

THE EFFECT OF CUTTING HEIGHT AND MOWING
FREQUENCY, STAGE OF DEVELOPMENT, AND REDUCED
LIGHT INTENSITY ON NET PHOTOSYNTHESIS, DARK
RESPIRATION AND DISTRIBUTION OF ^{14}C -
PHOTOSYNTHATE IN COOL SEASON TURFGRASSES.

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ABSTRACT

THE EFFECT OF CUTTING HEIGHT AND MOWING FREQUENCY, STAGE OF DEVELOPMENT, AND REDUCED LIGHT INTENSITY ON NET PHOTOSYNTHESIS DARK RESPIRATION, AND DISTRIBUTION OF ^{14}C -PHOTOSYNTHATE IN COOL SEASON TURFGRASSES

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Net photosynthesis, dark respiration, and distribution of ^{14}C -photosynthate were chosen as key parameters for determining a plant's overall physiological status. This study evaluated these physiological responses on turfgrass subjected to mowing stress, during seedling growth and development, and under reduced light intensity. It was anticipated that this information would aid in developing more effective cultural systems in turf management.

In Merion Kentucky bluegrass (*Poa pratensis* L.), lower cutting heights and increased mowing frequencies resulted in reduced root production, decreased shoot growth, increased net photosynthesis, and increased dark respiration. Enhanced accumulation of ^{14}C -photosynthate in the root and stem fractions and lower incorporation of labelled photosynthate in the leaf fractions occurred as mowing frequencies increased. The trends in net photosynthate and distribution of ^{14}C -photosynthate were attributed mainly to the relative location and proportions of assimilate supply and demand. The effect of mowing on accelerated dark respiration and defoliation of leaf area are suggested as the major contributing factors associated with

mowing stress. Proper mowing frequency (semi-weekly) and cutting height (6.25 cm) may alleviate mowing stress and improve turfgrass quality in Kentucky bluegