glomerata) made some growth at 40 F. Optimum top growth occurred at 80-90 F for the bluegrass, 70 F for the orchardgrass, and 100 F for bermudagrass. Roots and rhizomes developed best at 50 F for Canada bluegrass, 60 F for Kentucky bluegrass, 70 F for orchardgrass, and 100 F for bermudagrass (Brown, 1939). The optimum temperature for root growth is generally lower or similar as for herbage growth (Darrow, 1939; Brown, 1939; Harrison, 1934; Sullivan and Sprague, 1949; and Lovvorn, 1945). However, Beard (1961) observed that roots of bentgrass were reduced in yield with temperatures above 80 F but maximum top growth occurred at 70 F.

Went (1944) reported optimum growth of several grasses with night temperature several degrees lower than the day temperature. Adverse effects of high day temperatures on barley growth were offset by low night temperatures (Gregory, 1926). However, Brown (1939) found that bermudagrass and Kentucky and Canada bluegrasses were less influenced by night temperatures.

Beevers and Cooper (1964a) indicated that a low day:low night temperature regime was associated with a better root development than for a high day:high night or high day:low night regime. Ryegrass root/top ratios were reduced or increased by temperatures above and below those for optimum dry matter production. Beard (1959) reported that temperature controlled bentgrass root initiation. Root initiation occurred during late summer when temperatures dropped sharply. Low light intensities and high temperatures reduced roots more than shoots (Soper, 1957).

Kentucky bluegrass made little top growth until the temperature in the top half inch of soil rose to 50 F (Brown, 1943). Maximum growth occurred in early May when soil temperature averaged 62 F. The lowest herbage yields occurred in July when soil temperatures averaged 74 F. Top growth declined during September and remained low in October even though the mean temperature was similar to that of May.

Two peak periods of growth, the first from mid-April to mid-May, and the second from mid-June to late July, occurred with bentgrass putting turf (Musser and Duich, 1958). Growth then decreased progressively from mid-August until early October.

Kentucky bluegrass with adequate nitrogen at 60 F initially produced less new foliage after defoliation than grass at 80 F (Harrison, 1934). However, after several defoliations this relationship reversed. Alberta (1956-57) and Beevers and Cooper (1964a) reported similar findings for ryegrass. They attributed this to faster leaf maturation in warm than for cool regimes. Several researchers have shown that the photosynthetic efficiency of senescent leaves is lower than for young ones (Barua, 1960; Miller, 1960).

### Carbohydrate and Nitrogen Constituents:

At temperatures above optimum for growth, carbohydrate reserves of certain plants are utilized in respiration faster than  $\text{CO}_2$  can be assimilated (Brown, 1939; Harrison, 1934; Kendall, 1958; Gist, 1957; and Alberta 1956-57). Plants growing at temperatures below optimum eventually outyield those grown at optimum growth temperatures (Harrison, 1934; Sprague and Sullivan, 1950; and Sullivan and Sprague, 1953). Growth and respiration that take place at expense of food storage can be stimulated only to a degree before growth is decreased by exhausting the food reserves (Madison, 1962). (This effect caused bentgrass growth rate and sugar levels to have an inverse relationship (Jordan, 1959)).

Brown (1939) found that the N-free extract of orchardgrass, Kentucky and Canada bluegrass declined with rising temperatures. However, N-free extract in bermudagrass did not decrease with temperature increase. These results are possibly explained with Lundegarth's (1931) statement that tropical plants have a higher assimilation rate than temperate species.

DeCugnac (1931) and Weinmann (1947) placed perennial grasses in two groups; those which accumulate fructosan and sucrose with no starch (cool season grasses) and those which store non-reducing sugars and starch with no fructose (grasses adapted to semi-tropics). Total available carbohydrates decrease in bermudagrass foliage from spring to fall. The carbohydrates in the rhizomes were reduced in early spring, increased during the summer, and then decreased during the winter (Weinmann and Goldsmith, 1948).

Carbohydrates in cool season grasses were high during the fall and winter (Brown, 1943; McCarty and Price, 1942; Sampson and McCarty, 1931; and Alberta, 1956-57), decreased when leaf growth was rapid in the spring and early summer, had a peak in June or July, and then a slight decline in August (Reynolds and Smith, 1962). Alberta (1956-57) reported that high night temperatures may have adverse effects on recovery of the carbohydrate reserves. Rapid regrowth occurred when the carbohydrate content was adequate (Ward and Blaser, 1961) and when temperatures were favorable for growth (McCarty, 1942; Norman, 1939).

Sullivan and Sprague (1949) found that total N, amino acids, and nitrogenous salts increased with temperature. However, the authors explained this may have been apparent since carbohydrates were reduced with increased temperatures. Ryegrass growing continuously at 12 C had higher carbohydrate, ammonium, and total nitrogen contents, but a lower nitrate content than for warmer regimes (Beever and Cooper, 1964b). They hypothesized that the low nitrate content was caused by efficient nitrate reduction at lower than at higher temperatures. This theory was supported by the ammonium content (probably derived from the reduction of nitrate) being the greatest at the low temperature regimes. The lower total N of plants growing in warm regimes may be associated with production of other cell constituents, thus diluting the nitrogenous components.

Carbohydrate accumulation at low temperatures may be due to the decreased respiration which causes less energy conversion by adenosine triphosphate (ATP). The free amino-N accumulation has been attributed to the reduction of ATP which is needed to synthesize proteins from amino acids (Webster, 1959).

Beard (1961) reported with bentgrass that non-protein N was lowest at 70 F and increased as temperature was raised or lowered, while with bermudagrass the non-protein N level increased with temperature. He indicated that maximum growth utilized more nitrogen; therefore, decreased the level of non protein N.

#### Photosynthesis and Respiration:

With sufficient carbon dioxide, light, water, and fertility the rate of photosynthesis generally increases with temperature up to a point then decreases with further rise in temperature (Meyer et al., 1961; Ormrod, 1961; Murata, 1961; and El-Sharkawy and Hesketh, 1964). Yet other workers reported either a slight increase in photosynthesis or no significant effect with increased temperature (Beinhart, 1962; Yamada et al., 1955; Verduin and Loomis, 1944; Chapman et al., 1954; Thomas and Hill, 1949; and Moss et al., 1961). The latter data were apparently obtained at temperatures in the optimum range, since both Yamada et al. (1955) and Murata (1961) found photosynthesis of "excised rice" was not affected when grown from 20 to 33 C. However, Murata also reported photosynthesis was retarded below 20 and above 40 C.

Murata (1961) proposed two explanations for temperature effects below 20 C. The first is that carbon dioxide diffusion is limited

under low temperature because low temperature reduces the dark reaction. The second is that the  $Q_{10}$  value is increased by a factor (i.e. closing of the stomata) that affects the temperature independent diffusion process. Moss (1961) found that the drop in net assimilation rates at high temperature was too large to be attributed to increased respiration alone. Decker (1944) claimed that photosynthesis became "heat inactivated" at high temperatures. Meyer et al. (1961) explained that NAR reduction at higher temperature may be due to one or more of the following: (1) inactivation of enzymes, (2) oxygen may be limited, and (3) carbon dioxide may accumulate and check respiration.

### Responses of Grass to Nitrogen

#### Growth:

Troughton (1957) states that in general grasses grown with limited nitrogen levels have well developed roots, but poorly developed shoots. The reverse generally occurs where excess nitrogen is available (Lovvorn, 1947; Oswalt et al., 1959; Juska et al., 1955; Hylton et al., 1965; Harrison, 1934; Sprague, 1934; and Madison, 1962). Root growth is reduced under high nitrogen because less sugar is translocated from the stimulated growing shoot (Harrison, 1934; Sprague, 1934; Jones et al., 1961; and Nowakowski, 1962).

Bluegrass, conditioned to low N, gave a rapid growth increase during hot weather while no response was obtained with high N conditioned plants when additional high nitrogen was applied. These growth

responses were attributed to the higher carbohydrate reserve content within the low N conditioned plant (Pellett and Roberts, 1963).

Roberts and Bredakis (1960) found that when defoliation occurred regularly, nitrogen was not only essential to promote top growth; but it also had a beneficial effect on root development of bentgrass. Applications of nitrogen to Kentucky bluegrass prior to periods of low temperature improved root development without excessively stimulating top growth (Hanson and Juska, 1961).

Hylton et al. (1965) found that Lolium multiflorum L. top growth increased with added increments of N to 128 mg per plant. Root weight reached a maximum with 32 mg and decreased in absolute amount with the addition of 64 mg of N per plant.

#### Carbohydrate and Nitrogen Constituents:

Depletion of carbohydrates in grasses with increased nitrogen assimilation is well established (Burton and DeVance, 1952; Gregory and Sen, 1937; Alberta, 1960; Benedict and Brown, 1944; and Sprague and Sullivan, 1950). Sprague and Sullivan (1950) found that the percentages of fructosan and sucrose were lowered, but the percentage of reducing sugars increased as nitrogen decreased. Weinmann and Goldsmith (1948) reported that Cynodon dactylon turf increased 40% in total available carbohydrates with low rates of nitrogen as compared to unfertilized grass.

Carbohydrates are utilized to supply energy for respiration (Nightingale, 1937) and for nitrate reduction, amino synthesis, and growth which are stimulated by high nitrogen (Vose and Breese, 1964).

Koontz and Vose (1960) postulated that high nitrogen stimulates phosphorus uptake, which increases carbohydrate utilization for oxidative phosphorylation.

Blackman and Templeman (1940), Roberts and Bredakis (1960), and Iotzenko (1961) working with cool season grasses and Prine and Burton (1956), Fisher and Caldwell (1959), Vicente-Chandler et al. (1959), and Miller et al. (1961) working with tropical grasses found that total nitrogen and protein nitrogen increased as nitrogen fertilizer increased.

Total organic and nitrate nitrogen was found to increase with added N fertilizer (Hylton et al., 1965). The nitrogen status of the plant may best be related to its nitrate-N content, since nitrate accumulated when growth was no longer stimulated. Vose and Breese (1964) found plants high in nitrogen content to accumulate amino-N when nitrate was added. If the nitrogen content was low, then amino-N was synthesized into more complex nitrogen compounds.

#### Photosynthesis and Respiration:

The relationship between N in leaves and photosynthetic activity as reported by Burstromn (1943), Loustalot et al. (1950), and Murata (1961) indicates that as the nitrogen in the leaves decreased below a specific point photosynthesis decreased. In contrast Ishizuka (1947), Gregory and Richards (1929), and Murata (1961) observed that a deficiency of nitrogen did not lower photosynthetic activity. Murata (1961) explained that contrasting reports are compatible. He showed

that nitrogen improved photosynthesis, principally through changing the activity of protoplasmic protein rather than respiration. When nitrogen supply was increased for a relatively short period, the protoplasm was increased per unit area which caused changes in photosynthetic activity. However, with liberal nitrogen, portions of the nitrogen were converted and stored as protein; therefore, the volume of protoplasm per unit leaf area may not fluctuate significantly. Nitrogen deficient leaves are dwarfed and the protoplasm per unit area does not change significantly.

Plants deficient in nitrogen have low respiration rates, but plants stimulated with nitrogen to produce new tissue have high respiration rates. (Gregory and Richards, 1929; Gregory and Sen, 1937).

### Responses of Grass to Light

#### Growth:

It has been claimed that light sets the ceiling for dry matter production on heavily fertilized grasses (Burton et al., 1954). Generally, shading reduces the number of shoots and rhizomes the dry weight of all grass parts (Watkins, 1940; Burton et al., 1949; Knipmeyer, et al., 1962; Juska, 1963; Madison, 1962; Mitchell, 1953; Reid, 1933; and Sullivan and Sprague, 1943 and 1953). Shade decreased the dry weight of leaf surface of young rice plants (Murata, 1961). Shading reduced bermudagrass yields, this was pronounced when fertilized with high as compared with low nitrogen (Burton et al., 1949). Several workers (Watkins,

1940; Mitchell, 1954; and Reid, 1933) have shown that shade reduced root growth more severely than top growth of various grasses.

Lovvorn (1945) suggested that plant development is dependent upon photoperiod which is influenced by temperature. Heavily fertilized Cynodon dactylon produced the greatest root weight with long photoperiod when subjected to 60-70 F. However, when subjected to 80-90 F the greatest root weight occurred with short photoperiods. Younger (1959) reported that the dormancy of bermudagrass is associated with low temperatures and high light intensity.

Shaded plants take longer to mature than plants in high light intensities (Mitchell, 1954; and Beinhart, 1964).

#### Carbohydrate and Nitrogen Constituents:

Grasses grown under low light intensity caused a lowering of carbohydrates and nitrate to accumulate. However, protein or total nitrogen did not increase (Sullivan and Sprague, 1943 and 1953; Blackman and Templeman, 1940; and Knipmeyer et al., 1962). It has been implied that proteolysis may be accelerated if plants are grown in the darkness where carbohydrates are rapidly decreased (Nightingale, 1937).

Watkins (1940), with Bromus inermis, found when carbohydrate content was reduced, the total nitrogen content increased when light intensity was decreased. Burton et al. (1959) similarly found that low nitrogen fertilized bermudagrass increased in protein and decreased in carbohydrates as light intensity decreased. However, heavy nitrogen fertilization of bermudagrass had little effect upon composition of shaded bermudagrass, except that the carbohydrates were decreased.

Certain plant species can metabolize nitrate or hyponitrate in both light and darkness; however, the rate is accelerated in the light (Frear and Burrell, 1958; and Mendel and Visser, 1951). Others have shown that light is essential to maintain the enzyme nitrate reductase in the active state (Candella et al., 1957; and Hagamar and Flesher, 1960). Light energy may be coupled via triphosphopyridine nucleotide and nitrate reductase in nitrate reduction (Evans and Nason, 1953). Arnon et al. (1948) implies that light energy may be also converted directly via "cyclic photophosphorylation" to chemical bond energy. Knipmeyer et al. (1962) proposed that endergonic reactions such as assimilation of  $\text{CO}_2$ , nitrate reduction, or protein synthesis are being driven by a common energy pool of reduced pyridine nucleotides and high energy phosphate. These energy carriers may be supplied either directly by light or indirectly by carbohydrates. These authors also suggested that nitrogen metabolism is more adversely affected by shading than is carbohydrate metabolism.

It has been shown that there may be a depression of photosynthesis when soluble carbohydrates accumulate in leaves (Moss, 1962; Humphries, 1963; and Kurssanow, 1933). This condition has been reported to be particularly true under high light intensity (Burt, 1964).

#### Photosynthesis and Respiration:

Alexander and McCloud (1962) and Hesketh and Musgrave (1962) found that the response curves for uptake of  $\text{CO}_2$  as a function of light intensity agreed closely with the rectangular hyperbola theory derived by Rabinowitch (1951). The light assimilation curves of rice

varieties having a low photosynthetic activity at low light intensity also fit the rectangular hyperbolic curve. But not all plant light assimilation curves fit the rectangular hyperbolic curve. Plants having a relatively high photosynthetic value at low light intensity produced curves that take form of a combination of three straight lines (Murata, 1961).

Plants differ in photosynthetic capacity with increasing illumination (Bohning and Burnsides, 1956; Hesketh and Moss, 1963). NAR and relative growth in subtropical and tropical plants can greatly exceed those of cool temperature regimes (Blackman and Black, 1959). Burnside and Bohning (1957) pointed out from the comparative light saturation curves of apparent photosynthesis given by Lundegarth (1931), Rabinowitch (1951), and Bohning and Burnside (1956) that plants whose natural environment is full sun generally have a higher compensation point and are saturated at higher light intensities than those plants which naturally grow in the shade.

"Sun plants" grown at a low light intensity had a lower compensation point than when grown in full light. Ormrod (1961) further showed that saturation and compensation points seem to depend upon environment; for example, he reported that rice plants grown at low light intensity had a net loss of  $\text{CO}_2$  as temperatures increased. However, at high light intensities net photosynthesis increased as temperatures increased to 80 F, the highest temperatures studied.

## EXPERIMENT I

The Effect of Temperature and Nitrogen on  
Growth and Composition of Bentgrass and Bermudagrass

## PROCEDURE

Plugs (four-inch diameter, 1 inch of soil) of Tifgreen bermudagrass and Cohansey bentgrass taken from low N plots were planted in #10 metal cans filled with 5:1 sand-soil mixture on September 28, 1963. This mixture had a pH of 7.1, 35 lb P and 90 lb available K per acre. Additional P and K were applied at rates of 0.88 and 1.66 lb per 1,000 sq ft, respectively.

Experiment A: During 45 days each of the two grasses were grown at three temperature regimes (environmental control chambers at day: night temperatures 95:85, 75:65, and 55:50 F) with each of two nitrogen rates (N-1, 1/10 lb per 1,000 sq ft applied on September 29, November 7, and November 14; N-2, 1 lb per 1,000 sq ft on September 29, October 9, October 18, November 7, and November 14). Three replications of each treatment were harvested at 45 days to obtain data on root and top growth and organic analysis of various morphological parts. All chambers had 14-hour day lengths with 3,000 ft-c light intensity. The grasses were clipped seven times from about a height of 1-3/4 inch to 1 inch.

Experiment B: After the two grasses had been grown for 45 days with the factorial treatments given for Experiment A, the pots were switched to obtain all possible temperature combinations for 10 additional days. For example, the treatments with the highest temperature

were arranged at random to continue with the high temperature and switched to each of the other two temperatures. Thus, for the last 10 days there were 9 temperature treatments with each of 2 N rates and 2 replications. The grasses were clipped to 1 inch when temperature switches were made with no other clipping.

The grasses for both experiments were washed free of soil in cold water and frozen at -20 C to kill the tissue. Later the samples were thawed, separated into stolons, leaves, and rhizomes, and refrozen until they could be dried by lyophilization. The plant material was then finely ground and analyzed for carbohydrate and nitrogen fractions.

Analyses for acid extractable carbohydrates (AEC) were made by boiling in 2%  $\text{H}_2\text{SO}_4$  as outlined by Smith (1962). Reducing sugars were determined by the method of Nelson-Somgyi (Somgyi, 1952). Monosaccharides were determined by refluxing with 80% ethanol for one hour in 80 C water bath, and then using the AEC procedure. Oligosaccharides were calculated from the increase in reducing sugars by hydrolyzing the ethanol extract with 2%  $\text{H}_2\text{SO}_4$ .

Polysaccharide analysis for samples harvested at 45 days were made by analyzing the residue from ethanol extractions. Other polysaccharide analyses were obtained by analyzing ethanol extractions for oligosaccharides and monosaccharides and then subtracting these ethanol soluble sugars from AEC.

Total and protein N were obtained by micro-dumas procedure similar to that outlined by Steward et al. (1963) using a Coleman nitrogen analyzer model 29. Total nitrogen was determined from the frozen dry samples and protein nitrogen from the ethanol extracted residue.

Net assimilation rate (NAR) and respiration rates of grasses were made after about 40 days in the growth chambers. A basal plastic board with inlet and outlet tubes and a rubber band sealed to the board to seal an inverted 1,000 cc petri dish, served as light chamber of a closed gas system. Freshly clipped leaves (1/2 to 1 inch long) were spread on a moist blotting paper on the plastic board to expose nearly all leaf surfaces. A diaphragm pump circulated the air which was passed through a silica gel drying column before obtaining CO<sub>2</sub> data. A Beckman model 15 non-dispersive infrared gas analyzer measured the CO<sub>2</sub> during 6 minutes. All CO<sub>2</sub> measurements were made at the day temperatures and in the chambers. Air temperature in the system was partially controlled by passing it through a copper coil emersed in an ice bath after the air was analyzed. The temperature was maintained at about 10 F above that of the environmental control chambers at 3,000 ft -c. Respiration was calculated by measuring CO<sub>2</sub> increases by placing a light tight jacket over the inverted petri dish.

## RESULTS

## Bentgrass, Experiment IA

Carbohydrates:

Acid extractable carbohydrates (AEC) and polysaccharides of bentgrass leaves and stolons decreased as temperatures increased (Table 1). AEC in stolons averaged 43.5% for 55 F and 31.8% for grass grown at 95 F.

Stolons and leaves with N-2, were 18.4 and 34.0%, respectively, lower in AEC than those with N-1. Stolons and leaves with N-2 were 13.8 and 37.3%, respectively, lower in polysaccharides than with N-1. The monosaccharides of leaves and stolons were not significantly affected by temperatures. There was a tendency for monosaccharides in stolons to be higher with N-2 than for N-1.

Nitrogen Content:

Total nitrogen content of stolons and leaves significantly increased with temperature and N increases (Table 2). Protein nitrogen content of leaves and stolons increased with high nitrogen, but only the protein nitrogen in stolons increased with temperature increases.

Top and Foot Growth:

Clipping yields were significantly lower with N-1 than for N-2 and at 55 F than at higher temperatures (Table 3). Root growth responded opposite to top growth mentioned for the temperature and N treatments (Table 4).

TABLE 1. Carbohydrates (% of dry matter) in bentgrass leaves and stolons with two nitrogen rates and each of three temperatures.

| Day-night<br>temp F | Nitrogen treatments <sup>1</sup> |        |        |                   |      |      |                   |         |        |
|---------------------|----------------------------------|--------|--------|-------------------|------|------|-------------------|---------|--------|
|                     | N-1                              | N-2    | Mean   | N-1               | N-2  | Mean | N-1               | N-2     | Mean   |
|                     | AEC %                            |        |        | Monosaccharides % |      |      | Polysaccharides % |         |        |
|                     | <u>Leaves</u>                    |        |        |                   |      |      |                   |         |        |
| 55-50               | 46.8 c                           | 22.8   | 34.8 c | 1.92              | 3.13 | 2.52 | 27.2 b            | 16.4    | 21.8 b |
| 75-65               | 35.0 b                           | 23.1   | 29.0 b | 3.12              | 2.41 | 2.76 | 26.6 b            | 16.2    | 21.4 b |
| 95-85               | 22.2 a                           | 22.9   | 22.5 a | 2.73              | 2.00 | 2.36 | 19.5 a            | 12.6    | 16.1 a |
| Mean                | 34.7                             | 22.9   | 28.8   | 2.59              | 2.51 | 2.55 | 24.4              | 15.1    | 19.8   |
|                     | <u>Stolons</u>                   |        |        |                   |      |      |                   |         |        |
| 55-50               | 46.9 b                           | 37.8 b | 42.4 c | 3.13              | 4.14 | 3.63 | 27.6 b            | 24.9 b  | 26.1 b |
| 75-65               | 42.6 b                           | 34.7 b | 38.7 b | 3.73              | 5.24 | 4.49 | 22.1 a            | 21.6 ab | 21.8 a |
| 95-85               | 36.0 a                           | 27.7 a | 31.8 a | 3.38              | 4.83 | 4.11 | 26.6 b            | 19.2 a  | 22.9 a |
| Mean                | 41.8                             | 33.4   | 37.6   | 3.41              | 4.74 | 4.08 | 25.4              | 21.9    | 23.6   |

<sup>1</sup>Treatments within N rates with the same letter do not differ significantly.

Significant (\*) and highly significant (\*\*) differences for the two grasses and other factorial combinations:

AEC - Leaves: Temperature (T), Grass (G), and Nitrogen (N) and their interactions\*\*; Stolons: T\*, G\*\*, TG\*, and N\*\*.

Monosaccharides - Leaves: G\* and N\*; Stolons: G\*\*, N\*\*, and GN\*\*.

Polysaccharides - Leaves: T\*, G\*\*, and TG\*; Stolons: G\*\* and N\*\*.

(See Table 9 for bermudagrass data.)

TABLE 2. Nitrogen fractions (% of dry matter) in bentgrass leaves and stolons with two nitrogen rates and each of three temperatures.

| Day-night<br>temp F | Nitrogen treatments <sup>1</sup> |         |        |             |      |        |
|---------------------|----------------------------------|---------|--------|-------------|------|--------|
|                     | N-1                              | N-2     | Mean   | N-1         | N-2  | Mean   |
|                     | Total N %                        |         |        | Protein N % |      |        |
|                     | <u>Leaves</u>                    |         |        |             |      |        |
| 55-50               | 1.14 a                           | 3.80 a  | 2.47 a | 1.15        | 3.06 | 2.10   |
| 75-65               | 1.59 a                           | 4.03 ab | 2.81 a | 1.62        | 3.95 | 2.78   |
| 95-85               | 2.29 b                           | 4.44 b  | 3.36 b | 1.97        | 3.18 | 2.58   |
| Mean                | 1.67                             | 4.09    | 2.88   | 1.58        | 3.40 | 2.49   |
|                     | <u>Stolons</u>                   |         |        |             |      |        |
| 55-50               | 0.95 a                           | 1.79 a  | 1.37 a | 0.94 ab     | 1.46 | 1.20 a |
| 75-65               | 0.96 a                           | 2.01 ab | 1.48 a | 0.66 a      | 1.55 | 1.11 a |
| 95-85               | 1.25 b                           | 2.19 b  | 1.72 b | 1.21 b      | 1.62 | 1.41 b |
| Mean                | 1.05                             | 2.00    | 1.53   | 0.94        | 1.55 | 1.25   |

<sup>1</sup>Treatments within N rates with the same letter do not differ significantly.

Significant (\*) and highly significant (\*\*) differences for the two grasses and other factorial combinations:

Total N- Leaves: N\*\*, GN\*, and TN\*; Stolons: T\*, G\*\*, N\*\*, GN\*\*, TG\*\*, and TN\*\*.

Protein N - Leaves: N\*\*; Stolons: T\*, G\*\*, N\*\*, GN\*\*, and TG\*.

(See Table 10 for bermudagrass data.)

TABLE 3. Effect of nitrogen rates and temperatures on bentgrass and bermudagrass clippings  
(average dry weight in grams per pot for 7 clippings) during 45 days.

| Day-night<br>temp F | Nitrogen treatments <sup>1</sup> |         |         | Nitrogen treatments <sup>1</sup> |         |         |
|---------------------|----------------------------------|---------|---------|----------------------------------|---------|---------|
|                     | N-1                              | N-2     | Mean    | N-1                              | N-2     | Mean    |
|                     | Bentgrass, grams                 |         |         | Bermudagrass, grams              |         |         |
| 55-50               | 4.59 a                           | 21.94 a | 13.28 a | 0.82 a                           | 2.76 a  | 1.79 a  |
| 75-65               | 6.91 b                           | 25.18 b | 16.06 b | 9.44 b                           | 28.23 b | 18.85 b |
| 95-85               | 8.59 b                           | 25.80 b | 17.23 b | 16.46 b                          | 42.21 b | 29.36 c |
| Mean                | 6.71                             | 24.31   | 15.51   | 8.91                             | 24.40   | 16.66   |

<sup>1</sup>Treatments within N rates with the same letter do not differ significantly.

Significant (\*) and highly significant (\*\*) difference when the two grass and other factorial treatments were combined: T\*\*, G\*\*, N\*\*, TG\*\*, and TN\*\*.

TABLE 4. Effect of nitrogen rates and temperatures on bentgrass and bermudagrass roots during 45 days.

| Day-night<br>temp F | Nitrogen treatments <sup>1</sup> |         |        | Nitrogen treatments <sup>1</sup> |        |        |
|---------------------|----------------------------------|---------|--------|----------------------------------|--------|--------|
|                     | N-1                              | N-2     | Mean   | N-1                              | N-2    | Mean   |
|                     | Bentgrass, grams                 |         |        | Bermudagrass, grams              |        |        |
| 55-50               | 1.44 b                           | 0.96 b  | 1.21 b | 0.66                             | 0.07 a | 0.37 a |
| 75-65               | 1.51 b                           | 0.71 ab | 1.12 b | 0.85                             | 0.74 b | 0.80 b |
| 95-85               | 0.82 a                           | 0.55 a  | 0.69 a | 0.77                             | 0.47 b | 0.62 b |
| Mean                | 1.27                             | 0.75    | 1.01   | 0.76                             | 0.42   | 0.59   |

<sup>1</sup> Treatments within N rates with the same letter do not differ significantly.

The significant (\*) and highly significant (\*\*) differences when the two grass and other factorial treatments were combined: T\*\*, G\*\*, N\*\*, and TG\*\*.

Respiration and Net Assimilation Rates (NAR):

Bentgrass grown at 75 F had a higher NAR than at 55 or 95 F with both N treatments (Fig. 1). Approximately 180% more CO<sub>2</sub> was fixed at 75 F than at either 55 or 95 F. Grass fertilized with N-2 took up over 220% more CO<sub>2</sub> than with N-1.

Respiration increased as temperatures or N levels increased. These trends were consistent as the interactions were not significant.

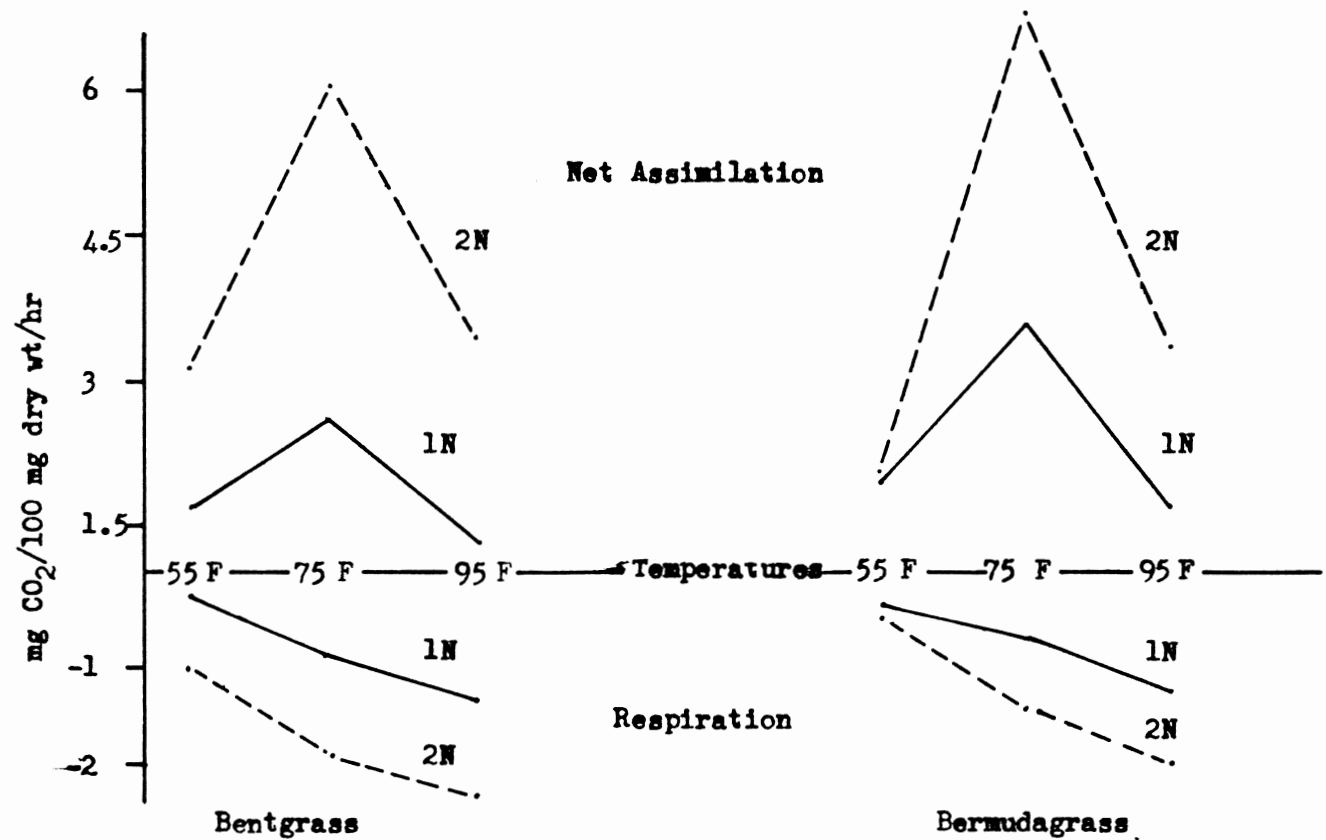


FIG. 1. Effect of temperature and nitrogen rates on net assimilation (NAR) and respiration of bentgrass and bermudagrass.

Significant (\*) and highly significant (\*\*) differences for the two grasses and other factorial combinations: NAR - T\*\*, N\*\*, TG\*, and TN\*\*; respiration - T\*\*, N\*\*, and NG\*\*

### Bentgrass, Experiment IB

The influence of each of three temperatures with two nitrogen treatments during 45 days, plus 10 subsequent days with the original and the two other temperatures on composition and growth are given in this section.

#### Carbohydrates:

The AEC content of stolons (Table 5) and leaves (Table 6) significantly increased with day-night temperature decreases during the last 10 days, irrespective of the temperatures during the first 45 days. With one exception, these relationships were statistically consistent for the two N levels. Subjecting plants to 55 F for 10 days, irrespective of previous temperature, caused the stolons or leaves to be about one-fourth higher in AEC than for 95 F final temperatures. The 55 and 75 F temperatures during the first 45 days caused stolons or leaves to be about 25% higher in AEC than at the highest temperature, irrespective of the final 10 day temperature.

When temperature treatments for final 10 days were pooled, the oligosaccharides in stolons increased as temperatures decreased (Table 5). When the data for the first 45-day temperatures were pooled, oligosaccharides were lower in stolons at 95 F than for the lower two temperatures.

When the data for the first 45-day temperatures were pooled, irrespective of the last 10-day temperatures, the stolons for plants grown at 95 F were lower in AEC than those for the other two temperatures. These results were consistent with N-1 and N-2 (Table 5) and similar relationships occurred with leaves (Table 6).

TABLE 5. Carbohydrates (% dry weight) in bentgrass stolons with two nitrogen rates with each of three temperatures for 45 days plus 10 subsequent days with the original and two other temperatures.

| Day temp F |         | Nitrogen treatments <sup>1</sup> |        |        |                    |        |        |                   |     |      |                   |        |        |
|------------|---------|----------------------------------|--------|--------|--------------------|--------|--------|-------------------|-----|------|-------------------|--------|--------|
| First      | Plus 10 | N-1                              | N-2    | Mean   | N-1                | N-2    | Mean   | N-1               | N-2 | Mean | N-1               | N-2    | Mean   |
| 45 days    | days    | AFC %                            |        |        | Oligosaccharides % |        |        | Monosaccharides % |     |      | Polysaccharides % |        |        |
| 55         | 55      | 56.0                             | 57.8   | 56.9   | 19.5               | 19.9   | 19.7   | 2.7               | 2.4 | 2.6  | 33.8              | 35.2   | 34.5   |
| 55         | 75      | 51.5                             | 45.6   | 48.5   | 25.1               | 13.9   | 19.0   | 2.5               | 5.6 | 4.1  | 24.9              | 26.1   | 25.5   |
| 55         | 95      | 49.1                             | 37.8   | 43.4   | 11.9               | 10.9   | 11.4   | 3.3               | 3.5 | 3.4  | 33.9              | 23.5   | 28.1   |
| Mean       |         | 52.2 b                           | 47.0 b | 49.6 b | 18.8 b             | 14.9 b | 16.7 b | 2.8 a             | 3.8 | 3.4  | 30.8 b            | 28.2 b | 29.4 b |
| 75         | 55      | 55.8                             | 54.3   | 55.0   | 23.9               | 23.8   | 23.8   | 2.8               | 2.3 | 2.5  | 29.2              | 28.2   | 28.7   |
| 75         | 75      | 52.3                             | 46.1   | 49.2   | 16.1               | 15.3   | 15.7   | 2.2               | 5.5 | 3.9  | 34.0              | 29.3   | 31.6   |
| 75         | 95      | 46.8                             | 38.9   | 42.8   | 19.1               | 10.2   | 14.7   | 2.3               | 4.9 | 3.6  | 25.3              | 23.8   | 24.5   |
| Mean       |         | 51.6 b                           | 46.4 b | 49.0 b | 19.7 b             | 16.4 b | 18.0 b | 2.4 a             | 4.2 | 3.3  | 29.5 b            | 27.1 b | 28.3 b |
| 95         | 55      | 47.4                             | 45.3   | 46.3   | 19.4               | 20.5   | 20.0   | 2.2               | 3.0 | 2.6  | 25.8              | 21.8   | 23.8   |
| 95         | 75      | 38.1                             | 28.6   | 33.4   | 6.2                | 2.6    | 4.4    | 9.4               | 5.2 | 7.3  | 22.5              | 20.8   | 21.6   |
| 95         | 95      | 36.7                             | 27.9   | 32.3   | 6.4                | 4.4    | 5.4    | 1.9               | 2.8 | 2.3  | 28.5              | 19.6   | 24.0   |
| Mean       |         | 40.7 a                           | 33.9 a | 37.3 a | 10.7 a             | 9.2 a  | 9.9 a  | 4.5 b             | 3.7 | 4.1  | 25.6 a            | 20.7 a | 23.1 a |

35

Temperature effects for final 10 days, irrespective of previous 45 days.

|        |    |        |        |        |        |        |        |       |       |       |      |        |        |
|--------|----|--------|--------|--------|--------|--------|--------|-------|-------|-------|------|--------|--------|
| Pooled | 55 | 53.1 c | 52.5 c | 52.7 c | 20.9 c | 21.4 c | 21.2 c | 2.6 a | 2.6 a | 2.6 a | 29.6 | 28.4 c | 29.0 b |
| Pooled | 75 | 47.3 b | 40.1 b | 43.7 b | 15.8 b | 10.6 b | 13.0 b | 4.7 b | 5.4 b | 5.1 b | 27.1 | 25.4 b | 26.2 a |
| Pooled | 95 | 44.2 a | 34.9 a | 39.5 a | 12.5 a | 8.5 a  | 10.5 a | 2.5 a | 3.7 a | 3.1 a | 29.2 | 22.3 a | 25.8 a |

<sup>1</sup>Treatments within N rates with the same letter do not differ significantly.

Significant (\*) and highly significant (\*\*) differences for the two grasses and other factorial combinations:

AFC - G\*\*, N\*\*, T\*\*, TG\*\*, and TN\*\*  
Oligosaccharides - G\*\*, N\*\*, NG\*\*, T\*\*, TG\*\*, and TN\*\*  
Monosaccharides - G\*\*, T\*\*, TG\*\*, and TN\*\*  
Polysaccharides - G\*\*, N\*\*, T\*\*, TG\*\* and TN\*\*  
(See Table 11 for bermudagrass data.)

TABLE 6. Carbohydrate (% dry weight) in bentgrass leaves with two nitrogen rates with each of three temperatures for 45 days plus 10 subsequent days with the original and two other temperatures.

| Day temp F    |              | Nitrogen treatments <sup>1</sup> |        |                   |        |        |        |
|---------------|--------------|----------------------------------|--------|-------------------|--------|--------|--------|
| First 45 days | Plus 10 days | N-1                              | N-2    | Mean              | N-1    | N-2    | Mean   |
| AEC %         |              |                                  |        | Monosaccharides % |        |        |        |
| 55            | 55           | 46.9                             | 33.1   | 40.0              | 2.02   | 1.95   | 1.98   |
| 55            | 75           | 40.6                             | 23.2   | 31.9              | 1.88   | 7.08   | 4.48   |
| 55            | 95           | 31.0                             | 21.6   | 26.3              | 1.78   | 2.48   | 2.13   |
| Mean          |              | 39.5 c                           | 25.9 b | 32.7 b            | 1.89 a | 3.84 c | 2.86 b |
| 75            | 55           | 41.2                             | 39.2   | 40.2              | 1.80   | 1.95   | 1.87   |
| 75            | 75           | 38.5                             | 26.0   | 32.3              | 1.85   | 2.48   | 2.17   |
| 75            | 95           | 30.6                             | 19.5   | 25.0              | 1.34   | 2.85   | 2.09   |
| Mean          |              | 36.7 b                           | 28.2 c | 32.5 b            | 1.66 a | 2.42 a | 2.04 a |
| 95            | 55           | 31.6                             | 28.6   | 30.1              | 2.03   | 1.64   | 1.84   |
| 95            | 75           | 28.4                             | 17.8   | 23.1              | 7.04   | 4.35   | 5.69   |
| 95            | 95           | 22.5                             | 21.8   | 22.2              | 1.65   | 2.81   | 2.23   |
| Mean          |              | 27.5 a                           | 22.7 a | 25.1 a            | 3.57 b | 2.93 b | 3.25 c |
| Pooled        | 55           | 39.9 c                           | 33.6 b | 36.8 c            | 1.9 a  | 1.8 a  | 1.9 a  |
| Pooled        | 75           | 35.8 b                           | 22.3 a | 29.1 b            | 3.6 b  | 4.6 c  | 4.1 b  |
| Pooled        | 95           | 28.0 a                           | 21.0 a | 24.4 a            | 1.6 a  | 2.7 b  | 2.1 a  |

Temperature effect for final 10 days, irrespective of previous 45 days.

<sup>1</sup>Treatments within N rates with the same letter do not differ significantly.

Significant (\*) and highly significant (\*\*) differences for the two grasses and other factorial combinations:

AEC - G\*, N\*\*, T\*\*, NG\*\*, TG\*\*, and TN\*\*.

Monosaccharides - G\*\*, N\*\*, T\*\*, TG\*\*, and TN\*\*.

(See Table 12 for bermudagrass data.)

Monosaccharides in leaves and stolons were quite variable. When temperature treatments for the final 10 days were pooled, monosaccharides were higher in stolons and leaves for grass grown at 75 F than for the lower and higher temperatures. This occurred with both N rates.

High temperatures caused drastic reductions of polysaccharides in stolons. The trends for polysaccharides were similar to those for AEC (Table 5). When the data for the first 45 or the final 10 day temperatures were pooled, the stolons were lower in polysaccharides for 95 F than for the lowest temperature.

#### Nitrogen:

Statistical comparisons when the temperature effects for the last 10 days were pooled, show that 95 F temperature during the first 45 days caused bentgrass stolons and leaves to be higher in total nitrogen than for the two lower temperatures (Fig. 2). The total nitrogen content of leaves and stolons for the last 10 days (previous temperature effects for 45 days pooled) was lower for 55 F than for the higher temperatures. Total nitrogen in leaves and stolons was higher with N-2 than for N-1. The data for protein nitrogen were similar to those for total nitrogen with minor deviations (Fig. 3).

#### Top and Root Growth

There was considerable variation for top growth and with only two replications the differences due to temperature were not significant (Table 7). However, grass grown at 95 F for 55 days, had less top growth than those at lower temperatures. Liberal nitrogen fertilization increased top growth consistently.

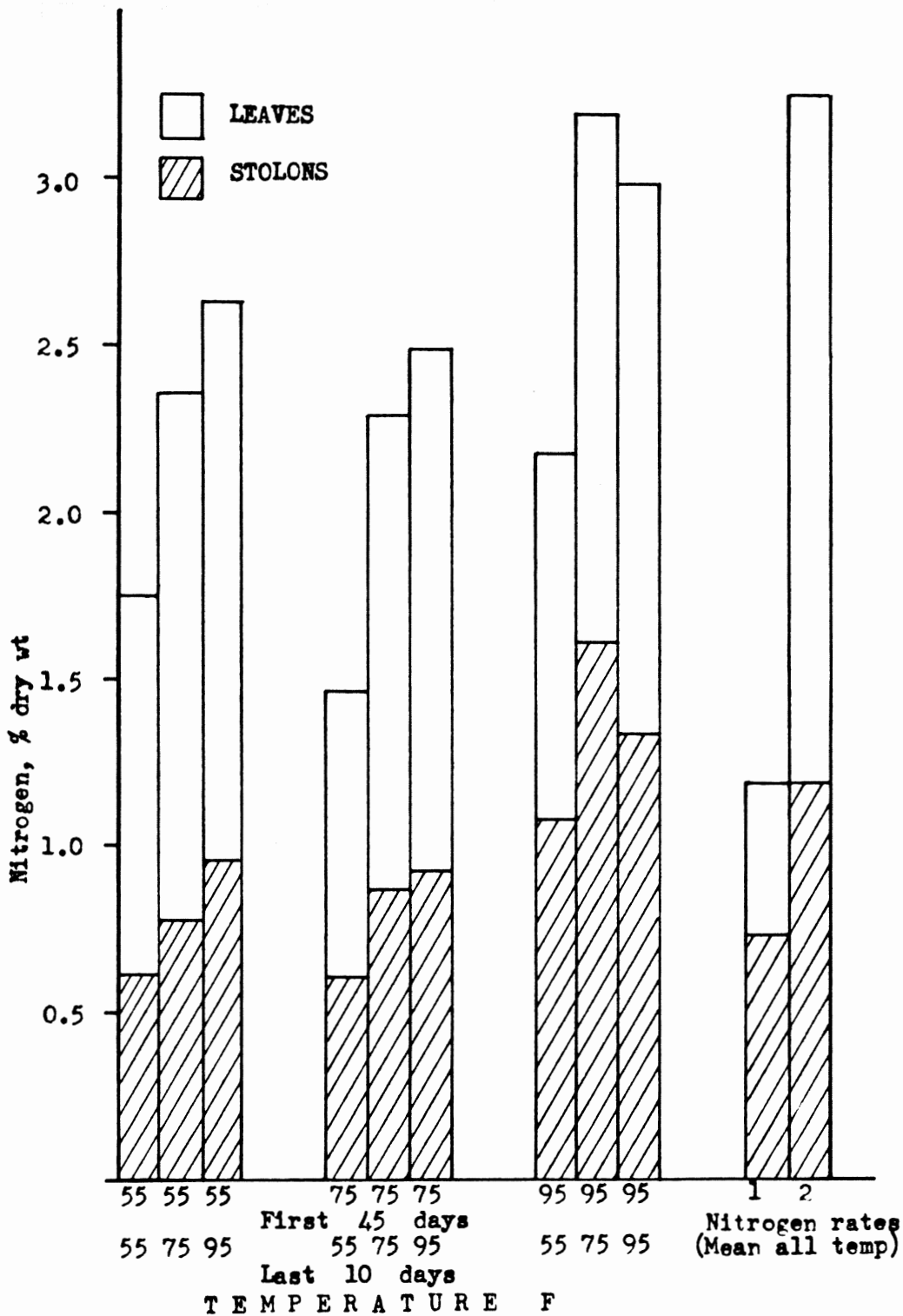


FIG. 2. Total nitrogen content of bentgrass stolons and leaves with two nitrogen rates with each of three temperatures for 45 days plus 10 subsequent days with the original and two other temperatures. Significant (\*) and highly significant (\*\*) differences for two grasses and factorial combinations: Leaves - N\*\*, NG\*\*, TG\*\*, and TN\*; Stolons - N\*\*, T\*\*, G\*\*, NT\*\*, NG\*\*, and TG\*\*.

(See Fig. 4 for bermudagrass.)

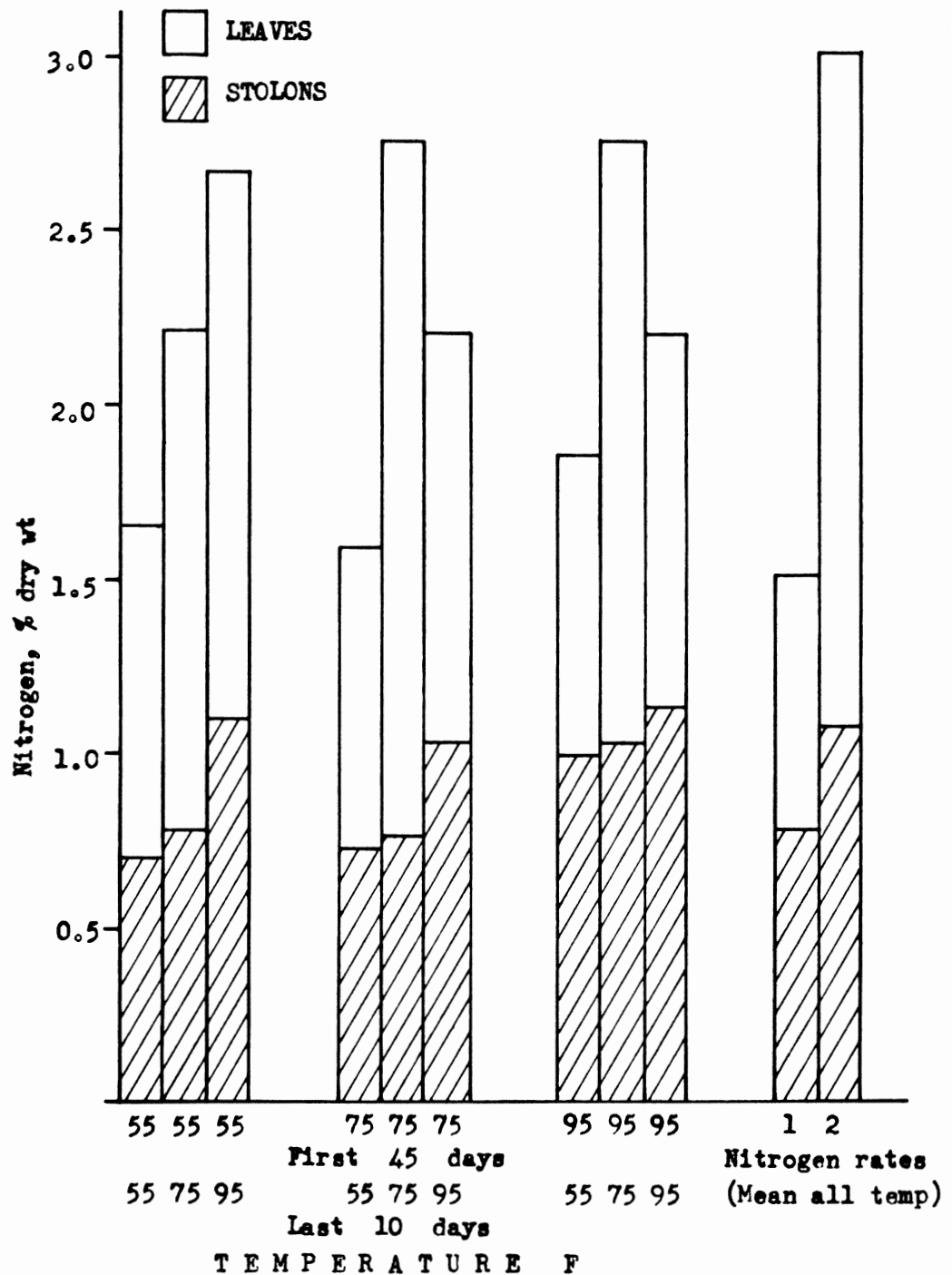


FIG. 3. Protein nitrogen content of bentgrass leaves and stolons with two nitrogen rates with each of three temperatures for 45 days plus 10 subsequent days with the original and two other temperatures. Significant (\*) and highly significant (\*\*) differences for two grasses and factorial combinations: Leaves - G\*\*, N\*\*, T\*, NG\*\*, and TG\*\*; stolons - G\*\*, N\*\*, T\*\*, NG\*\*, NT\*\*, and TG\*\*. (See Fig. 5 for bermudagrass.)

TABLE 7. Ten-day clipping yields (average dry weight in grams per pot for last 10 days) of bentgrass and bermudagrass from two nitrogen rates with each of three temperatures for 45 days plus 10 subsequent days with the original and other temperatures.

| Day temp F                                                               |              | Nitrogen treatments <sup>1</sup> |      |              |      |        |        |
|--------------------------------------------------------------------------|--------------|----------------------------------|------|--------------|------|--------|--------|
| First 45 days                                                            | Plus 10 days | N-1                              | N-2  | Mean         | N-1  | N-2    | Mean   |
| Bentgrass                                                                |              |                                  |      | Bermudagrass |      |        |        |
| 55                                                                       | 55           | 0.11                             | 1.18 | 0.64         | 0.09 | 0.82   | 0.46   |
| 55                                                                       | 75           | 0.07                             | 1.46 | 0.76         | 0.59 | 2.05   | 1.32   |
| 55                                                                       | 95           | 0.09                             | 1.27 | 0.68         | 1.24 | 1.46   | 1.35   |
| Mean                                                                     |              | 0.09                             | 1.30 | 0.69         | 0.64 | 1.44 b | 1.04 b |
| 75                                                                       | 55           | 0.11                             | 1.29 | 0.70         | 0.17 | 0.64   | 0.40   |
| 75                                                                       | 75           | 0.11                             | 1.38 | 0.74         | 0.23 | 0.86   | 0.55   |
| 75                                                                       | 95           | 0.10                             | 1.08 | 0.59         | 0.46 | 0.90   | 0.68   |
| Mean                                                                     |              | 0.11                             | 1.25 | 0.68         | 0.29 | 0.80 a | 0.54 a |
| 95                                                                       | 55           | 0.12                             | 1.23 | 0.67         | 0.18 | 0.41   | 0.30   |
| 95                                                                       | 75           | 0.17                             | 0.96 | 0.57         | 0.33 | 0.90   | 0.62   |
| 95                                                                       | 95           | 0.11                             | 0.25 | 0.18         | 0.30 | 1.08   | 0.69   |
| Mean                                                                     |              | 0.13                             | 0.81 | 0.47         | 0.27 | 0.80 a | 0.54 a |
| Temperature effects for final 10 days, irrespective of previous 45 days. |              |                                  |      |              |      |        |        |
| Pooled                                                                   | 55           | 0.11                             | 1.23 | 0.67         | 0.15 | 0.62 a | 0.39 a |
| Pooled                                                                   | 75           | 0.12                             | 1.27 | 0.69         | 0.38 | 1.27 b | 0.83 b |
| Pooled                                                                   | 95           | 0.10                             | 0.87 | 0.48         | 0.67 | 1.15 b | 0.91 b |

<sup>1</sup> Treatments within N rates with the same letter do not differ significantly.

Significant (\*) and highly significant (\*\*) differences for the two grasses and other factorial combinations: N\*\*, T\*, and TG\*.

Roots weighed more for the N-1 than the N-2 treatments (Table 8). When data were pooled for the last 10 days there was a rather distinct trend for root weights to be reduced by temperature elevations, but differences were not significant due to considerable variability and the low degrees of freedom. When data for the 45 days temperatures were pooled, the root weights for N-1 and N-2 were reduced by 95 F as compared with the two lower temperatures.

TABLE 8. Root weights (average dry weight in grams per pot) of bentgrass and bermudagrass from two nitrogen rates with each of three temperatures during 45 days plus 10 subsequent days with the original and two other temperatures.

| Day temp F    |              | Nitrogen treatments <sup>1</sup> |        |              |      |      |        |
|---------------|--------------|----------------------------------|--------|--------------|------|------|--------|
| First 45 days | Plus 10 days | N-1                              | N-2    | Mean         | N-1  | N-2  | Mean   |
| Bentgrass     |              |                                  |        | Bermudagrass |      |      |        |
| 55            | 55           | 2.02                             | 1.87   | 1.95         | 0.97 | 0.93 | 0.95   |
| 55            | 75           | 1.84                             | 1.44   | 1.64         | 0.95 | 0.49 | 0.72   |
| 55            | 95           | 1.87                             | 1.41   | 1.64         | 1.11 | 0.80 | 0.96   |
| Mean          |              | 1.91 b                           | 1.57 b | 1.74         | 1.01 | 0.74 | 0.88 b |
| 75            | 55           | 1.65                             | 0.80   | 1.23         | 1.22 | 0.81 | 1.02   |
| 75            | 75           | 1.51                             | 1.42   | 1.47         | 0.92 | 0.76 | 0.84   |
| 75            | 95           | 2.30                             | 1.77   | 2.04         | 1.26 | 0.71 | 0.98   |
| Mean          |              | 1.82 b                           | 1.33 b | 1.58         | 1.13 | 0.76 | 0.95 c |
| 95            | 55           | 1.39                             | 0.88   | 1.13         | 0.63 | 0.68 | 0.65   |
| 95            | 75           | 1.02                             | 1.07   | 1.04         | 1.00 | 0.72 | 0.86   |
| 95            | 95           | 1.46                             | 0.50   | 0.98         | 1.06 | 0.80 | 0.93   |
| Mean          |              | 1.29 a                           | 0.82 a | 1.05         | 0.90 | 0.73 | 0.81 a |

<sup>1</sup>Treatments within N rates with the same letter do not differ significantly.

Significant (\*) and highly significant (\*\*) differences for the two grasses and other factorial combinations: G\*\*, N\*\*, and T\*.

## Bermudagrass, Experiment IA

### Carbohydrates:

The AEC and polysaccharides of bermudagrass leaves and stolons did not differ significantly with different temperatures (Table 9). Rhizomes grown at 55 F were higher in AEC and polysaccharides than those grown at 75 or 95 F. Temperature did not influence the monosaccharide content of any of the bermudagrass parts.

The AEC and the polysaccharides of leaves, stolons, and rhizomes were decreased by high N. Monosaccharides in stolons showed a definite increase with high N.

Monosaccharides were highest in the leaves (2% of dry matter) and the lowest in the rhizomes (0.63%). However, rhizomes contained 75 and 7% more AEC and 57 and 10% more polysaccharides than bermudagrass leaves and stolons, respectively.

### Nitrogen Content:

Total nitrogen and protein nitrogen of the leaves were not effected by temperature (Table 10). Both nitrogen fractions of the stolons were higher in plants at 55 than at 75 or 95F. The total nitrogen in rhizomes decreased with high temperatures, but the protein nitrogen was not significantly affected by temperature. Both the total and protein nitrogen of leaves, stolons, and rhizomes increased with high N.

Total nitrogen of leaves, stolons, and rhizomes averaged 3.01%, 1.23% and 0.93%, respectively. Protein nitrogen content was lower than total nitrogen but of a similar trend.

TABLE 9. Carbohydrates (% of dry matter) in bermudagrass leaves, stolons, and rhizomes with two nitrogen rates with each of three temperatures.

| Day-night<br>temp F | Nitrogen treatments <sup>1</sup> |        |        |                   |      |      |                   |        |        |
|---------------------|----------------------------------|--------|--------|-------------------|------|------|-------------------|--------|--------|
|                     | N-1                              | N-2    | Mean   | N-1               | N-2  | Mean | N-1               | N-2    | Mean   |
|                     | AFC %                            |        |        | Monosaccharides % |      |      | Polysaccharides % |        |        |
|                     |                                  |        |        | Leaves            |      |      |                   |        |        |
| 55-50               | 26.7                             | 23.7   | 25.2   | 1.81              | 2.52 | 2.16 | 28.3              | 24.5   | 26.4   |
| 75-65               | 26.8                             | 20.0   | 23.4   | 1.69              | 1.97 | 1.83 | 29.8              | 19.8   | 24.8   |
| 95-85               | 25.9                             | 21.1   | 23.5   | 1.28              | 2.75 | 2.02 | 29.9              | 21.9   | 25.9   |
| Mean                | 26.5                             | 21.6   | 24.0   | 1.59              | 2.41 | 2.00 | 29.3              | 22.1   | 25.7   |
|                     |                                  |        |        | Stolons           |      |      |                   |        |        |
| 55-50               | 38.7                             | 37.3   | 38.0   | 0.61              | 0.93 | 0.77 | 41.0              | 30.6   | 35.8   |
| 75-65               | 38.8                             | 38.0   | 38.4   | 0.76              | 0.99 | 0.87 | 36.8              | 35.0   | 35.9   |
| 95-85               | 43.3                             | 38.8   | 41.0   | 0.61              | 1.23 | 0.92 | 40.2              | 35.4   | 37.8   |
| Mean                | 40.1                             | 38.1   | 39.1   | 0.66              | 1.05 | 0.85 | 39.3              | 33.6   | 36.5   |
|                     |                                  |        |        | Rhizomes          |      |      |                   |        |        |
| 55-50               | 45.0                             | 44.3 b | 44.6 b | 0.51              | 0.57 | 0.54 | 46.6 b            | 44.6 c | 45.6 b |
| 75-65               | 42.8                             | 37.9 a | 40.3 a | 0.39              | 0.76 | 0.58 | 40.1 a            | 37.1 b | 38.6 a |
| 95-85               | 46.0                             | 36.2 a | 41.1 a | 0.66              | 0.90 | 0.78 | 41.1 a            | 32.1 a | 36.6 a |
| Mean                | 44.6                             | 39.4   | 42.0   | 0.52              | 0.74 | 0.63 | 42.6              | 38.0   | 40.3   |

<sup>1</sup>Treatments within N rates with the same letter do not differ significantly.

Significant (\*) and highly significant (\*\*) differences for the two grasses and other factorial combinations:

AFC - T\*\*, N\*\*, and NT\*\*

Monosaccharides - N\*

Polysaccharides - T\*\*, N\*\*, and NT\*

(See Table 1 for statistical differences of factorial treatments.)

TABLE 10. Nitrogen fractions (% of dry matter) in bermudagrass leaves, stolons, and rhizomes with two nitrogen rates with each of three temperatures.

| Day-night<br>temp F | Nitrogen treatments <sup>1</sup> |        |        |                             |        |        |
|---------------------|----------------------------------|--------|--------|-----------------------------|--------|--------|
|                     | N-1                              | N-2    | Mean   | N-1                         | N-2    | Mean   |
|                     | Total N %                        |        |        | Protein N %                 |        |        |
|                     |                                  |        |        | <u>Leaves<sup>2</sup></u>   |        |        |
| 55-50               | 2.58                             | 3.87   | 3.22   | 2.31                        | 2.92   | 2.62   |
| 75-65               | 2.07                             | 4.09   | 3.08   | 2.05                        | 3.39   | 2.72   |
| 95-85               | 1.72                             | 3.68   | 2.74   | 1.55                        | 3.35   | 2.45   |
| Mean                | 2.15                             | 3.88   | 3.01   | 1.97                        | 3.22   | 2.60   |
|                     |                                  |        |        | <u>Stolons<sup>2</sup></u>  |        |        |
| 55-50               | 1.13 b                           | 2.04 b | 1.59 b | 0.93                        | 1.35 b | 1.14 b |
| 75-65               | 1.31 b                           | 1.10 a | 1.21 b | 0.83                        | 0.86 a | 0.84 a |
| 95-85               | 0.71 a                           | 1.06 a | 0.89 a | 0.73                        | 0.66 a | 0.70 a |
| Mean                | 1.05                             | 1.40   | 1.23   | 0.83                        | 0.96   | 0.90   |
|                     |                                  |        |        | <u>Rhizomes<sup>3</sup></u> |        |        |
| 55-50               | 0.96 b                           | 1.56 b | 1.26 b | 0.61                        | 0.86   | 0.74   |
| 75-65               | 0.66 a                           | 0.87 a | 0.76 a | 0.68                        | 0.78   | 0.73   |
| 95-85               | 0.61 a                           | 0.91 a | 0.76 a | 0.57                        | 0.71   | 0.64   |
| Mean                | 0.74                             | 1.11   | 0.93   | 0.62                        | 0.78   | 0.70   |

<sup>1</sup> Treatments within N rates with the same letter do not differ significantly.

<sup>2</sup> The significant (\*) and highly significant (\*\*) differences for the two grasses and other factorial combinations:

Total N - Leaves: N\*\*, GN\*, and TG\*; Stolons: T\*, G\*\*, N\*\*, GN\*\*, TG\*\*, and TN\*\*.

Protein N - Leaves: N\*\*; Stolons: T\*, G\*\*, N\*\*, GN\*\*, TG\*\*, and TN\*\*.

(See Table 2 for statistical differences of factorial treatments of bentgrass.)

<sup>3</sup> The significant (\*) and highly significant (\*\*) differences for bermudagrass rhizome factorial combinations: N\*\*, T\*\*, and NT\*.

### Top and Root Growth:

Clipping yields were approximately 2.5 times greater with N-2 than N-1 (Table 3). However, clipping yields were significantly lower at 55 F than at higher temperatures. Roots reacted opposite of top growth with the nitrogen treatments, but had trends similar to top growth for the temperature treatments (Table 4). Roots at 55 F were 46% and 60% of those at 75 and 95 F, respectively, for nitrogen factorial combinations.

### Respiration and Net Assimilation Rate (NAR):

Bermudagrass grown at 75 F gave 172% and 96% higher NAR than at 55 and 95 F, respectively (Fig. 1). NAR for grass fertilized with N-2 at 55 was lower than at 95 F, but no significant effect was noted with N-1. Grass fertilized with N-1 was about 40% lower in CO<sub>2</sub> uptake than that fertilized with N-2.

Respiration increased as both N and temperature increased, but differences at 55 F between N-1 and N-2 were nil.

## Bermudagrass, Experiment IB

Carbohydrates:

The AEC contents of bermudagrass stolons were significantly lower at 55 F (Table 11) and those in rhizomes and leaves were significantly increased at 95 F (Table 12) as compared to the other two temperatures for the first 45 days, irrespective of the temperature the last 10 days. The AEC of grass grown at 95 F for the first 45 days, irrespective of subsequent temperatures, increased about 14%, 17%, and 7.3% in leaves, stolons, and rhizomes, respectively, over those at 55 F.

When data for the last 10 days temperatures were pooled, the AEC for stolons and rhizomes tended to be higher at 55 F than at the higher temperatures. On the other hand, the leaves tended to be higher in AEC when subjected to 95 F than for lower temperatures for the final 10 days, irrespective of previous temperatures. N-2 consistently lowered the AEC in all parts when compared with N-1.

The monosaccharides and oligosaccharides of the stolons were not significantly affected by the various temperatures (Table 11). The monosaccharides of the leaves showed no temperature influence with data pooled for the last 10 days. When data for the first 45 day temperatures were pooled, irrespective of the final 10 day temperatures, the leaves grown at 55 F had higher monosaccharides than at higher temperatures. This was not consistent among nitrogen treatments, as shown by a significant interaction. The N-2 grass had a higher percent of monosaccharides than N-1.

TABLE 11. Carbohydrates (% dry weight) in bermudagrass stolons with two nitrogen rates with each of three temperatures for 45 days plus 10 subsequent days with the original and two other temperatures.

| Day temp F    |              | Nitrogen treatments <sup>1</sup> |        |        |                    |     |      |                   |      |      |                   |        |        |
|---------------|--------------|----------------------------------|--------|--------|--------------------|-----|------|-------------------|------|------|-------------------|--------|--------|
| First 45 days | Plus 10 days | N-1                              | N-2    | Mean   | N-1                | N-2 | Mean | N-1               | N-2  | Mean | N-1               | N-2    | Mean   |
|               |              | AEC %                            |        |        | Oligosaccharides % |     |      | Monosaccharides % |      |      | Polysaccharides % |        |        |
| 55            | 55           | 41.6                             | 39.6   | 40.6   | 4.0                | 5.0 | 4.5  | 0.59              | 0.76 | 0.67 | 37.0              | 33.9   | 35.4   |
| 55            | 75           | 36.0                             | 33.7   | 34.8   | 2.6                | 3.7 | 3.2  | 0.83              | 0.86 | 0.84 | 32.5              | 29.2   | 30.8   |
| 55            | 95           | 39.3                             | 34.6   | 36.9   | 5.4                | 4.8 | 5.1  | 0.47              | 0.59 | 0.53 | 33.1              | 29.2   | 31.5   |
| Mean          |              | 38.9 a                           | 35.9 a | 37.4 a | 4.0                | 4.5 | 4.3  | 0.63              | 0.74 | 0.68 | 34.4 a            | 30.7 a | 32.5 a |
| 75            | 55           | 47.1                             | 44.1   | 45.5   | 4.7                | 5.4 | 5.0  | 0.44              | 0.41 | 0.42 | 41.9              | 38.2   | 40.1   |
| 75            | 75           | 47.8                             | 38.8   | 43.3   | 4.9                | 4.9 | 4.9  | 0.54              | 0.42 | 0.48 | 42.2              | 33.5   | 37.8   |
| 75            | 95           | 44.8                             | 35.5   | 40.1   | 5.7                | 4.7 | 5.2  | 0.28              | 0.63 | 0.45 | 38.6              | 30.2   | 34.4   |
| Mean          |              | 46.5 b                           | 39.4 b | 42.9 b | 5.1                | 5.0 | 5.0  | 0.42              | 0.48 | 0.45 | 40.9 b            | 33.9 b | 37.4 b |
| 95            | 55           | 42.6                             | 42.2   | 42.4   | 4.6                | 6.2 | 5.4  | 0.45              | 0.44 | 0.45 | 37.5              | 35.6   | 36.5   |
| 95            | 75           | 44.2                             | 41.9   | 43.0   | 4.0                | 4.7 | 4.3  | 0.41              | 0.32 | 0.36 | 39.8              | 36.9   | 38.3   |
| 95            | 95           | 47.8                             | 43.5   | 45.8   | 6.4                | 6.0 | 6.3  | 0.49              | 1.74 | 1.12 | 40.9              | 36.0   | 38.4   |
| Mean          |              | 44.8 b                           | 42.5 c | 43.7 b | 5.0                | 5.6 | 5.3  | 0.45              | 0.83 | 0.64 | 39.4 b            | 36.2 b | 37.7 b |

Temperature effects for final 10 days, irrespective of previous 45 days.

|        |    |      |        |        |     |     |     |      |      |      |      |        |        |
|--------|----|------|--------|--------|-----|-----|-----|------|------|------|------|--------|--------|
| Pooled | 55 | 43.8 | 42.0 b | 42.8 b | 4.4 | 5.5 | 5.0 | 0.49 | 0.54 | 0.51 | 38.8 | 35.9 b | 37.3 b |
| Pooled | 75 | 42.7 | 38.1 a | 40.4 a | 3.8 | 4.4 | 4.1 | 0.59 | 0.53 | 0.56 | 38.2 | 33.2ab | 35.6ab |
| Pooled | 95 | 44.0 | 37.9 a | 40.9 a | 5.8 | 5.2 | 5.5 | 0.41 | 0.99 | 0.70 | 37.5 | 31.8 a | 34.8 a |

<sup>1</sup> Treatments within N rates with the same letter do not differ significantly.

Significant (\*) and highly significant (\*\*) differences for the two grasses and other factorial combinations:

AEC - G\*\*, N\*\*, T\*\*, TG\*\*, and TN\*\*  
 Oligosaccharides - G\*\*, N\*\*, T\*\*, TG\*\*, NG\*\*, and TN\*\*  
 Monosaccharides - G\*\*, T\*\*, TG\*\*, and TN\*\*  
 Polysaccharides - G\*\*, N\*\*, T\*\*, TG\*\*, and TN\*\*  
 (See Table 5 for bentgrass data.)

TABLE 12. Carbohydrate (% dry weight) in bermudagrass leaves and rhizomes with two nitrogen rates with each of three temperatures for 45 days plus 10 subsequent days to the original and two other temperatures.

| Day temp F |         | Nitrogen treatments <sup>1</sup> |      |        |                     |        |        |                       |      |        |                     |        |        |
|------------|---------|----------------------------------|------|--------|---------------------|--------|--------|-----------------------|------|--------|---------------------|--------|--------|
| First      | Plus 10 | AFC %                            |      |        | Monosaccharides %   |        |        | AFC %                 |      |        | Monosaccharides %   |        |        |
| 45 days    | days    | N-1                              | N-2  | Mean   | N-1                 | N-2    | Mean   | N-1                   | N-2  | Mean   | N-1                 | N-2    | Mean   |
|            |         | Rhizomes <sup>3</sup>            |      |        | Leaves <sup>2</sup> |        |        | Rhizomes <sup>3</sup> |      |        | Leaves <sup>2</sup> |        |        |
| 55         | 55      | 47.5                             | 44.4 | 46.0   | 28.3                | 28.7   | 28.5   | 0.68                  | 0.57 | 0.62   | 0.88                | 1.44   | 1.16   |
| 55         | 75      | 43.1                             | 43.2 | 43.1   | 26.5                | 24.4   | 25.4   | 0.60                  | 0.33 | 0.46   | 1.39                | 1.91   | 1.65   |
| 55         | 95      | 43.1                             | 39.8 | 41.4   | 28.2                | 28.4   | 28.3   | 0.39                  | 0.37 | 0.38   | 1.67                | 2.46   | 2.07   |
| Mean       |         | 44.5 a                           | 42.4 | 43.6 a | 27.6 a              | 27.1 b | 27.4 a | 0.56 b                | 0.42 | 0.49 b | 1.31 b              | 1.93 b | 1.62 b |
| 75         | 55      | 49.4                             | 47.7 | 48.5   | 27.8                | 27.3   | 27.5   | 0.41                  | 0.48 | 0.45   | 0.49                | 1.64   | 1.06   |
| 75         | 75      | 46.4                             | 39.7 | 43.0   | 30.4                | 27.2   | 28.8   | 0.30                  | 0.29 | 0.29   | 0.81                | 1.15   | 0.98   |
| 75         | 95      | 41.6                             | 40.5 | 41.0   | 33.9                | 25.6   | 29.8   | 0.28                  | 0.42 | 0.35   | 0.87                | 1.66   | 1.26   |
| Mean       |         | 45.8 a                           | 42.6 | 44.1 a | 30.7 b              | 26.7 a | 28.7 a | 0.33 a                | 0.40 | 0.36 a | 0.72 a              | 1.48ab | 1.10 a |
| 95         | 55      | 51.2                             | 47.3 | 49.3   | 32.3                | 30.6   | 31.5   | 0.63                  | 0.78 | 0.70   | 1.94                | 1.34   | 1.64   |
| 95         | 75      | 45.9                             | 43.8 | 44.8   | 30.5                | 28.6   | 29.6   | 0.44                  | 0.28 | 0.36   | 0.86                | 0.97   | 0.92   |
| 95         | 95      | 48.7                             | 43.1 | 45.9   | 33.9                | 32.0   | 32.9   | 0.42                  | 0.44 | 0.43   | 0.94                | 1.34   | 1.14   |
| Mean       |         | 48.6 b                           | 44.7 | 46.6 b | 32.2 b              | 30.4 b | 31.3 b | 0.50 b                | 0.50 | 0.50 b | 1.25 b              | 1.22 a | 1.23 a |

Temperature effects for final 10 days, irrespective of previous 45 days.

|        |    |        |        |        |        |      |        |        |        |        |      |      |      |
|--------|----|--------|--------|--------|--------|------|--------|--------|--------|--------|------|------|------|
| Pooled | 55 | 49.4 b | 46.5 b | 47.9 b | 29.5 a | 28.9 | 29.2ab | 0.57 b | 0.61 b | 0.59 b | 1.10 | 1.47 | 1.29 |
| Pooled | 75 | 45.0 a | 42.2 a | 43.6 a | 29.1 a | 26.7 | 27.9 a | 0.45 a | 0.30 a | 0.37 a | 1.02 | 1.34 | 1.18 |
| Pooled | 95 | 44.5 a | 41.1 a | 42.8 a | 32.0 b | 28.7 | 30.3 b | 0.36 a | 0.41 a | 0.39 a | 1.16 | 1.82 | 1.49 |

<sup>1</sup>Treatments within N rates with the same letter do not differ significantly.

<sup>2</sup>See Table 6 for statistical differences.

<sup>3</sup>Significant (\*) and highly significant (\*\*) differences for bermudagrass rhizomes and factorial combinations: AFC - N\*\* and T\*\*, Monosaccharides - T\*.

When data for the final 10 days temperature treatments were pooled, the rhizome monosaccharides were higher when grown at 55 F than at higher temperatures for both N treatments. When data for the first 45-day temperatures were pooled, the rhizome monosaccharides were lower at 75 F than the other two temperatures. This occurred at N-1 but was not significant at N-2.

#### Nitrogen Content:

When the temperature data were pooled the last 10 days, the highest total nitrogen occurred in leaves for grass grown at 95 F (Fig. 4). No significant total nitrogen content differences, due to final 10 day temperatures were evident in stolons or rhizomes. Data pooled for the first 45 days, showed that the lowest total N content in leaves occurred at 95 F and the highest values in stolons and rhizomes occurred at 55 F. Generally, N-2 increased total N content in all plant parts.

The pooled temperature effect for the last 10 days showed that temperatures did not significantly influence protein nitrogen content of leaves, stolons, or rhizomes (Fig. 5). However, data pooled for the first 45-day temperatures, irrespective of the final temperature, showed that protein nitrogen was higher in stolons, rhizomes, and leaves at 55 F than at higher temperatures. Protein nitrogen in all the bermudagrass parts was higher with N-2 than for N-1.

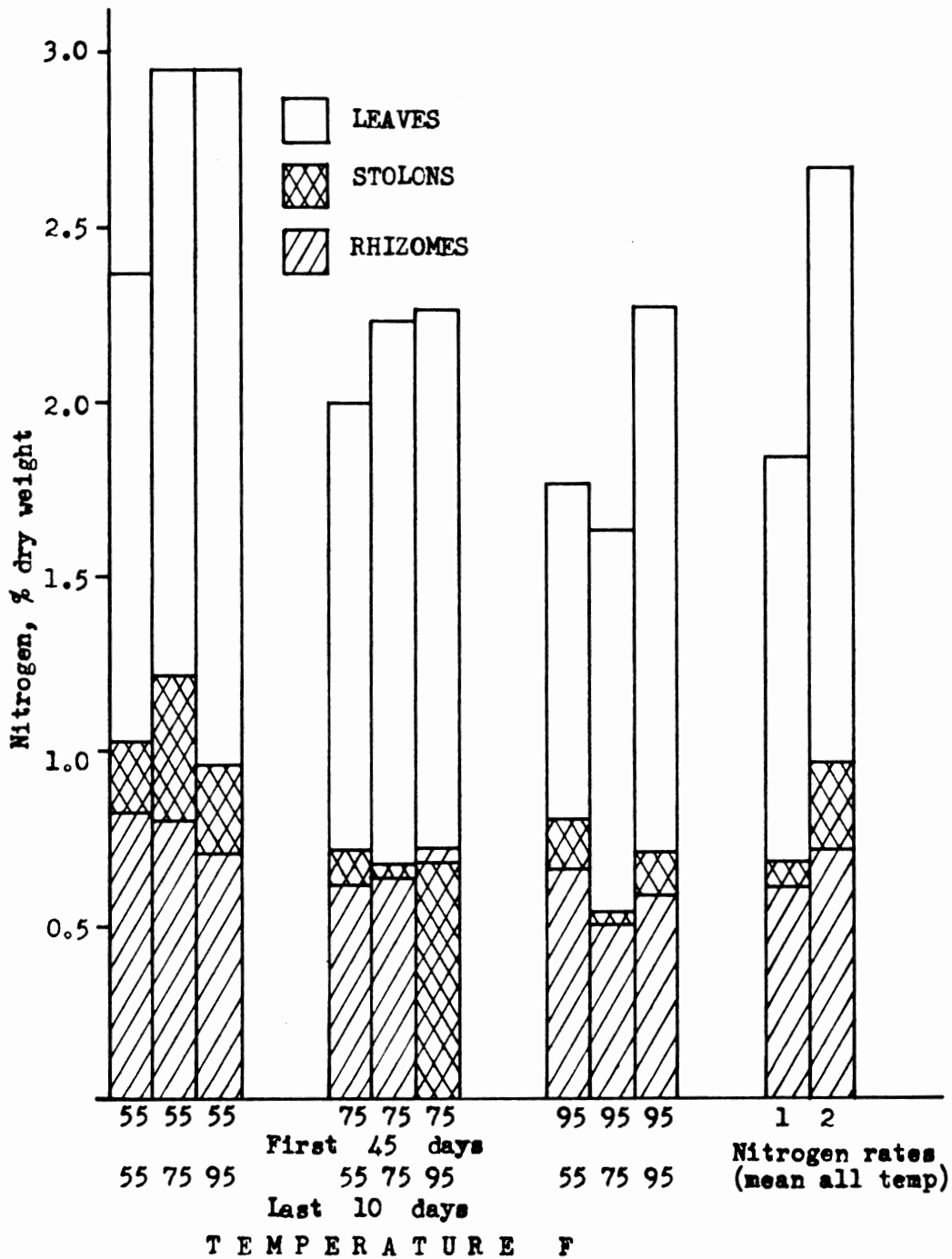


FIG. 4. Total nitrogen content of bermudagrass leaves, stolons, and rhizomes with two nitrogen rates with each of three temperatures for 45 days plus 10 subsequent days with the original and two other temperatures.

Nitrogen and temperature treatments caused highly significant differences on rhizomes. (See Fig. 2 for data of leaves and stolons.)

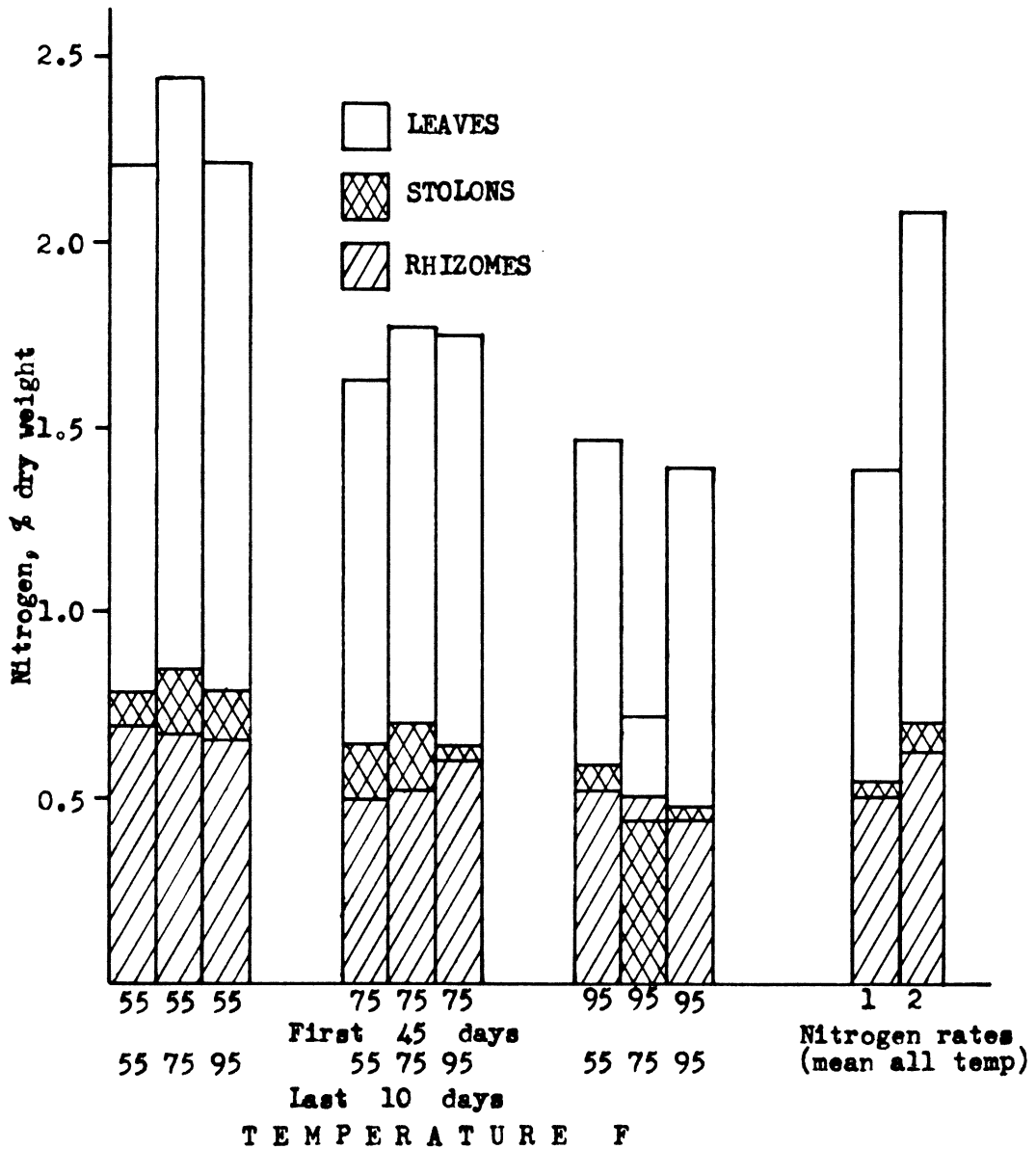


FIG. 5. Protein nitrogen of bermudagrass leaves, stolons, and rhizomes with two nitrogen rates with each of three temperatures for 45 days plus 10 subsequent days with the original and two other temperatures.

No significant differences in rhizome protein N content due to temperature, nitrogen, or their interactions were found. (See Fig. 3 for data of leaves and stolons.)

Top and Root Growth:

Clipping yields for temperatures during the last 10 days, irrespective of the previous 45-day temperatures, were lower at 55 F than at higher temperatures (Table 7). When the data for the first 45-day temperatures were pooled, irrespective of the final 10-day temperatures, the clipping yields were significantly higher at 55 F than at higher temperatures. These results were significant with the N-2, and the trend also occurred with N-1. Liberal nitrogen fertilization increased top growth consistently.

When data for the first 45-day temperatures were pooled, irrespective of the final 10-day temperatures, roots (average of N-1 and N-2) weighed less at 95 F than at the lower temperatures (Table 8). The root weights were consistently higher for N-1 than N-2. The temperature switches for the final 10 days did not affect root yields significantly.

## DISCUSSION

Bentgrass:

Rapid growth, increased respiration, and decreased NAR that coincided with temperature elevations possibly caused the reductions in polysaccharides, AEC, and oligosaccharides that occurred in stolons and leaves. Carbohydrate reduction occurred quite rapidly as shown by significant changes from high-low or low-high temperature alterations during 10 days. Monosaccharides and oligosaccharides made up a large portion of carbohydrates in bentgrass; thus, the rapid decline of total carbohydrate at the high temperature may be attributed to mobility and ease of utilization of the simple carbohydrates. The high monosaccharide content that eventually accumulated in the grass at 75 F, compared to higher and lower temperatures, may be attributed to the high NAR and newly formed sugars.

Optimum temperatures for NAR and growth differ as carbohydrates accumulated at 55 F, even though there was little growth. With high temperatures the NAR was reduced whereas growth and respiration increased causing a reduction in carbohydrates. When temperatures are sub-optimum, growth and respiration apparently use less energy than is being supplied by photosynthesis; thus carbohydrates increase which reduces the total and protein nitrogen content.

Deep roots are very desirable because closely mowed fine turf-grasses often have shallow roots causing serious injury during drought in the absence of frequent watering. The poor root growth with the high temperature and high N may be attributed to their combined influence on high respiration, high yields of top growth that utilize

stored and newly fixed energy, and low NAR. These interrelationships apparently account for the reduction in carbohydrates in plant tissue that could reduce root growth.

It is interesting to note that top growth for mid- and high-temperatures was similar, but roots were significantly better at mid-temperature. This may be attributed to the higher NAR and a trend for lower respiration at the mid-temperature. With high N, the best root development at the low temperature may be attributed to low top growth and concurrent carbohydrate accumulation due to relatively high NAR. Also, the low respiration apparently conserved carbohydrate energy for improved root growth.

Roots weighing 69% more for N-1 than N-2 may be attributed to slow top growth (low demand for energy) and high accumulation of carbohydrates, even though NAR was rather low. Also, the low respiration would conserve carbohydrates. Lowering of plant carbohydrates when nitrogen fertility increases top growth is a well established principle (Alberta, 1960 and Sprague and Sullivan, 1950). Total and protein N increased with high N fertilization because of increased N intake and reduced carbohydrate content. Increase of total nitrogen at high temperature was also reported for ryegrass by Sullivan and Sprague (1949). These authors stated that such increases in nitrogen may be apparent because of the decreased carbohydrates. It is possible that high temperatures stimulated N uptake as nutrient uptake is a function of respiration rate (Bryer, 1951).

Although liberal N as compared to low N fertilized grass had higher NAR at high temperature, the root growth and eventually top growth were drastically reduced. This growth reduction may be attributed to extremely low carbohydrate content which was caused by high energy requirements for respiration and top growth, and by the reduced NAR at high temperature. When top growth was stimulated by N at high temperature, synthesized carbohydrates were apparently utilized for leaf and vegetative growth and not translocated to the roots. This was indicated by the consistently low carbohydrates and high N content of leaves in with liberal N applications at all temperatures. Carbohydrates accumulated at low temperature even with high N, because apparently more energy was supplied by photosynthesis than was utilized for respiration and growth.

#### Bermudagrass:

Carbohydrates in bermudagrass were largely polysaccharides, thus the changes in the simpler sugars probably had small physiological effect on the grass. Bermudagrass apparently was near carbohydrate saturation as the significant carbohydrate differences were very small. There were no significant carbohydrate differences in the leaves and stolons due to temperature after 45 days. Rhizomes from grass with liberal N were higher in AEC and polysaccharides at low temperatures than at the two higher temperatures during the first 45 days. However, during the last 10 days switching from the low to the higher temperatures caused carbohydrate decreases in rhizomes and

stolons. This may be attributed to stimulated top growth with higher temperatures. It is speculated that this change was temporary since carbohydrates in bermudagrass tended to increase with temperature.

The reduced total nitrogen in stolons and rhizomes with increased temperature is possibly caused by: (1) large removal of nitrogen by clipping (Roberts and Bredakis, 1960) and (2) apparent decreases associated with the production and accumulation of other cell constituents that diluted the nitrogenous compounds (Beavers and Cooper 1964b). This was confirmed as grass switched from low to high temperatures increased in nitrogen content with a carbohydrate decrease.

Although not significant, roots were higher and top yields were lower at the mid than at high temperature. The low sub-optimum temperature inhibited top and root growth, respiration, and NAR. The drop in carbohydrates that occurred when plants were switched from low to high temperature may be attributed to stimulated top growth.

Because yields at 95 were higher than at 75 F, it seems that carbohydrates should have been lower at 95 F. However, carbohydrates did not differ significantly at these two temperatures even though NAR was higher at 75 F. The slightly higher root weights at 75 than at 95 F may have counteracted carbohydrate accumulation.

The increases in monosaccharides with liberal nitrogen fertilization may be attributed to hydrolyzation of polysaccharides or increased CO<sub>2</sub> uptake. However, the increased top growth and respiration accompanied by high nitrogen fertilization cause high energy demand

and thus lowering AEC. This possibly caused reduced root growth. The increased total and protein nitrogen with high N fertilization may be attributed to low AEC and increased N uptake.

## EXPERIMENT II

The Effect of Light Intensity, Night Temperature, and Nitrogen on Bentgrass and Bermudagrass Growth, NAR, Respiration, Nitrogen Content and Carbohydrate Reserves

## PROCEDURE

Tifgreen bermudagrass and Cohansey bentgrass sod samples were placed in No. 10 cans as described for Experiment I. These grasses were placed in three environmental control chambers at 60, 75, and 90 F. night temperatures, during 10 hours of darkness. One-half of each chamber was shaded to obtain L-0.5 (1,500 ft-c) and L-1 (3,000 ft-c). Two N levels were used with the factorial combinations (two grasses, two light intensities, and three night temperatures). All day temperatures during 14-hr. light periods were 95 F. The N rates were: N-1 (one-tenth pound per 1,000 sq ft) and N-2 (one pound per 1,000 sq ft) applied on the first, tenth, and twentieth day after the plants were placed in growth chambers. Three pots (replications) of each treatment combination were harvested at the end of 10, 20, and 30 days. There were three additional pots of all factorial combinations at 60 and 90 F. night temperatures to switch and continue these temperature treatments for the last 10 days.

The grasses were clipped to a 1-inch height every three or four days and the roots were harvested at 30 days, when the experiment terminated. Stolons were analyzed for carbohydrates and total nitrogen as described for Experiment I.

After 27 days respiration and net assimilation rates (NAR) were measured as described in Experiment I. NAR's were measured during the 95 F day temperatures under L-1 and L-0.5 in each chamber. Respiration rate was measured in the same chamber as the NAR was measured, immediately following the NAR determination.

## RESULTS

## Bentgrass, Experiment II

Carbohydrates:

High N and low light intensity significantly reduced AEC (Figures 6 and 7 and Table 13). Night temperatures on bentgrass grown in L-1 had inconsistent effect on AEC for the sampling dates (Fig. 6). At 10 days with L-1, grass at 90 F had 12.1 and 16.8% less AEC than at 60 and 75 F, respectively. At 20 days AEC did not differ significantly among the night temperatures. After 30 days, bentgrass grown at 75 F averaged 14.8 and 8.9% higher in AEC than for 60 and 90 F, respectively. Grass grown under L-1 that was switched from 90 to 60 F had a higher AEC content than that grown continuously at 90 F. However, when plants were switched from 60 to 90 F, there was not a significant reduction in AEC during this 10-day period.

Polysaccharides in grass stolons at L-0.5 increased with switches of temperature from the higher to the lower (last 10 days Fig. 7). With grass grown in L-1, polysaccharides were lower for 60 F than at the higher constant temperatures for the 20 and 30 day sampling periods. Switching temperatures from high or low (the last 10 days) increased polysaccharides with L-1. Polysaccharides were lower for N-2 than N-1 when light intensities and temperatures were averaged.

Monosaccharides and the oligosaccharides were higher in grasses grown in L-1 than L-0.5 for all dates. High N reduced the monosaccharides of stolons at L-1 for all dates measured. The oligosaccharides

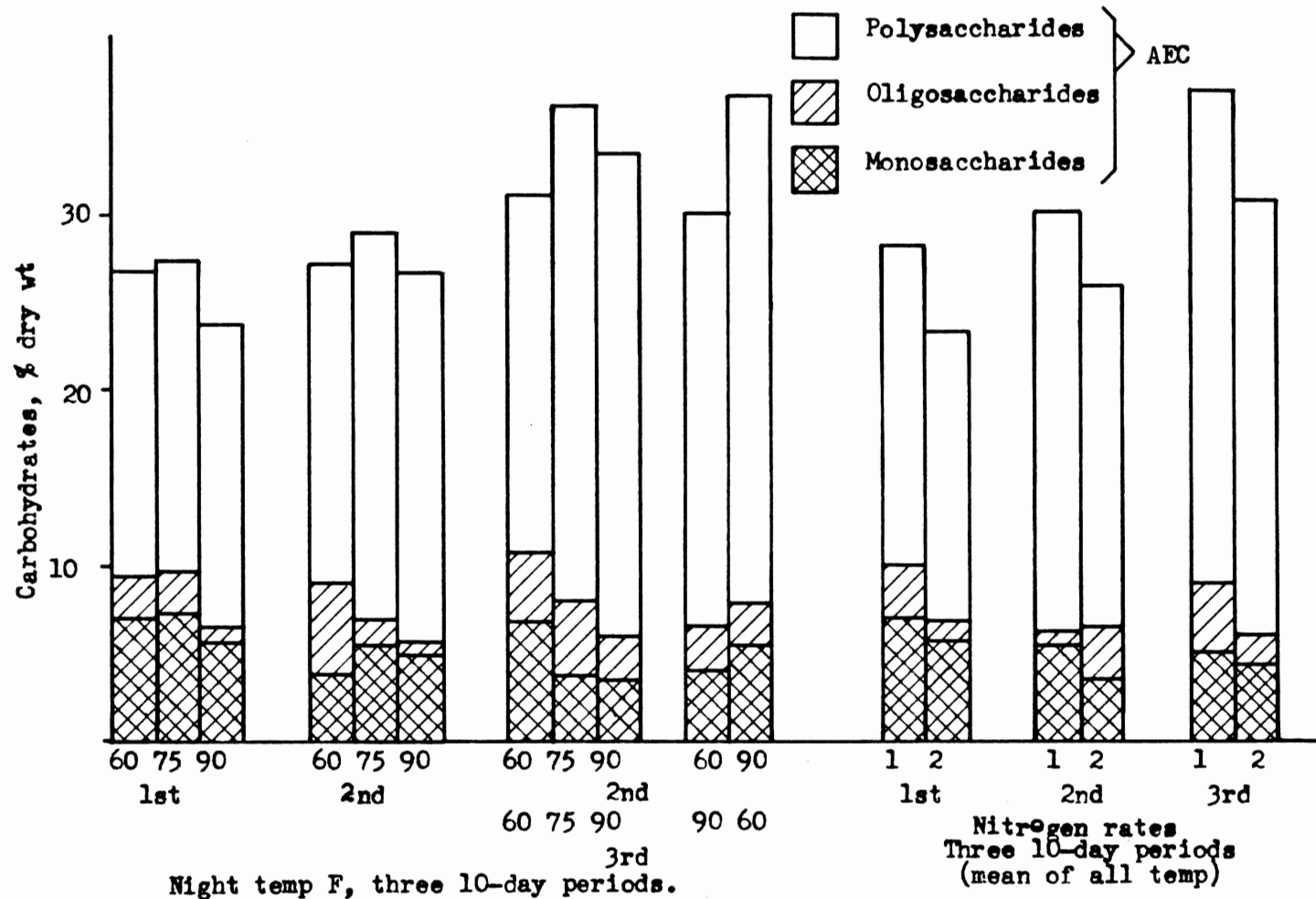


FIG. 6. Carbohydrates (% dry weight) in stolons of bentgrass grown at 95 F for 14 hours at (3,000 ft-c) L-1 with two N rates at each of three night temperatures for three 10 day periods and also switching the high-low temperatures for the last 10 days. (See Fig. 7 for L-0.5 factorial combinations and Table 13 for statistical significance.)

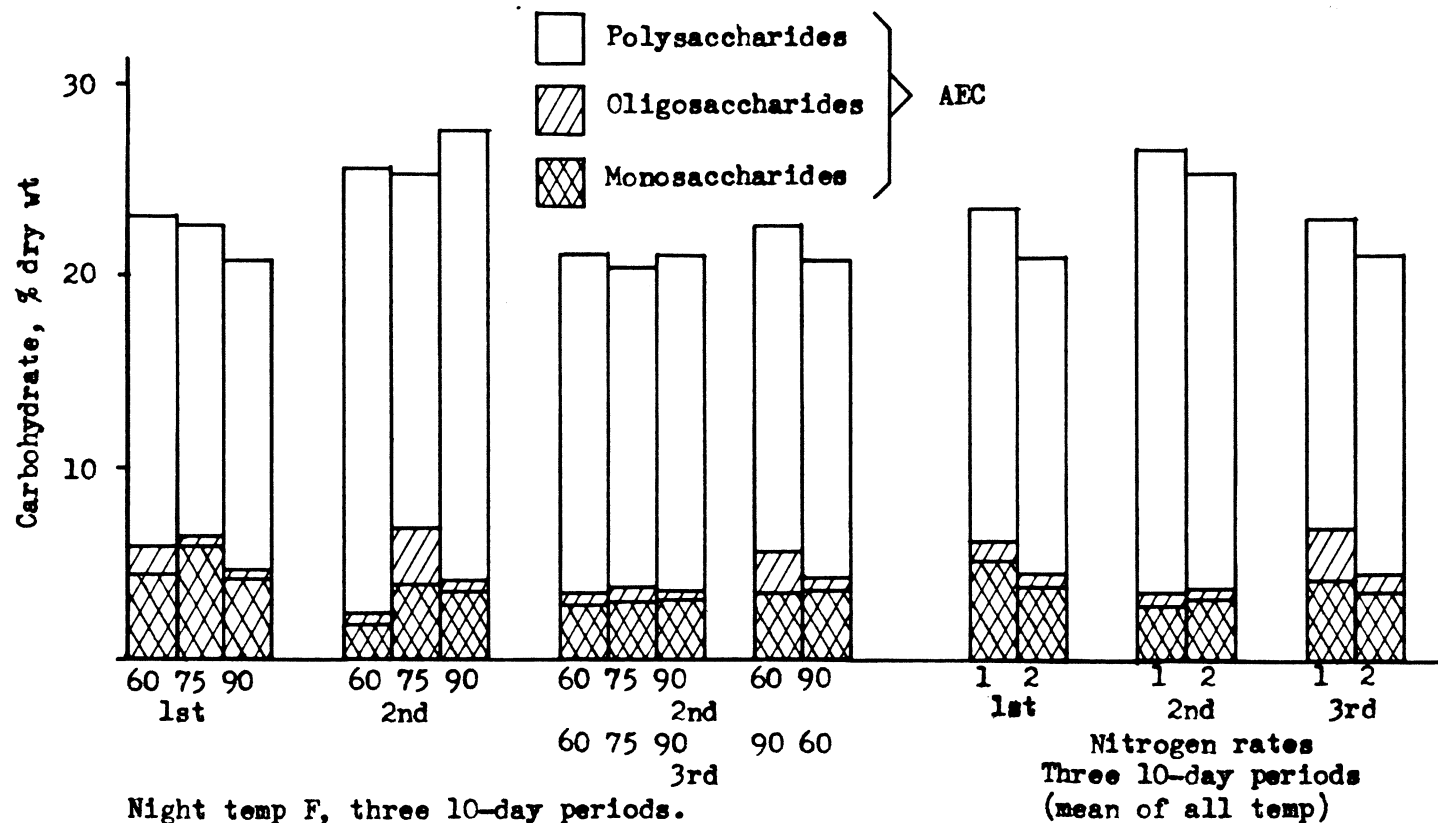


FIG. 7. Carbohydrates (% dry weight) in stolons of bentgrass grown at 95 F for 14 hours at (1,500 ft-c) L-0.5 with two N rates at each of three night temperatures for three 10-day periods and also switching the high-low temperatures for the last 10 days. (See Fig. 6 for L-1 factorial combinations and Table 13 for statistical significance.)

TABLE 13. Significant (\*) and highly significant (\*\*) differences for carbohydrate data in Figures 6 and 7.

| Carbohydrates    | Sampling Periods | Factorial treatments  |            |               |    |    |    |
|------------------|------------------|-----------------------|------------|---------------|----|----|----|
|                  |                  | Tempera-<br>ture<br>T | Light<br>L | Nitrogen<br>N | TL | LN | TN |
| AEC              | First 10 days    | **                    | **         | **            | NS | NS | NS |
|                  | Second 10 days   | NS                    | **         | **            | ** | ** | NS |
|                  | Third 10 days    | **                    | **         | **            | ** | ** | ** |
| Monosaccharides  | First 10 days    | **                    | **         | **            | *  | NS | NS |
|                  | Second 10 days   | **                    | **         | **            | NS | ** | *  |
|                  | Third 10 days    | **                    | **         | NS            | *  | NS | NS |
| Oligosaccharides | First 10 days    | **                    | **         | **            | NS | NS | NS |
|                  | Second 10 days   | **                    | **         | *             | ** | *  | ** |
|                  | Third 10 days    | NS                    | **         | **            | *  | ** | ** |
| Polysaccharides  | First 10 days    | NS                    | NS         | NS            | NS | NS | NS |
|                  | Second 10 days   | NS                    | NS         | **            | ** | *  | ** |
|                  | Third 10 days    | **                    | **         | **            | ** | ** | ** |

were also reduced with N-2, except at 20 days. Monosaccharides and oligosaccharides generally decreased as the night temperature increased at L-1. Switching temperatures at L-1 had little influence on oligosaccharides; but monosaccharides decreased when switching to the higher temperature during 10 days. There were no consistent differences for the monosaccharides because of temperatures for grass grown at L-0.5. Temperature switches at L-0.5, caused the oligosaccharides to increase with the higher temperature.

#### Nitrogen Content:

Total nitrogen content was not affected significantly by night temperatures (Fig. 8). High N or low light intensities generally caused total nitrogen content of stolons to increase.

#### Top Growth:

N-2 as compared with N-1 increased top growth 100 and 27% for L-1 and L-0.5, respectively (Table 14). Top growth was reduced by the lower light intensity at all temperatures, when nitrogen was liberal during the last two sampling periods. Yields were reduced by 90 F night temperatures as compared to the two lower temperatures. This occurred for L-0.5 and L-1 at all sampling periods, except for high light intensity during the first 10 days.

Switching from 60 to 90 F, during the last 10 days, reduced top growth as compared to grass maintained at the lower temperature (Table 14). Conversely, switching from 90 to 60 F increased top growth over grass maintained at 90 F. These data were consistent for L-1 and L-0.5. The yields were consistently higher for L-1 than L-0.5 except for plants switched from 90 to 60 F.

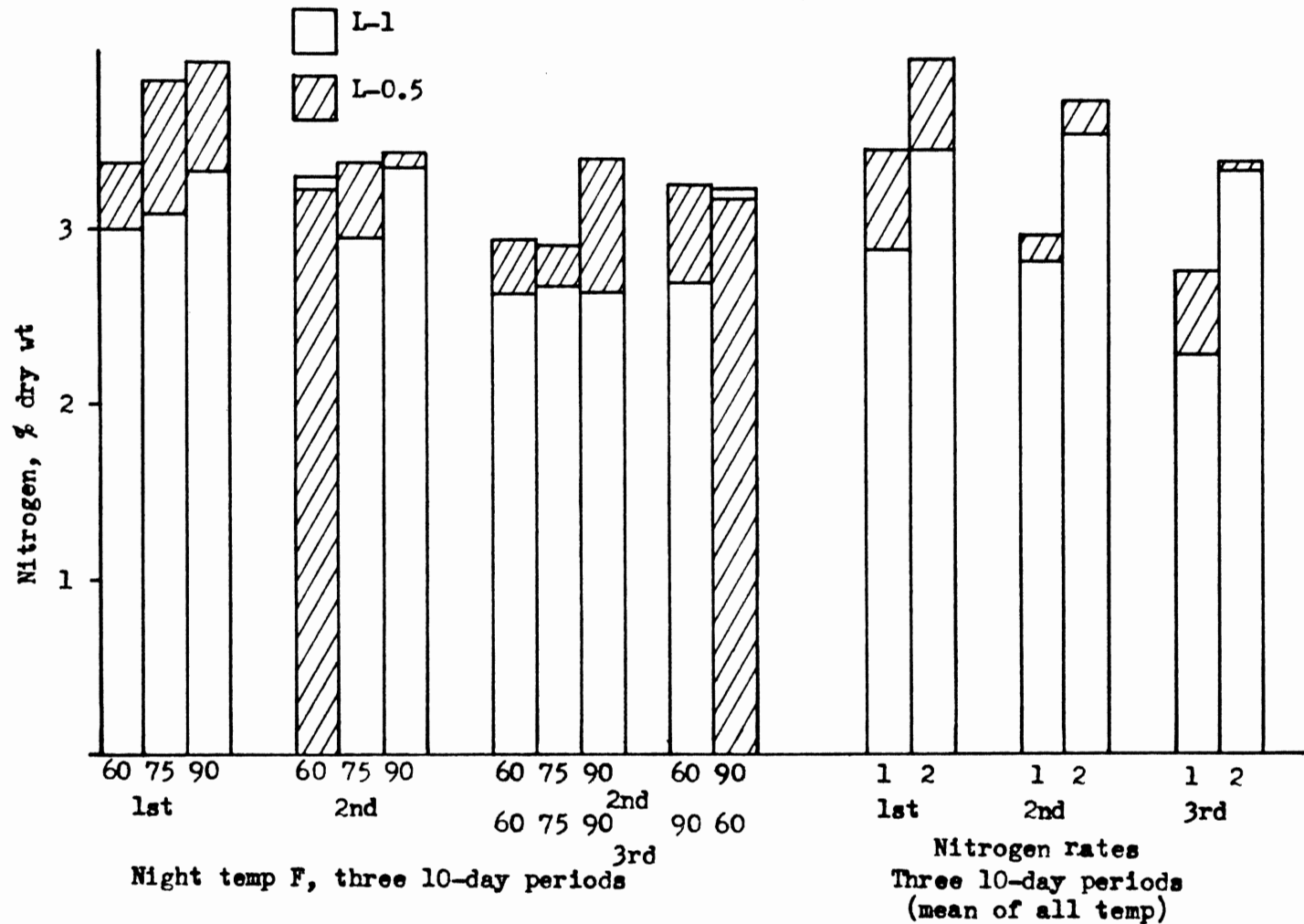


FIG. 8. Total nitrogen content (% dry weight) in bentgrass stolons grown at 95 F for 14 hours at L-1 (3,000 ft-c) and L-0.5 (1,500 ft-c) with two N rates at each of three night temperatures for three 10-day periods also switching the high and low temperatures for the last 10 days.

Significant (\*) and highly significant (\*\*) differences for the factorial treatments: 1st period - L\*, N\*; 2nd period - N\*\*; 3rd period - L\* and N\*\*.

TABLE 14. Top growth (mg dry matter) of bentgrass grown at L-1 and L-0.5 with two nitrogen rates at each of three night temperatures for three 10-day periods and also for switching the high-low temperatures for the last 10 days. (Temperature during 14 hrs. light was 95 F.)

| Night<br>temp F           | 10-day sampling periods and nitrogen treatments <sup>2</sup> |     |       |        |     |        |       |       |        |
|---------------------------|--------------------------------------------------------------|-----|-------|--------|-----|--------|-------|-------|--------|
|                           | First                                                        |     |       | Second |     |        | Third |       |        |
|                           | N-1                                                          | N-2 | Mean  | N-1    | N-2 | Mean   | N-1   | N-2   | Mean   |
|                           | mg                                                           | mg  | mg    | mg     | mg  | mg     | mg    | mg    | mg     |
| <u>L-1 (3,000 ft-c)</u>   |                                                              |     |       |        |     |        |       |       |        |
| 60                        | 94                                                           | 268 | 181   | 331    | 826 | 579 c  | 601   | 942   | 772 c  |
| 75                        | 67                                                           | 209 | 138   | 148    | 653 | 401 b  | 420   | 1,056 | 738 c  |
| 90                        | 113                                                          | 164 | 139   | 232    | 305 | 269 a  | 450   | 506   | 478 a  |
| 60-90 <sup>1</sup>        | -                                                            | -   | -     | -      | -   | -      | 404   | 641   | 523 ab |
| 90-60                     | -                                                            | -   | -     | -      | -   | -      | 455   | 729   | 592 b  |
| Mean                      | 91                                                           | 214 | 153   | 237    | 595 | 416    | 466   | 775   | 621    |
| <u>L-0.5 (1,500 ft-c)</u> |                                                              |     |       |        |     |        |       |       |        |
| 60                        | 254                                                          | 288 | 271 b | 245    | 300 | 273 ab | 540   | 651   | 596 b  |
| 75                        | 129                                                          | 336 | 233 b | 204    | 381 | 293 b  | 510   | 637   | 574 b  |
| 90                        | 61                                                           | 104 | 83 a  | 237    | 217 | 227 a  | 334   | 308   | 321 a  |
| 60-90                     | -                                                            | -   | -     | -      | -   | -      | 286   | 347   | 317 a  |
| 90-60                     | -                                                            | -   | -     | -      | -   | -      | 616   | 617   | 617 b  |
| Mean                      | 148                                                          | 243 | 196   | 229    | 299 | 264    | 457   | 512   | 484    |

<sup>1</sup> Temperatures at 60 for the first 20 days, then switched to 90 F for the last 10 days.

<sup>2</sup> Combined N. treatment means having the same letters are not significant. Significant (\*) and highly significant (\*\*) differences: First 10 days - T\*\*, N\*\*, and TL\*\*; Second 10 days - T\*\*, L\*\*, N\*\*, and all first order interactions\*\*; and Third 10 days - T\*, L\*, N\*\*, TN\*\*, and SN\*\*.

Root Development:

Roots were harvested at the end of 30 days. Roots weighed less when the grass received high N at all temperatures or light treatments (Table 15). The roots at L-1 weighed 271% more than for L-0.5 when all treatments were averaged. Bentgrass roots weighed less for 90 F night temperatures than for 60 and 70 F. The trend was similar at L-1 and L-0.5, but not significant at L-0.5. Switching from 60 to 90 F reduced root yields, but grass switched from 90 to 60 F showed a non-significant increase in root weight. This lack of significance may be associated with the low root weights at 90 F before making the switch.

Respiration and Net Assimilation Rates(NAR):

Low light intensity or a high night temperature caused sharp decreases in NAR (Fig. 9). Bentgrass grown at L-1 and L-0.5 at 90 F was 65.7 and 37.8%, respectively, lower in NAR than those at 60 F. Grass grown at L-1 and L-0.5 increased in NAR when switched from night temperatures of 90 to 60 F during the final 10 days. NAR decreased when grass grown at L-1 was switched from 60 to 90 F, but the difference was not high enough for significance for L-0.5 grass.

When comparing N level, N-2 increased NAR 43% when the grass was grown at L-1, but was not significant for grass grown at L-0.5. Low light intensity reduced NAR approximately 33% (factorial treatment combinations averaged).

TABLE 15. Root weights (mg dry matter per pot) of bentgrass grown at two light intensities with two nitrogen rates at each of three night temperatures after 30 days and also for switching the high-low temperatures for the last 10 days. (Temperature during 14 hrs. light was 95 F.)

| Night<br>temp F    | Light and nitrogen treatments <sup>2</sup> |     |       |                    |     |      |
|--------------------|--------------------------------------------|-----|-------|--------------------|-----|------|
|                    | L-1 (3,000 ft-c)                           |     |       | L-0.5 (1,500 ft-c) |     |      |
|                    | N-1                                        | N-2 | Mean  | N-1                | N-2 | Mean |
|                    | mg                                         | mg  | mg    | mg                 | mg  | mg   |
| 60                 | 682                                        | 296 | 489 b | 202                | 75  | 139  |
| 75                 | 749                                        | 406 | 577 b | 231                | 203 | 217  |
| 90                 | 239                                        | 88  | 164 a | 80                 | 40  | 60   |
| 60-90 <sup>1</sup> | 385                                        | 156 | 271 a | 67                 | 37  | 52   |
| 90-60              | 345                                        | 99  | 222 a | 117                | 56  | 86   |
| Mean               | 428                                        | 173 | 301   | 139                | 82  | 111  |

<sup>1</sup>Temperature at 60 for the first 20 days, then switched to 90 F for the last 10 days.

<sup>2</sup>Combined N treatment means having the same letter are not significant.

Significant (\*) and highly significant (\*\*) differences: T\*\*, L\*\*, N\*\*, TS\*, and SN\*\*.

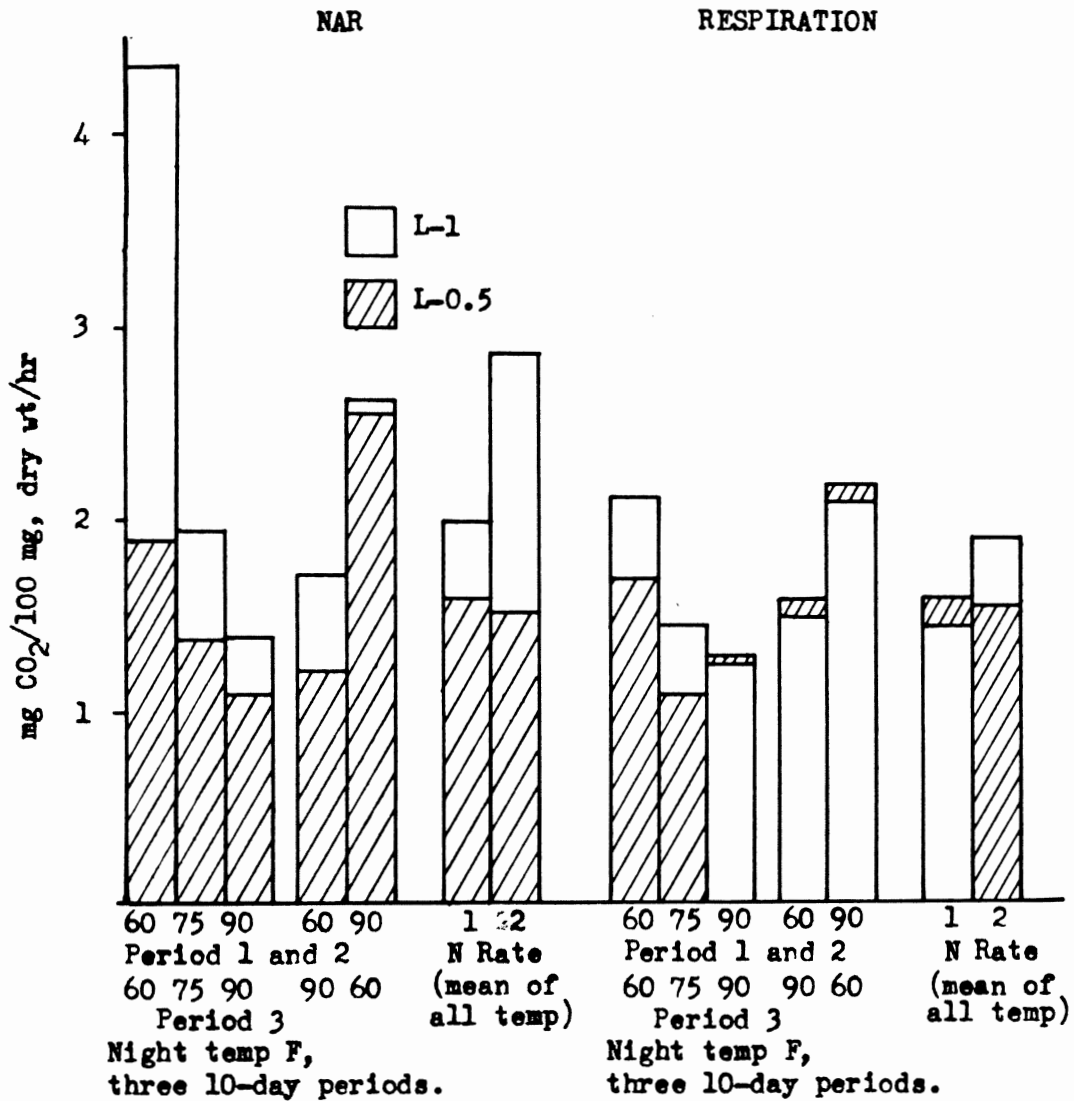


FIG. 9. NAR and respiration rates of bentgrass grown at L-1 (3,000 ft-c) and L-0.5 (1,500 ft-c) with two N rates at each of three night temperatures for 30 days and also for switching the high-low temperatures for the last 10-day period.

Highly significant differences for the factorial treatments:  
NAR - T, L, N, TL, and LN; and for respiration - T and LN.

Respiration rates were taken during the day when all temperatures were 95 F. Neither N fertilization nor the light intensity gave significant differences in respiration. When night temperatures were high the respiration rate was generally reduced as compared with low night temperatures. Switching grass that had been at 90 to 60 F night temperatures also caused increases in respiration.

## Bermudagrass, Experiment II

Carbohydrates:

Carbohydrates varied with time when grown at various night temperatures (Figures 10 and 11 and Table 16). After 30 days nitrogen fertilization, temperature, light, and their interactions had statistically significant effects on carbohydrate content, but the differences may be too small to be biologically significant. The highest AEC after 30 days ranged from 23.5 to 30.1% in L-1 and from 21.1 to 25.4% in L-0.5 for all N and temperature factorial combinations.

When considering all treatments, polysaccharides made up 86.2% and the simple sugars accounted for 13.8% of the AEC at 30 days. After 30 days, the AEC were lower at 60 than at 90 F for L-1 and L-0.5. Within L-1, AEC of stolons increased when the temperature was switched from low to high.

After 30 days high N lowered AEC less than 4.0 and 0.5 percentage units for L-1 and L-0.5 factorial treatments, respectively. By reducing light from L-1 to L-0.5, AEC were reduced 5.3 and 2.4 percentage units for N-1 and N-2, respectively.

Nitrogen Content:

Total N content of bermudagrass stolons (after 30 days for all factorial combinations) increased about 30% by either increasing N level or reducing light intensity (Fig. 12). Such trends were consistent for all periods. The highest night temperature (90 F) caused total N to increase for L-1, but not for L-0.5 grass stolons sampled after 20 and 30 days. Night temperatures did not effect N content of stolons

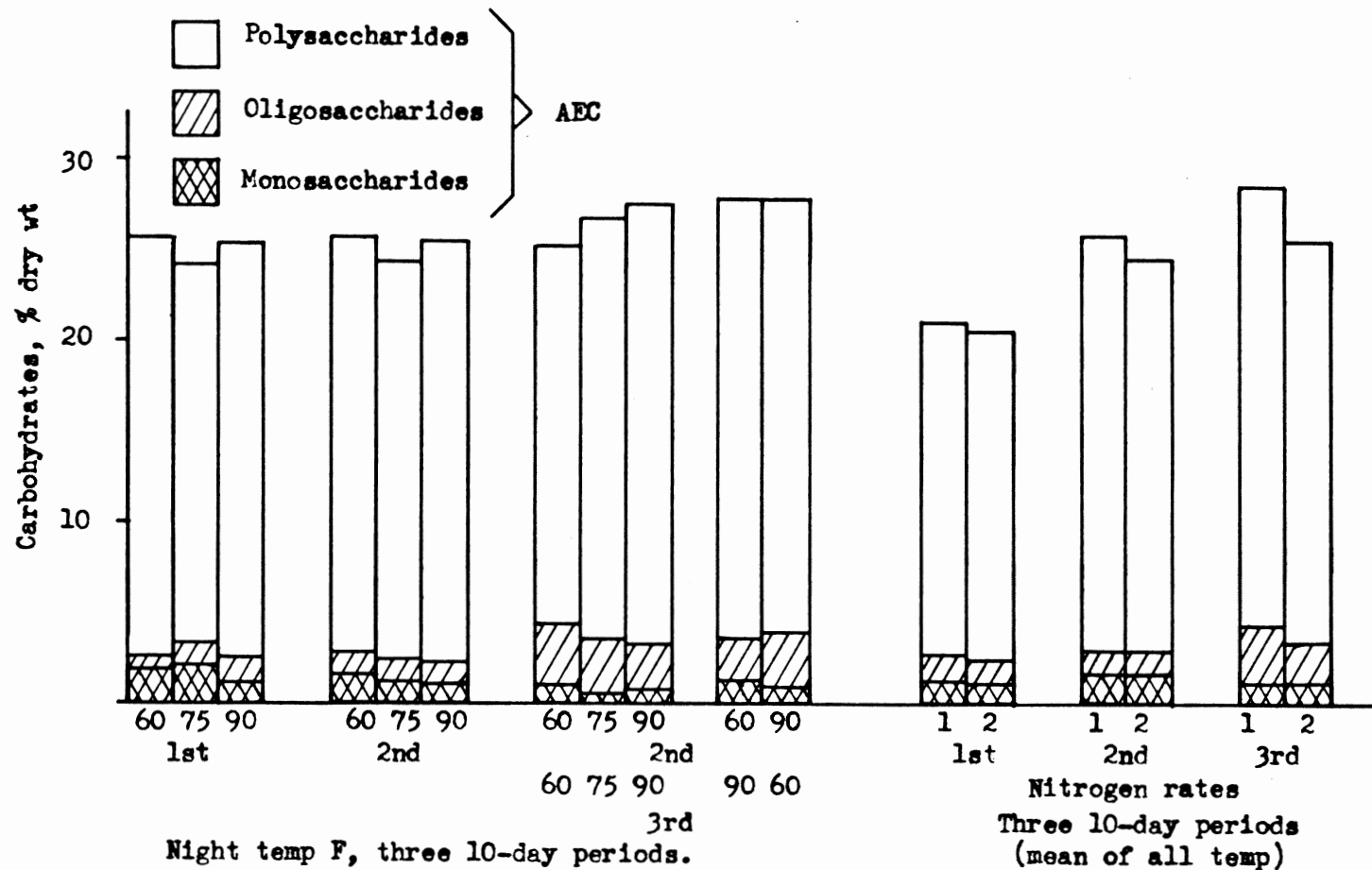


FIG. 10. Carbohydrates (% dry weight) in stolons of bermudagrass grown at 95 F for 14 hours at L-1 (3,000 ft-c) with two N rates at each of three night temperatures for three 10-day periods and also switching the high and low temperatures for the last 10 days. (See Fig. 11 for L-0.5 factorial combinations and Table 16 for statistical significance.)

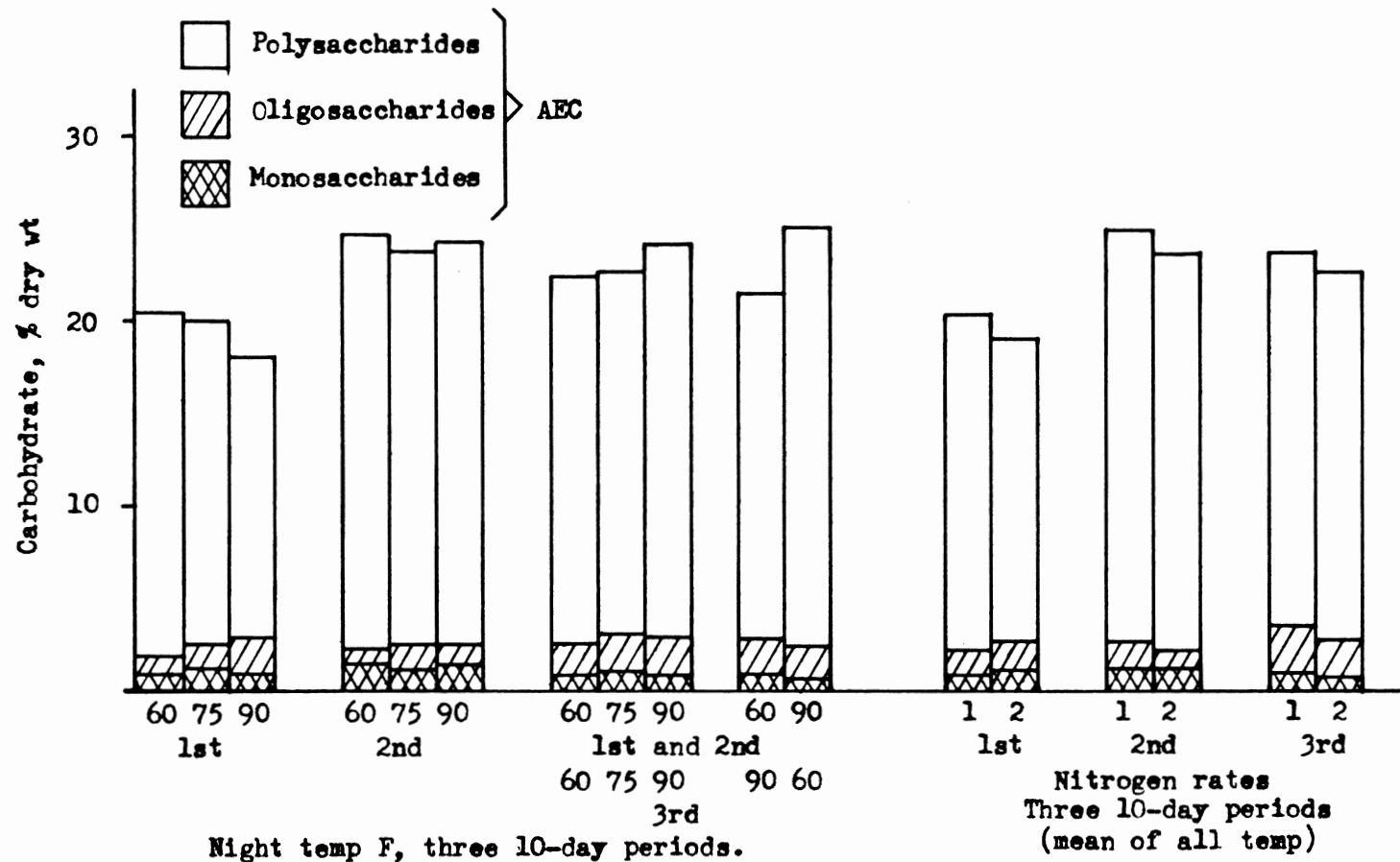


FIG. 11b. Carbohydrates (% dry weight) in stolons of bermudagrass grown at 95 F for 14 hours at L-0.5 (1,500 ft-c) with two N rates at each of three night temperatures for three 10-day periods and also switching the high and low temperatures for the last 10 days. (See Fig. 10 for L-1 factorial combinations and Table 16 for statistical significance.)

TABLE 16. Significant (\*) and highly significant (\*\*) differences for carbohydrate data in Figures 10 and 11.

| Carbohydrates    | Sampling Periods | Factorial treatments  |            |               |    |    |    |
|------------------|------------------|-----------------------|------------|---------------|----|----|----|
|                  |                  | Tempera-<br>ture<br>T | Light<br>L | Nitrogen<br>N | TL | LN | TN |
| AEC              | First 10 days    | NS                    | NS         | NS            | ** | NS | NS |
|                  | Second 10 days   | NS                    | **         | NS            | NS | NS | NS |
|                  | Third 10 days    | **                    | **         | **            | ** | ** | *  |
| Monosaccharides  | First 10 days    | **                    | NS         | NS            | *  | NS | NS |
|                  | Second 10 days   | *                     | **         | NS            | NS | NS | NS |
|                  | Third 10 days    | **                    | **         | NS            | NS | NS | NS |
| Oligosaccharides | First 10 days    | **                    | **         | NS            | ** | ** | NS |
|                  | Second 10 days   | NS                    | **         | *             | NS | NS | NS |
|                  | Third 10 days    | NS                    | **         | **            | NS | ** | NS |
| Polysaccharides  | First 10 days    | NS                    | *          | NS            | ** | NS | NS |
|                  | Second 10 days   | **                    | NS         | NS            | NS | NS | NS |
|                  | Third 10 days    | **                    | **         | **            | NS | NS | NS |

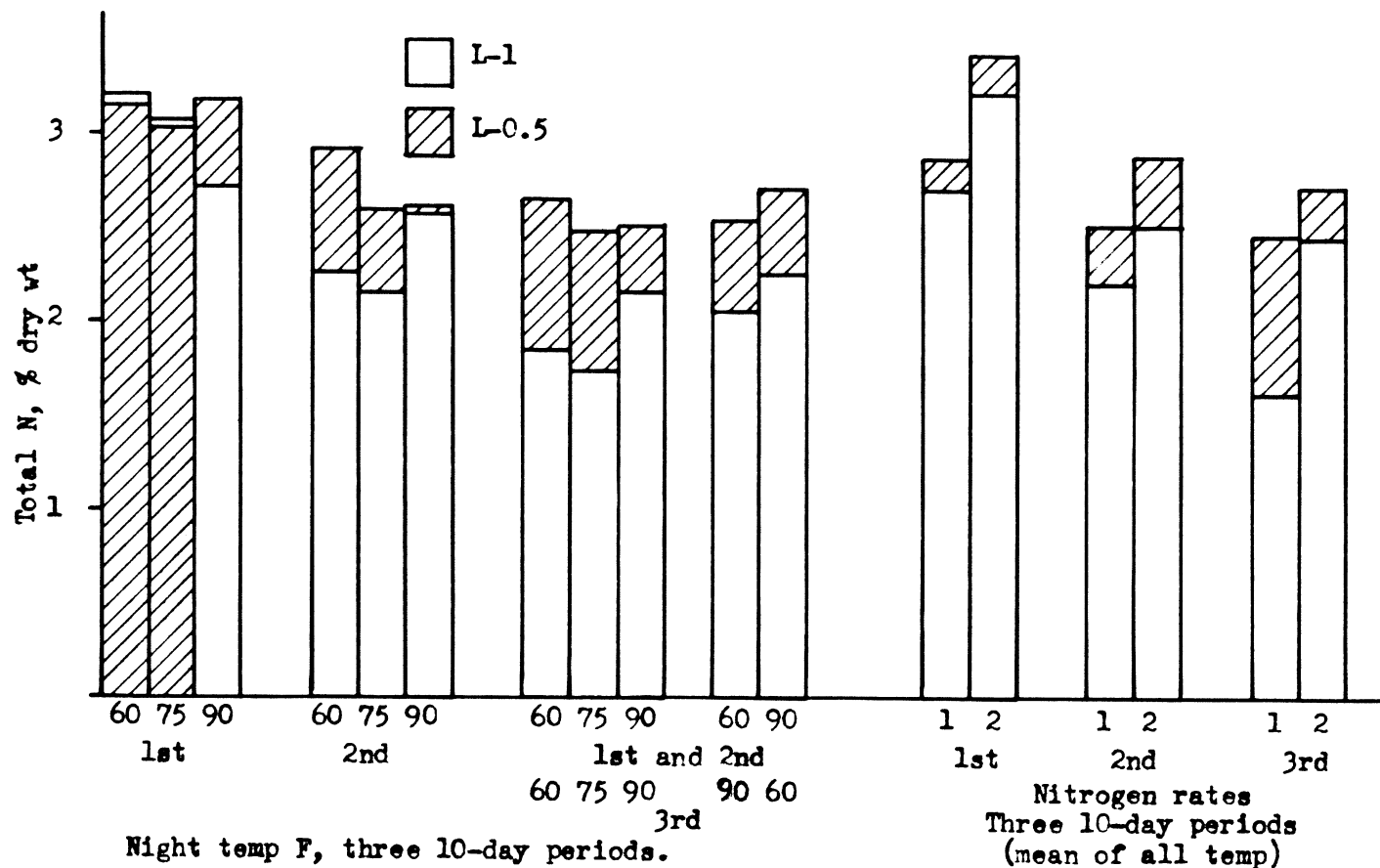


FIG. 12. Total nitrogen content (% dry weight) in bermudagrass grown at 95 F for 14 hours at L-1 (3,000 ft-c) and L-0.5 (1,500 ft-c) with two N rates at each of three night temperatures for three 10-day periods and also switching the high and low temperatures for the last 10 days. Significant (\*) and highly significant (\*\*) differences for the factorial treatments: 1st period - N\*\*; 2nd period - L\*\*, N\*\*, and TL\*; 3rd period - N\*\*, L\*\*, T\*\*, TL\*, TN\*, and LN\*\*.

during the first 10-days. Switching temperatures for the last 10 days did not significantly increase the N content above that in stolons maintained at the original temperatures.

#### Top Growth:

Top growth was generally higher for N-2 than N-1 (Table 17). Reduced light intensity (L-1 to L-0.5) decreased top growth for all treatments. The variable night temperatures with 95 F during the 14-hr. light period, caused decided yield differences. During the first 10 days grass under L-1 at 60 F had 27.3 and 32.2% lower clipping yields than for 75 and 90 F night temperatures, respectively. During the second 10 days with L-1 at 90 F, the grass clippings were 34.0 and 28.7% less than for 75 or 60 F, respectively. Under the same conditions during the last 10 days, top growth was greatest at 75 and lowest at 90 F.

There were residual night temperature effects from growing grass at given night temperatures for 20 days and then switching to different night temperatures for 10 days. Top growth (all treatments averaged) was not significantly influenced when night temperatures were switched from 60 to 90 F or the reverse.

#### Root Growth:

Root weights were greatly decreased by low light intensity and at high N at L-1 (Table 18). There was about an 11-fold increase in root weights for L-1 as compared to L-0.5 at 75 F night temperatures. Bermuda-grass grown in L-1 made the largest root yield at 75 F, seven time more

TABLE 17. Top growth (mg dry matter) of bermudagrass grown at L-1 and L-0.5 with two nitrogen rates at each of three night temperatures for three 10-day periods and also for switching the high-low temperatures for the last 10 days. (Temperature during 14 hrs. light was 95 F.)

| Night<br>temp F           | 10-day sampling periods and nitrogen treatments <sup>2</sup> |     |       |        |     |       |       |       |         |
|---------------------------|--------------------------------------------------------------|-----|-------|--------|-----|-------|-------|-------|---------|
|                           | First                                                        |     |       | Second |     |       | Third |       |         |
|                           | N-1                                                          | N-2 | Mean  | N-1    | N-2 | Mean  | N-1   | N-2   | Mean    |
|                           | mg                                                           | mg  | mg    | mg     | mg  | mg    | mg    | mg    | mg      |
| <u>L-1 (3,000 ft-c)</u>   |                                                              |     |       |        |     |       |       |       |         |
| 60                        | 427                                                          | 600 | 515 a | 599    | 692 | 646 b | 669   | 1,069 | 870 b   |
| 75                        | 680                                                          | 735 | 708 b | 550    | 844 | 698 b | 683   | 1,439 | 1,062 c |
| 90                        | 652                                                          | 866 | 760 b | 434    | 487 | 461 a | 511   | 664   | 588 a   |
| 60-90 <sup>1</sup>        | -                                                            | -   | -     | -      | -   | -     | 644   | 896   | 771 b   |
| 90-60                     | -                                                            | -   | -     | -      | -   | -     | 584   | 659   | 622 a   |
| Mean                      | 586                                                          | 734 | 661   | 528    | 674 | 602   | 618   | 945   | 783     |
| <u>L-0.5 (1,500 ft-c)</u> |                                                              |     |       |        |     |       |       |       |         |
| 60                        | 355                                                          | 386 | 371 a | 247    | 296 | 272   | 508   | 591   | 550 b   |
| 75                        | 459                                                          | 436 | 448 b | 389    | 260 | 325   | 526   | 578   | 552 b   |
| 90                        | 415                                                          | 487 | 451 b | 283    | 357 | 320   | 340   | 392   | 366 a   |
| 60-90                     | -                                                            | -   | -     | -      | -   | -     | 461   | 543   | 502 ab  |
| 90-60                     | -                                                            | -   | -     | -      | -   | -     | 333   | 417   | 375 a   |
| Mean                      | 410                                                          | 436 | 423   | 306    | 304 | 306   | 434   | 504   | 469     |

<sup>1</sup> Temperatures at 60 for the first 20 days then switched to 90 F for the last 10 days.

<sup>2</sup> Combined N treatment means having the same letter are not significant.

Significant (\*) and highly significant (\*\*) differences: First 10 days - T\* and L\*\*; Second 10 days - T\*\*, L\*\*, N\*, TL\*\*, and LN\*; Third 10 days - T\*\*, L\*\*, N\*\*, and their interactions\*\*.

TABLE 18. Root weights (mg dry matter per pot) of bermudagrass grown at two light intensities with two nitrogen rates at each of three night temperatures after 30 days and also for switching the high-low temperatures for the last 10 days. (Temperature during 14 hrs. light was 95 F.)

| Night<br>temp F    | Light and nitrogen treatments <sup>2</sup> |     |       |                    |     |      |
|--------------------|--------------------------------------------|-----|-------|--------------------|-----|------|
|                    | L-1 (3,000 ft-c)                           |     |       | L-C.5 (1,500 ft-c) |     |      |
|                    | N-1                                        | N-2 | Mean  | N-1                | N-2 | Mean |
|                    | mg                                         | mg  | mg    | mg                 | mg  | mg   |
| 60                 | 248                                        | 142 | 195 c | 16                 | 15  | 16   |
| 75                 | 323                                        | 173 | 248 d | 25                 | 16  | 22   |
| 90                 | 38                                         | 37  | 38 a  | 9                  | 6   | 8    |
| 60-90 <sup>1</sup> | 114                                        | 77  | 96 b  | 16                 | 10  | 13   |
| 90-60              | 55                                         | 53  | 54 ab | 2                  | 10  | 6    |
| Mean               | 156                                        | 96  | 126   | 14                 | 12  | 13   |

<sup>1</sup>Temperature at 60 for the first 20 days then, switched to 90 F for the last 10 days.

<sup>2</sup>Combined N treatment means having the same letter are not significant.

Significant (\*) and highly significant (\*\*) differences: T\*, N\*, L\*\*, TL\*, and LN\*\*.

than at 90 F night temperatures. After switching from 60 to 90 F (last 10 days), the root yield was reduced 52% of that kept at 60 F night temperature. Grass switched from 90 to 60 F (last 10 days) did not significantly differ in root weights when compared with grass remaining at 90 F.

#### Respiration and Net Assimilation Rates (NAR):

NAR was higher for N-2 than N-1 for all factorial combinations, but NAR for grass grown under L-0.5 was lower than L-1 (Fig. 13). Night temperatures caused large differences in NAR for grass grown under L-1, but not at L-0.5. Under L-1, NAR was 43% higher at 75 than at a 90 F night temperature. Switching bermudagrass from cool to warm night temperatures or vice versa (last 10 days) did not affect NAR appreciably.

All respiration data were obtained at 95 F daylight temperature (Fig. 13). Respiration was lower for grass grown at L-0.5 than L-1. Respiration was slightly higher for N-2 than N-1, but not statistically significant. The lowest respiration under L-1 occurred at 75 F, which was significantly lower than at 90 F. The residual effects of night temperatures for 20 days before switching temperatures influenced respiration, but the data were rather variable. The highest respiration occurred with grass switched from 60 to 90 F during the last 10 days; this was significantly higher than for other night temperatures, except for grass continuously at 90 F.

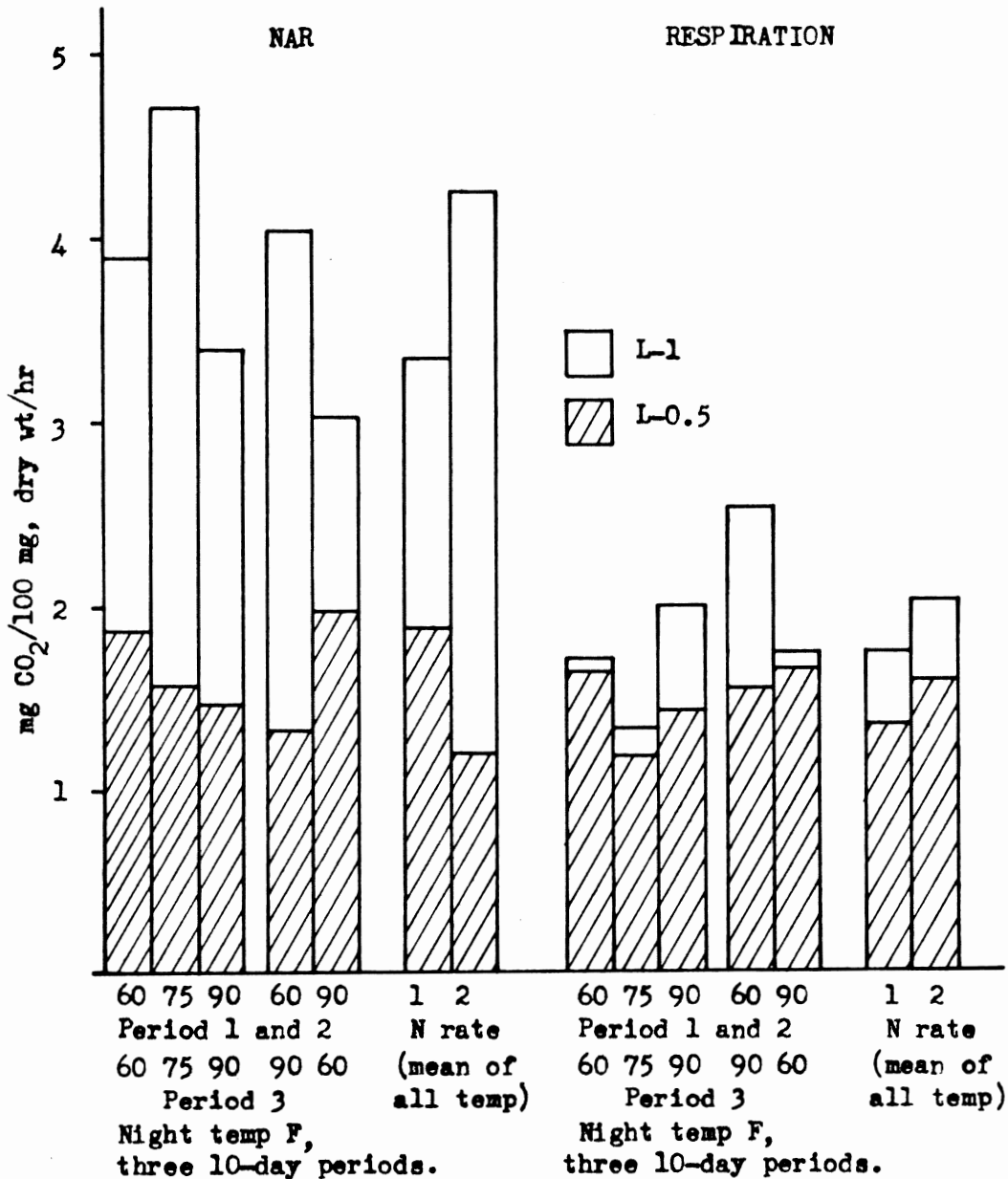


FIG. 13. NAR and respiration rates of bermudagrass grown at 95 F for 14 hours at L-1 (3,000 ft-c) and L-0.5 (1,500 ft-c) with two N rates at each of three night temperatures for 30 days and also for switching the high-low temperatures for the last 10 days.

Highly significant differences for the factorial treatments:  
NAR - L and LN; and for respiration - T and LN

## DISCUSSION

Bentgrass:

Night temperature, light intensity, and nitrogen fertilization influenced growth, morphology, and chemical composition of bentgrass. High night temperature or low light intensity decreased the daytime respiration rate, NAR, top and root growth, and ethanol soluble carbohydrates, but elevated the nitrogen content. High N fertilization increased top growth, NAR, respiration rate, nitrogen content, but reduced root development and all carbohydrates. Apparently because of high (95 F) day temperatures, carbohydrates were low for all treatments when compared to Experiment I.

The consistently better top growth of bentgrass at 60 F than at 90 F was probably influenced by the higher NAR at the lower temperature. Also, under full light intensity the accompanying high respiration at 60 as compared to 90 F night temperature is indicative of high metabolism which may account for the eventual low AEC. The increases in monosaccharides and oligosaccharides and concurrent decreases in polysaccharides indicate that the latter is readily hydrolyzed for growth and respiration at 60 F.

The small reduction in topgrowth even though NAR was sharply reduced at 75 as compared to 60 F, was apparently associated with reduced respiration. Evidently, grass at L-1 and 75 F for 30 days had a low energy demand associated with low respiration causing AEC to increase. These data are in agreement with Beard (1961) who reported

optimum root production of Agrostis species at temperatures higher than optimum for top growth. It was postulated that root growth was increased because more sugar was available (Jones et al, 1961 and Nowakowski, 1962).

At 90 F, NAR was drastically reduced. However, the concurrent low respiration and slow top and root growth at 90 F caused AEC to be slightly higher at 90 than for 60 F. Switching bentgrass grown at L-1 from 90 to 60 F night temperatures increased NAR and top growth, but these values were lower than for grass kept at 60 F. This implies that the original 90 F temperature had some retarding effect. However, grass switched from 60 to 90 F decreased NAR and top growth with little residual influence from the initial 60 F temperature.

Night temperatures did not influence the nitrogen content in bentgrass stolons. However, low light intensity or liberal nitrogen increased the nitrogen in stolons. Several workers (Knipmeyer, 1962; Sullivan and Sprague, 1949; and Burton et al., 1959) found that shading had little effect on N content of grasses. The increased total nitrogen obtained here may be due to the carbohydrate status. The low carbohydrates in grass were apparently caused by low NAR with low light intensity. With liberal nitrogen fertilization, the increases in top growth and respiration with concurrent high energy needs apparently caused a reduction in carbohydrates and root growth even though the NAR was high.

Bermudagrass:

Nitrogen fertilization, light intensity, and night temperatures greatly influenced bermudagrass growth. Growth responses from 60 F night temperatures with a warm season grass, such as bermudagrass, is of special interest. Top growth and root yield were best at 75 F and poorest at 90 F night temperatures. This may be explained by the highest NAR at 75 and lowest at 90 F night temperature. Root growth decreased for L-1 factorial treatment combinations when switched from 60 to 90 F. This may be attributed to the increase in respiration that occurred during the 95 F daylight temperature as a result of this high night temperature.

Polysaccharides made up a large portion of the AEC. Monosaccharides and oligosaccharides together made up a small portion (13 to 15%) of the AEC in bermudagrass. The differences of these two fractions for various treatments may be too small to be biologically significant. The highest AEC content of stolons occurring at 90 F after 30 days may be attributed to the low top growth (low energy needs) as compared to lower temperatures.

The higher total nitrogen content of stolons for L-0.5 as compared with L-1 factorial combinations may be attributed to the lower AEC for L-0.5. These lower AEC were apparently associated with low NAR that accompanied the low light intensity. The low yields of top and roots may also account for the higher nitrogen in grass stolons with L-0.5 than L-1. When considering L-1 factorial combinations

the high nitrogen of stolons with 90 F as compared to lower night temperatures may be associated with increased respiration and more nitrogen absorption at high temperatures.

Total nitrogen may have been increased in bermudagrass stolons with liberal N fertilization because of greater N uptake and also because of less accumulation of carbohydrates. Lower root weights with high N were apparently caused by the high energy demands for the stimulated top growth and the slightly increased respiration, which made less carbohydrates available for root growth.

## EXPERIMENT III

The Influence of Nitrogen and Season on the Carbohydrate Content  
of Bentgrass and Bermudagrass Stolons

## PROCEDURE

An area (2,000 sq ft) of Cohansey bentgrass, Agrostis palustris, was planted with stolons at Blacksburg on a Groseclose silt loam in spring 1962. The soil was limed to a pH of about 6.5 and fertilizer was applied at the rate of 45 lbs of P and 80 lbs of K per acre. Treatment variables were three rates of nitrogen designated as N-1, N-2, and N-3. The nitrogen treatments on plots 12 x 15 ft were replicated three times in randomized blocks. Nitrogen rates as pounds N per 1,000 sq ft (ammonium nitrate N source) were as follows: N-1 - 1/2 lb on August 18 and September 15, 1962, and 1/8 lb weekly from spring to fall in 1963 and 1964; N-2 as in N-1 except for 1 lb rates in 1962 and 1/4 lb weekly in 1963 and 1964; and N-3 same as N-2 except for 2 lbs rates in 1962 and 1/2 lbs weekly in 1963 and 1964.

The grass was mowed to 1/4 inch about three times each week and a broad spectrum fungicide was applied ever 10 to 14 days during the growing season. The area was watered periodically to obtain good growth.

Stolon samples were obtained 16 and 9 times during 1962 and 1963 growing seasons, respectively. The grasses were washed free of soil with cold water and then frozen at -20 C to kill the tissue. Later these materials were thawed and after making stolon separates, they were refrozen until they could be lyophilized. The dried stolons were

ground finely and analyzed for carbohydrates as described in Experiment I.

Tifgreen bermudagrass, Cynodon dactylon, was established near Richmond during spring 1963. The design and conduct of the experiment was similar to the one for bentgrass, except that 4-inch sod plugs were taken for rhizome and stolon analysis during May, 1963 to March, 1964. The samples were immediately packed in ice for transportation to the Blacksburg laboratory for washing and freezing. The three N rates (pounds N per 1,000 sq ft) were: N-1 - 1/2 lb N from urea in April 1963 and 1/4 lb N biweekly from mid-April to October 1963; N-2 as N-1, except for applying 1 lb in April and 0.5 lb thereafter; N-3 as N-1, except for using 2 lb in April and 3/4 lb thereafter plus ureaformaldehyde at 6 lb N on May 1, 1963.

## RESULTS

## Bentgrass, Experiment III

The seasonal variation of carbohydrate fractions in bentgrass are shown in Figures 14, 15, and 16. Oligosaccharides, polysaccharides and AEC increased during the fall and early winter and declined rapidly during spring. During the 1963 growing season, AEC decreased from a high of 57% on March 26 to a low of 24% on April 30 and then the trend was variable generally increasing somewhat during the summer months (Fig. 14).

The seasonal AEC cycle in 1964 was lowest in June and highest in January, but stolon samples were not taken often enough during the spring to ascertain the cyclic variation (Fig. 16). The AEC and oligosaccharides had similar trends, but polysaccharides did not peak during late fall and winter. The seasonal variation in monosaccharides was small as compared to the other carbohydrate fractions.

Rates of N did not significantly influence the percentages of oligosaccharides or polysaccharides for either year (Table 19 and Fig. 15). However, AEC and monosaccharides were generally decreased with high N.

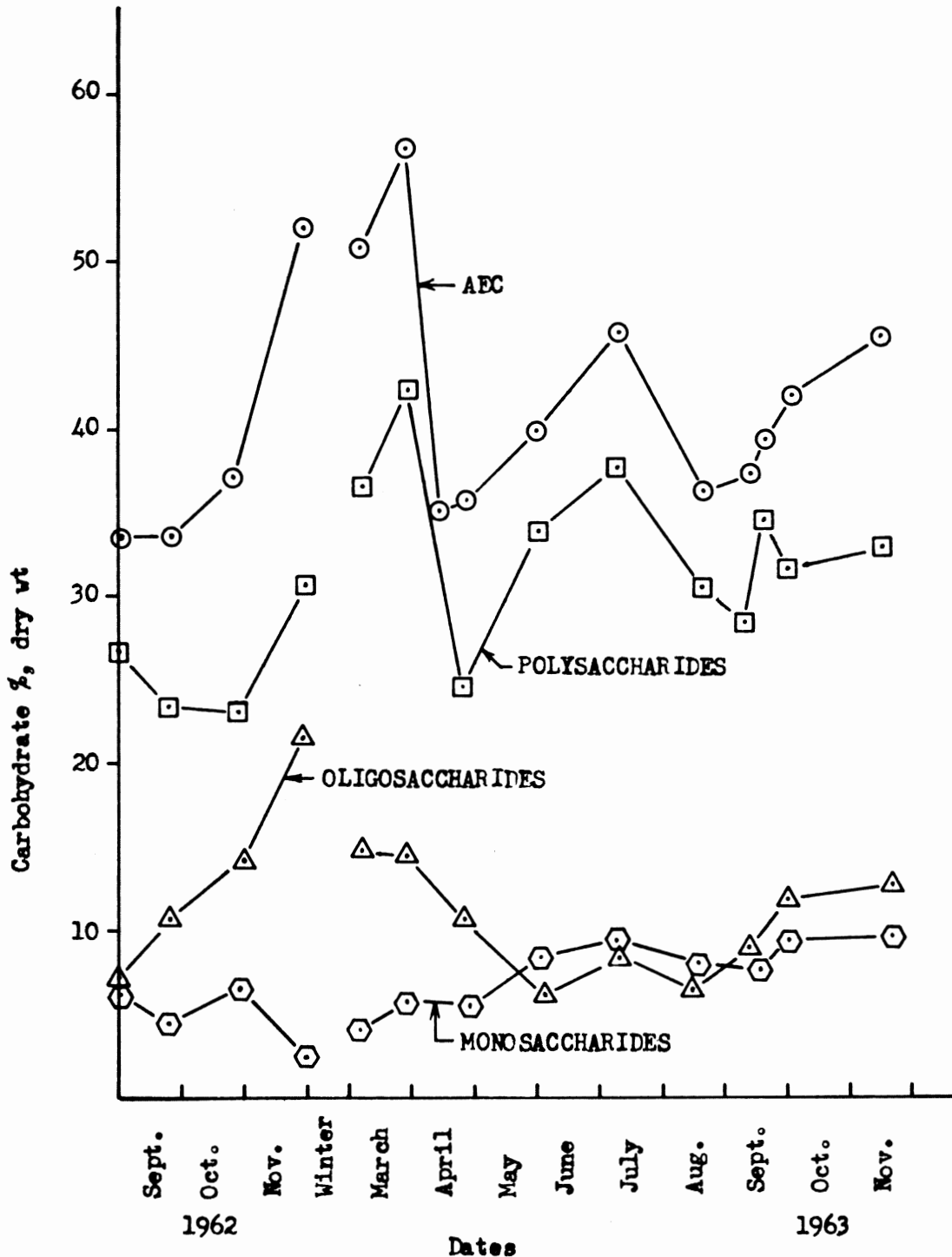


FIG. 14. Seasonal influence (1962-1963) on carbohydrates in stolons of creeping bentgrass (mean of three N rates).

Significant (\*) and highly significant (\*\*) differences: AEC - Nitrogen\*\*, Dates\*\*, and DN\*\*; polysaccharides - Dates\*\*; oligosaccharides - Dates\*\*; and monosaccharides - Nitrogen\*\* and Dates\*\*.

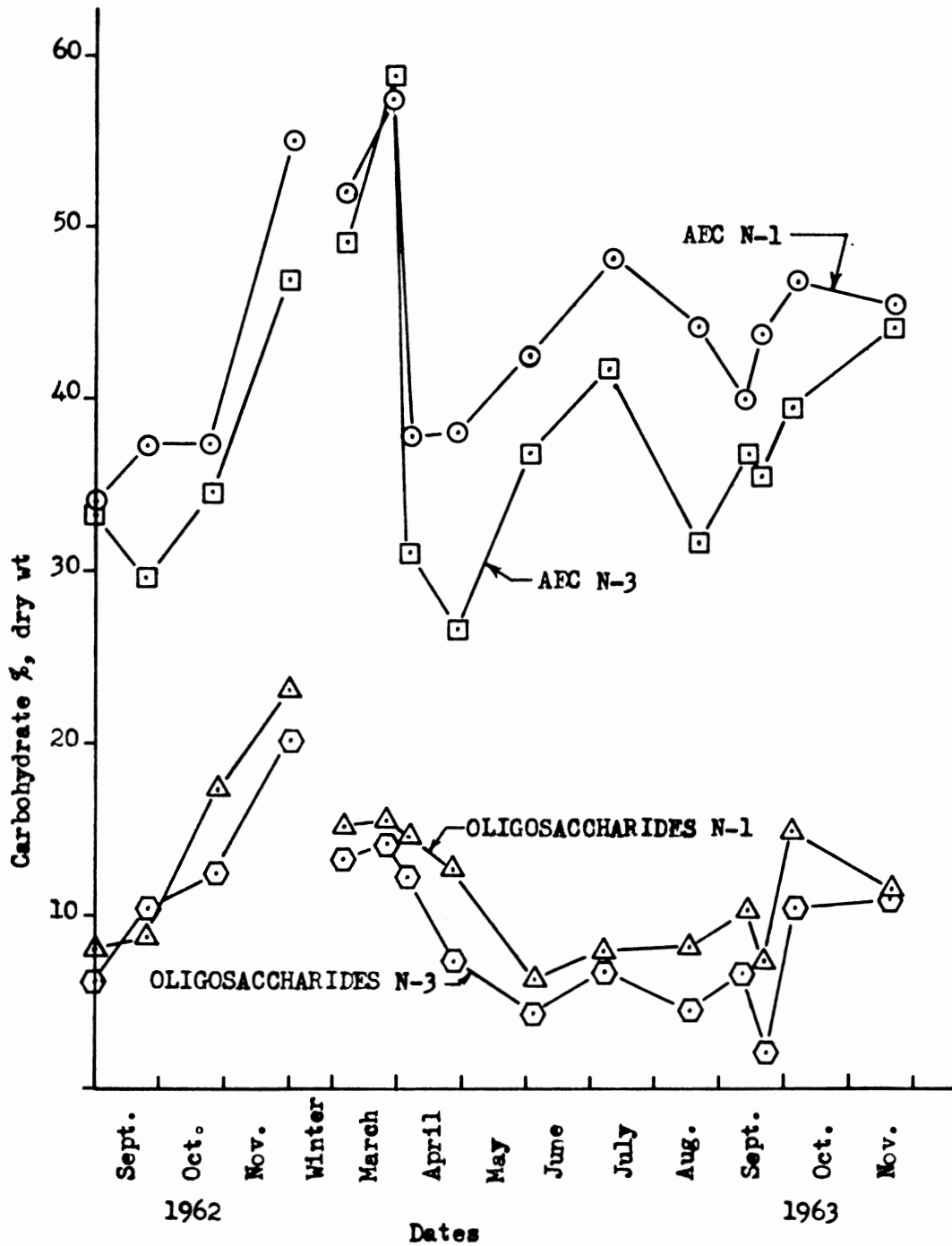


FIG. 15. Seasonal influence on carbohydrates in stolons of creeping bentgrass fertilized with high and low nitrogen rates.

Significant (\*) and highly significant (\*\*) differences:  
 AEC - Nitrogen\*\*, Dates\*\*, and DN\*\*; and oligosaccharides -  
 Dates\*\*

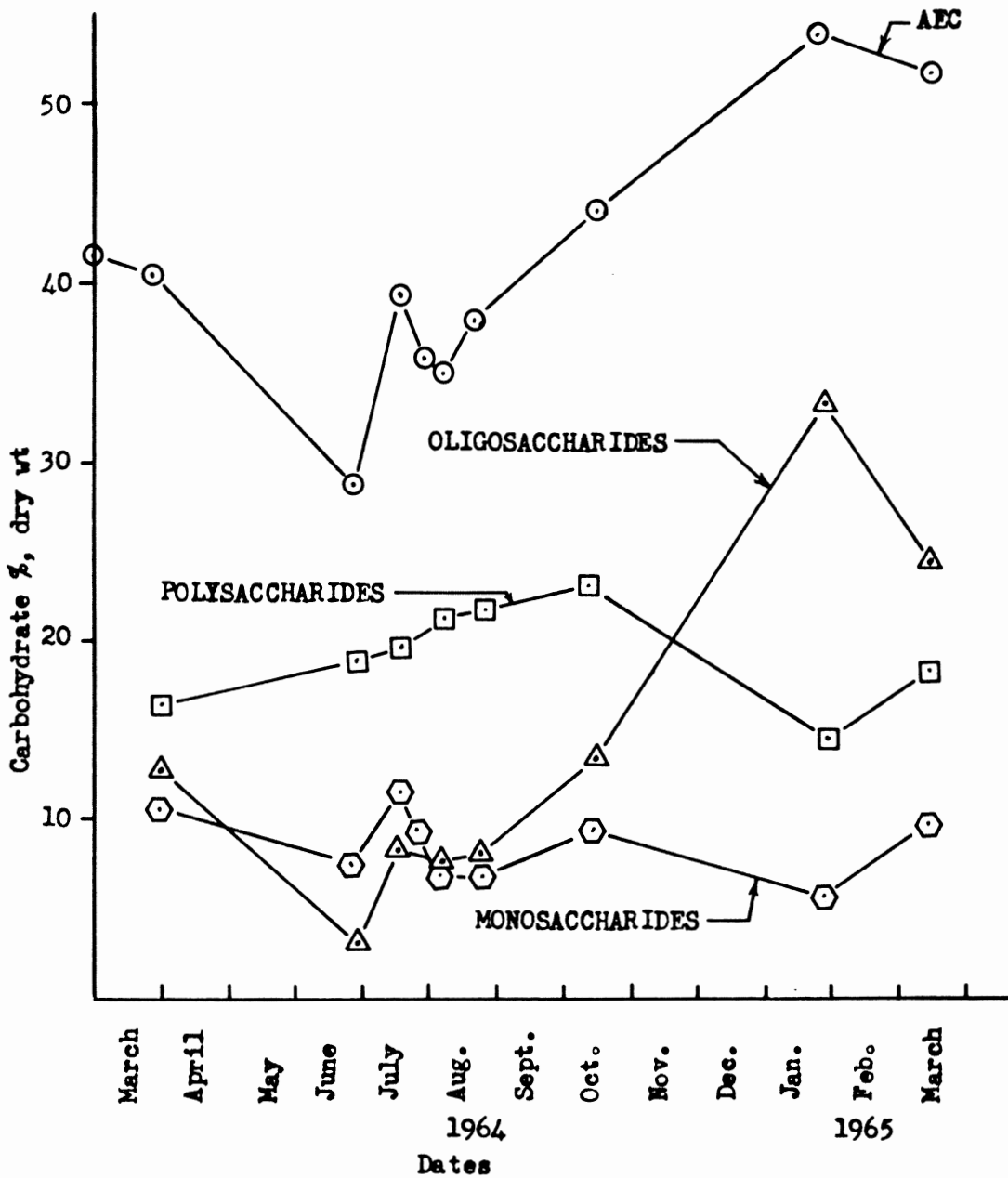


FIG. 16. Seasonal influence (1964-1965) on carbohydrates in stolons of creeping bentgrass (mean of three N rates).

Significant (\*) and highly significant (\*\*) differences:  
 AEC - Nitrogen\*\*, Dates\*\*, and DN\*; monosaccharides - Nitrogen\*\* and Dates\*\*;  
 oligosaccharides - Dates\*\*;  
 polysaccharides - Dates\*\*.

TABLE 19. Carbohydrate (% dry weight) in stolons of Cohansey bentgrass grown for two seasons at Blacksburg and Tifgreen bermudagrass grown for one season at Richmond with three nitrogen rates.

| Carbohydrate fractions      | No. of sampling dates | Nitrogen treatments <sup>1</sup> |        |        |
|-----------------------------|-----------------------|----------------------------------|--------|--------|
|                             |                       | N-1                              | N-2    | N-3    |
|                             |                       | %                                | %      | %      |
| <u>Bentgrass 1962-64</u>    |                       |                                  |        |        |
| AEC                         | 16                    | 43.5 c                           | 41.0 b | 38.2 a |
| Monosaccharides             | 16                    | 7.3 b                            | 6.9 b  | 5.6 a  |
| Oligosaccharides            | 16                    | 11.5                             | 10.8   | 9.2    |
| Polysaccharides             | 15                    | 32.0                             | 30.4   | 29.4   |
| <u>Bentgrass 1963-65</u>    |                       |                                  |        |        |
| AFC                         | 10                    | 44.0 c                           | 40.9 b | 39.0 a |
| Monosaccharides             | 10                    | 10.0 c                           | 8.6 b  | 7.3 a  |
| Oligosaccharides            | 10                    | 14.9                             | 13.7   | 14.0   |
| Polysaccharides             | 10                    | 19.3                             | 18.6   | 17.8   |
| <u>Bermudagrass 1963-64</u> |                       |                                  |        |        |
| AEC                         | 11                    | 40.5 b                           | 38.2 a | 38.1 a |
| Monosaccharides             | 9                     | 1.7                              | 1.7    | 1.7    |
| Oligosaccharides            | 9                     | 3.0                              | 2.6    | 2.6    |
| Polysaccharides             | 9                     | 39.6 b                           | 37.2 a | 36.2 a |

<sup>1</sup> Treatments between N rates with the same letter do not differ significantly.

### Bermudagrass, Experiment III

The seasonal variations of AEC and polysaccharides of bermudagrass stolons were similar (Fig. 17). These carbohydrates gradually increased during the spring, reached a maximum by late fall and then declined. The AEC values ranged from 24 to 48%. Oligosaccharides varied little, the values in spring and summer were a little lower than for the winter months. The values for monosaccharides were small averaging 1.7% and were highest in late winter.

AEC and polysaccharides in stolons were slightly but significantly reduced by liberal nitrogen fertilization (Table 19). Nitrogen fertilization did not influence the monosaccharides or oligosaccharides in bermudagrass stolons. The carbohydrates for the two higher levels of N were similar.

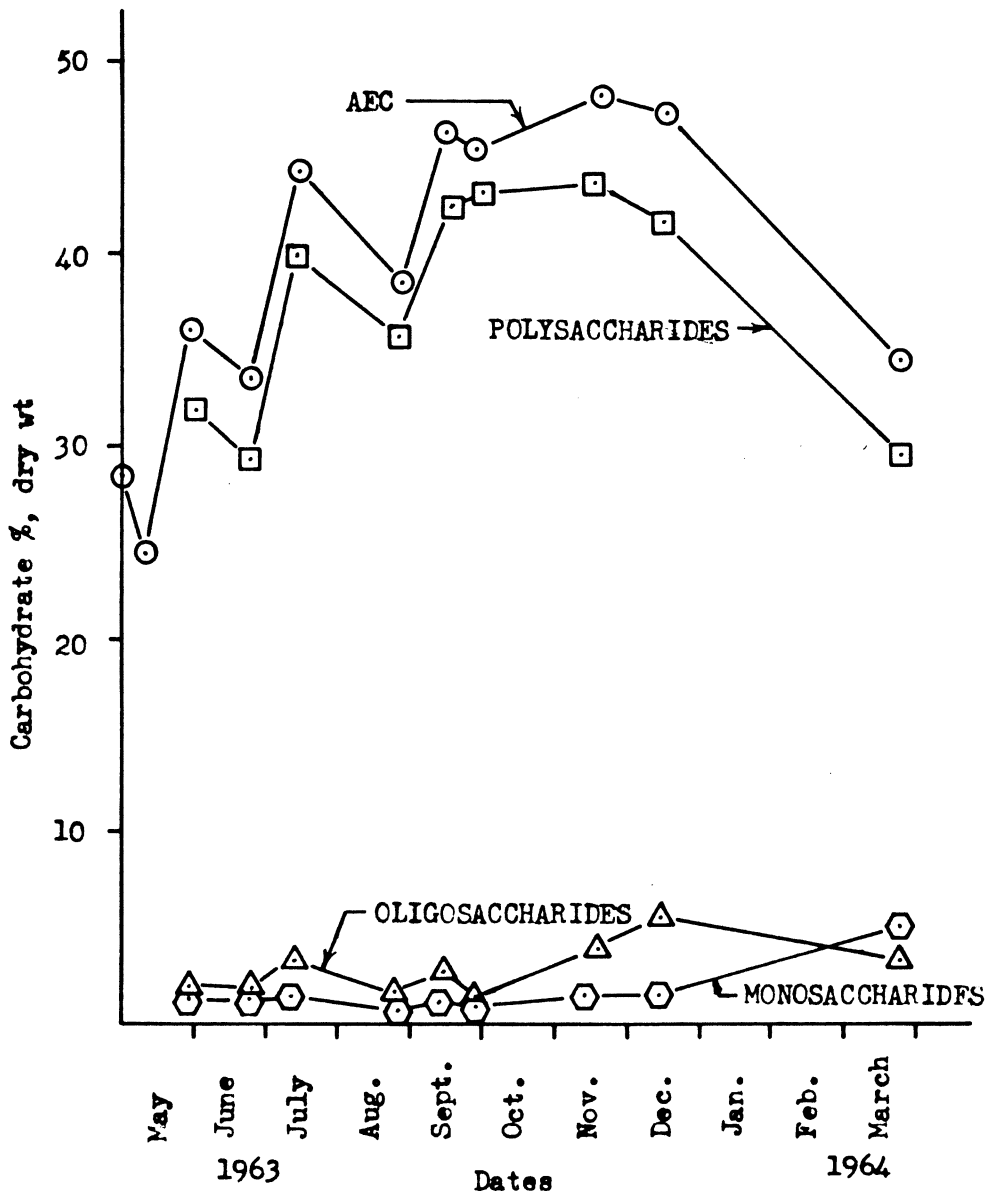


FIG. 17. Seasonal influence (1963-1964) on carbohydrates in stolons of bermudagrass (mean of three N rates).

Significant (\*) and highly significant (\*\*) differences:  
 AEC - Nitrogen\*, Dates\*\*, and DN\*\*;  
 polysaccharides - Nitrogen\*, Dates\*\*, and DN\*\*;  
 oligosaccharides - Dates\*\*;  
 and monosaccharides - Dates\*\*.

## DISCUSSION

Bentgrass:

Carbohydrates of bentgrass were drastically reduced in early spring. This may be attributed to the environmental conditions that stimulated rapid top growth where photosynthesis did not replenish carbohydrate reserves. In the growth chamber experiments with bentgrass, carbohydrates decreased concurrently with rapid growth. The rapid root and basal shoot tissue development during spring may also account for the rapid decline of AFC in spring (Hanson and Juska, 1961).

The AFC increases after the early spring decline which was more pronounced for 1963 than 1964, may be attributed to one or more of the following:

- (1) After the flush plant development in spring there was less top and root growth.

- (2) Possibly a series of temporary water stresses occurred where growth was retarded more than NAR.

- (3) High temperatures during hot days slowed growth causing carbohydrates to increase.

- (4) A low rainfall and rapid transpo-evaporation may have limited nitrogen uptake, causing a decrease in growth and a reduction in energy demand.

- (5) During slow growth the periods between clipping were extended a day or two. The lack of new tissue formation and higher leaf area caused a net energy increase.

- (6) Longer day length increased NAR.

Slight increases in carbohydrates after early spring decreases have been reported for forage grasses. Colby et al. (1965) attributed abnormally hot dry weather and heavy production of orchardgrass as factors reducing fructosan prior to and immediately after spring harvest of orchardgrass. After the second cuttings during late June and early July fructosan increased rapidly, but the yield was lower than the first harvest. The July decrease of AEC in bentgrass was possibly associated with an increase in respiration because of concurrent high temperatures (Fig. 18).

The carbohydrates in bentgrass during fall of 1962 and 1964 were higher than for 1963. This may be due to the high 1963 fall temperatures as compared with the other years (Figures 18 and 19). In 1963, the AFC remained low during winter and the next growing season as compared to the spring of 1962 and 1964.

Nitrogen fertilization as well as seasonal factors affected the carbohydrates of bentgrass. The controlled environmental chamber experiments showed that carbohydrates were reduced sharply in bentgrass with high N especially with high temperatures. Thus it appears that nitrogen should be restricted during high temperature periods.

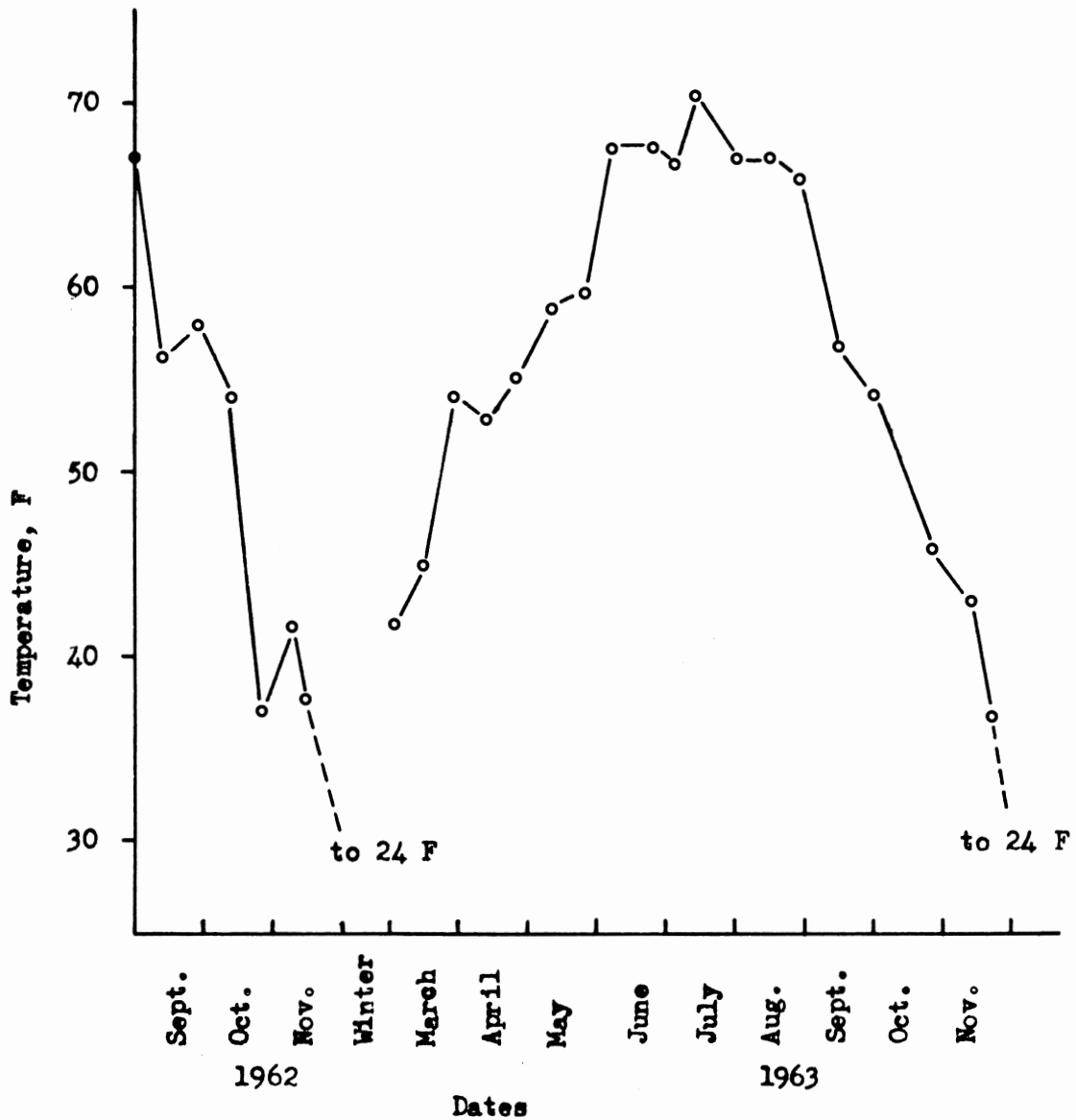


FIG. 18. Seasonal temperatures (14-day means of minimum and maximum) taken five feet above the soil at Blacksburg.

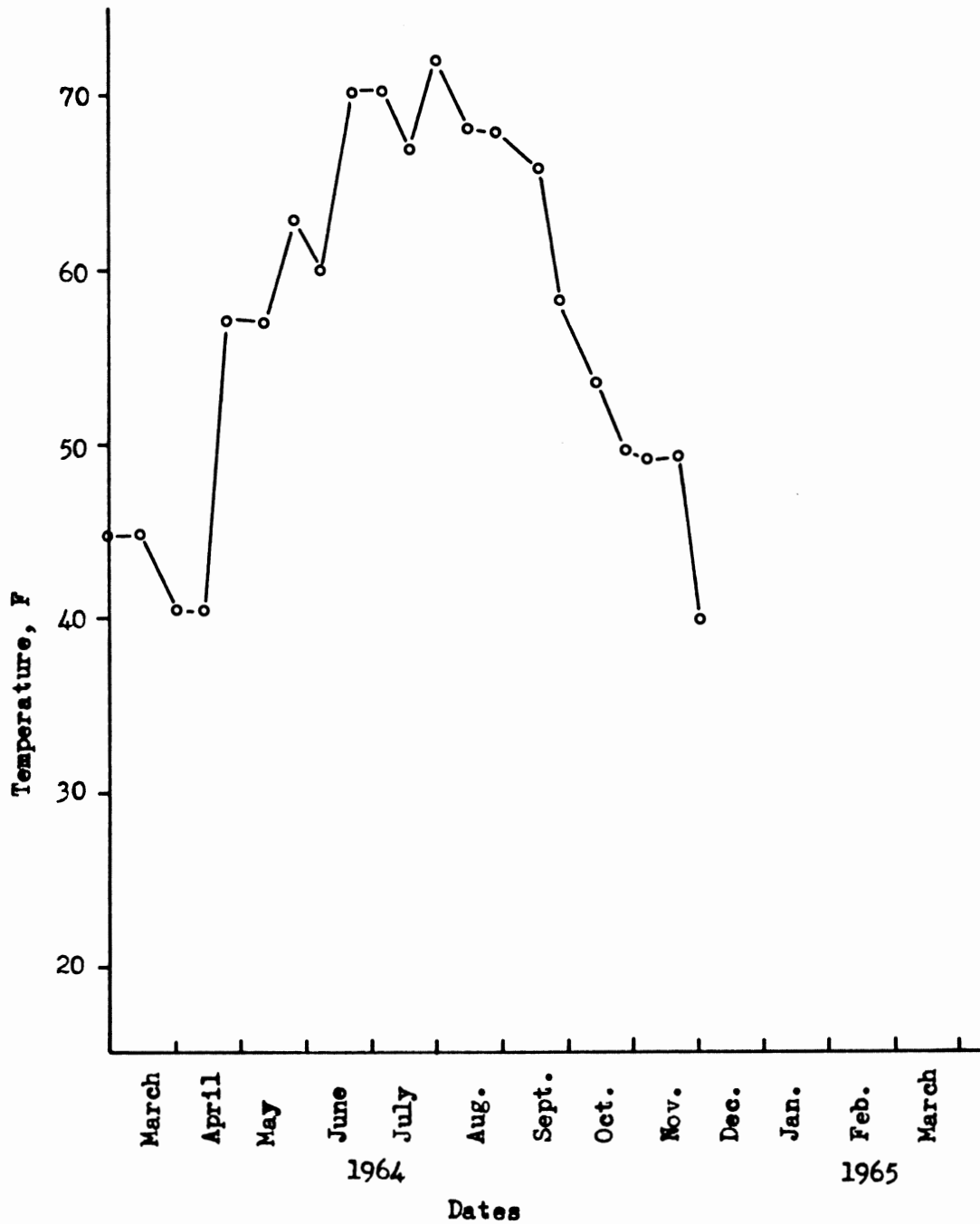


FIG. 19. Seasonal temperatures (14-day means of minimum and maximum) taken five feet above the sod at Blacksburg.

Bermudagrass:

The slow decline of AEC in bermudagrass during winter dormancy is attributed to slow respiration and little or no CO<sub>2</sub> synthesis by the frosted foliage. The rapid decline of carbohydrates during spring may be attributed to rapid energy utilization for metabolism in tissue formation and very low NAR because of obstruction from frosted tissue. High seasonal temperatures did not retard carbohydrate accumulation. Apparently NAR and metabolic growth processes of bermudagrass are highly efficient at high temperatures, there was a net accumulation of greater energy. Murata and Iyama (1963) showed that photosynthesis of bermudagrass increased rapidly as temperature increased to about 35 C then photosynthesis decreased slowly as temperature was further raised.

The undulations in AEC and polysaccharides in stolons during the summer may be attributed to growth variation caused by mowing schedule, soil moisture, and nutrient absorption. The highest AEC accumulation occurred during fall as temperatures decreased (Fig. 20). The increase is possibly associated with reduced growth (low energy requirements) and a relatively high NAR. The decrease in AEC and polysaccharides and the increase of monosaccharides of bermudagrass during the winter indicates hydrolysis of polysaccharides during the dormant period.

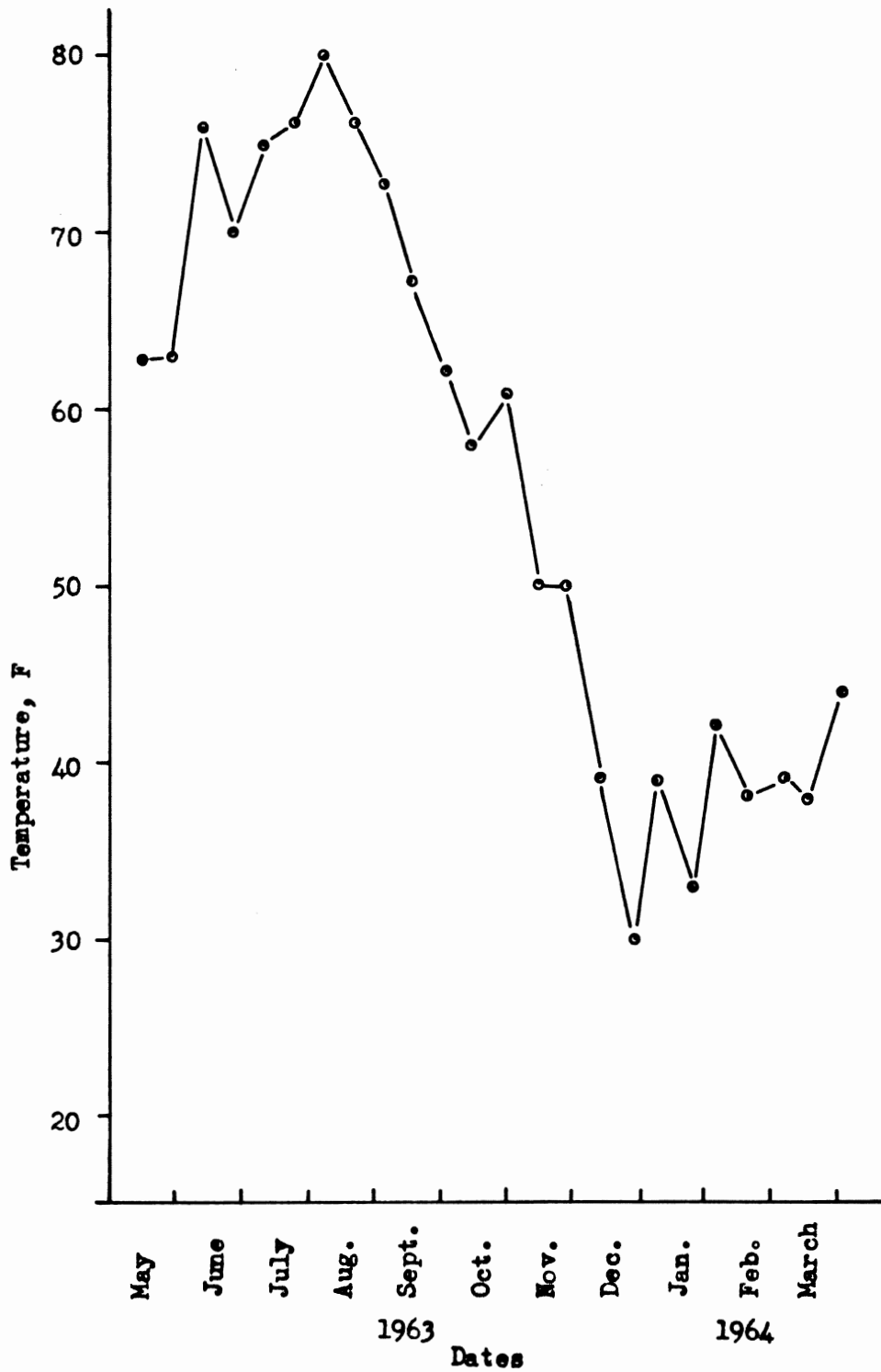


FIG. 20. Seasonal temperatures (14-day means of minimum and maximum) taken five feet above the sod at Richmond.

## GENERAL DISCUSSION

Carbohydrates were consistently lowered in both grasses with high N fertilization. This may be attributed to the larger energy demand caused by stimulated respiration and top growth, requiring more energy than was supplied by photosynthesis. Generally, a reduction of carbohydrates was associated with a decrease in root growth in both grasses.

Optimum temperatures for growth and NAR were lower for bentgrass than for bermudagrass. Lowering night temperatures improved root and top growth and NAR for both grasses. Carbohydrate reserves were improved by lower night than day temperatures with bentgrass, but not for bermudagrass.

AEC in bentgrass decreased at high day temperature; whereas, bermudagrass AEC showed a tendency to increase with temperature. Largest decreases in AEC of bermudagrass occurred when the grass was switched to medium or high temperatures after a period of low temperatures.

The monosaccharides and oligosaccharides of bermudagrass made up a relatively small percentage of the AEC, whereas a large percentage of the AEC in bentgrass consisted of monosaccharides and oligosaccharides. Possibly because of the high percentage of simple sugars in bentgrass, AEC was influenced more readily than in bermudagrass by environmental factors.

Low light intensity lowered NAR which caused top growth, root weight, and carbohydrates to be lowered and total nitrogen to be

increased in both grasses. Bentgrass was inhibited less by shade than bermudagrass.

Small differences could have been measured in the laboratory experiments with more replicates. Plugs the size of the opening of the container could have reduced border effects, increased sample size and possibly reduced variance. It may also have been desirable to clip the grass closer at shorter intervals to obtain a more uniform stress.

Carbohydrates of both grasses were high during the fall, declined during the winter in bermudagrass but not in bentgrass. Possibly, bentgrass was able to photosynthesize sufficiently to replenish utilized carbohydrates during the winter, but dormant bermudagrass was not. The lowest carbohydrate content of both grasses occurred after early spring growth. Carbohydrates in bermudagrass gradually increased throughout the summer months, but in bentgrass they remained low.

Obtaining root weights periodically and weighing the clippings taken from the field plots could have been useful in correlating growth with carbohydrate variations. Also, more frequent sampling for carbohydrates, especially during the second year, could have improved the data. Closer clipping of the field experiments at more frequent intervals could have lessened leaf area variation among treatments. Also, more precise watering management could have assured better growth control among the treatment variables.

It is difficult to associate physiological or growth functions with either total N or protein-N content. Several treatments (i.e.

bentgrass grown under low light intensity or high temperature) caused a high N content, apparently because of lowered carbohydrates. It is possible that some of the physiological changes as influenced by the various treatments could have been better determined if nitrate-N and amino-N had been measured. Accumulation of nitrate would infer inefficient nitrate reduction (Beever and Cooper, 1964b) and an accumulation of amino-N accumulation could be attributed to inefficient synthesis of protein from amino acids (Webster, 1959).

The carbohydrate status of grass is effected by a complex of interacting factors. One would not expect to find direct or reciprocal linear relationships for a single factor and carbohydrates. Monosaccharides and oligosaccharides may vary independently of the polysaccharides. For example, monosaccharides were higher and polysaccharides lower in bentgrass grown at 60 F compared to higher night temperatures. This monosaccharide increase may have been due to hydrolysis of polysaccharides, thus utilization rather than an accumulation of carbohydrates may have occurred.

Simple sugars may be of limited use when studying the physiological condition of a grass. Since monosaccharides and oligosaccharides may be utilized or synthesized into polysaccharides readily, the AEC probably gives a more accurate indication of the carbohydrate reserves of the grass. This appears so in bermudagrass, where only a small portion of the carbohydrates are simple sugars.

Carbohydrates within each grass for plant parts generally had similar trends for treatments. Therefore, it seems unnecessary to analyze all plant parts to determine the carbohydrate reserve status.

However, stolons contain larger percentages of carbohydrates than the leaves; and since it is difficult to sample and obtain sufficiently large quantities of similar age rhizomes, it is possibly sufficient to analyze stolons for carbohydrate reserves for both grasses. The nitrogen percentage of grasses is relatively low. Therefore, it seems preferable, when studying the general nitrogen metabolism of the grasses, to analyze the leaves since they contain the highest nitrogen percentage.

## SUMMARY

Two environmental control chamber experiments were conducted to study the growth behavior and some physiological effects on Tifgreen bermudagrass and Cohansey bentgrass. The variables were temperature and nitrogen rates (in the first experiment) and temperature, nitrogen rates, and light intensity (in the second experiment). Each of the grasses was included in a field experiment to study the influence of nitrogen rates on carbohydrate reserves at different seasons.

The following results were obtained for the growth chamber experiments:

Bentgrass:

Experiment I - By increasing the night:day temperatures, there were decreases in carbohydrates in leaves and stolons, root weights, and final growth rate of tops. Conversely, nitrogen content of plants and respiration increased. High nitrogen caused increased top growth, NAR, respiration, and a lowering of carbohydrates and root growth. The interrelationships of environmental factors with growth and composition were discussed. Oligosaccharides and monosaccharides made up a large portion of the AEC, with polysaccharides being the single largest fraction.

Experiment II - Yields, NAR, root growth, and respiration generally declined as night temperatures increased. AEC's were highest at the mid-temperature. Low light intensity caused decreases in yield of tops and roots, NAR, respiration, and carbohydrates; but N content of stolons increased. High nitrogen increased top growth, NAR, respiration, and N content; but reduced root yield and carbohydrates.

The more significant interrelationships of the environmental factors on growth and composition were discussed.

Bermudagrass:

Experiment I - Low temperatures inhibited top growth, root growth, respiration, NAR, and protein and total nitrogen content of leaves, stolons, and rhizomes. Carbohydrates in plant parts tended to increase with temperature, but root weights and NAR were highest at medium temperatures. The largest AEC content occurred when plants were switched from low to high temperatures.

High N rates generally caused increased top growth, NAR, respiration, and nitrogen content, but lowered carbohydrates and root growth. The interactions of the imposed variables with growth and plant constituents were discussed. Polysaccharides made up the largest portion of the AEC.

Experiment II - At a high day temperature, NAR, top growth, and root growth were highest at 75 F and lowest at 90 F night temperatures. The AEC of the stolons was highest at 90 F and lowest at 60 F night temperatures for all factorial treatments averaged. Nitrogen content was higher at 90 F night temperature than lower night temperatures.

Low light intensity decreased NAR, top growth, root growth, carbohydrates, and tended to reduce respiration. High nitrogen increased top growth, NAR, respiration, N content, but reduced root yield and carbohydrates. The interrelationships of the imposed factors with growth and grass constituents were discussed.

The following results were obtained in field experiments:

Bentgrass:

Carbohydrates of bentgrass stolons increased during the fall and early winter and declined rapidly during the spring. During the summer months the carbohydrate content was generally low and variable, increasing somewhat during early summer and generally decreasing in late summer. The possible causes of these fluctuations were discussed. Nitrogen fertilizer rates did not significantly affect the oligosaccharides or polysaccharides. However, the AEC and monosaccharides were generally decreased with high nitrogen fertilizer.

Bermudagrass:

The AEC and polysaccharides of bermudagrass stolons decreased during the spring, reached a maximum by late fall and then declined. These carbohydrates were slightly, but significantly, reduced by liberal N fertilization. The seasonal trend was discussed.

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## ABSTRACT

Two environmental control chamber experiments were conducted to study the effects of temperature, nitrogen, and light intensity on the growth and physiological effects on Tifgreen bermudagrass, Cynodon dactylon (L) Pers., and Cohansey bentgrass, Agrostis palustris Huds. Each of the grasses was included in a field experiment to study the influence of nitrogen rates on carbohydrate reserves at different seasons.

Increased temperatures with bentgrass caused decreased carbohydrates, root weights, and final growth of tops, but increased nitrogen content and respiration. NAR in bentgrass was highest at 75 F. The respiration rate, top growth, and carbohydrate content of bermudagrass tended to increase with temperature, but root weights and NAR were highest at medium temperatures. High N generally increased top growth, NAR, respiration, and nitrogen content, but lowered the carbohydrates and root growth for both grasses.

Bentgrass, grown at 95 F during the day, declined in yield, root growth, NAR, and respiration as night temperatures increased from 60 to 90 F. With bermudagrass NAR, top growth, and root growth were highest at 75 F and lowest at 90 F night temperatures. The AEC of bentgrass were highest at the mid-temperature, but the AEC for bermudagrass tended to increase with the high night temperature. Low light intensity generally decreased the yield of tops and roots, NAR, respiration, and carbohydrates, but increased the nitrogen content of both grasses.

Bentgrass stolons increased in carbohydrate content during the fall and early winter, and then declined rapidly during the spring. During the summer, the carbohydrates in bentgrass were low. The carbohydrates in bermudagrass stolons decreased during the winter and spring, increased during summer, and reached a maximum by late fall.

For all experiments the oligosaccharides and monosaccharides made up a rather large portion of the AEC in bentgrass, polysaccharides being the largest fraction. Polysaccharides in bermudagrass made up the largest fraction of the AEC, the monosaccharides and oligosaccharides being less than 10% of the dry weight.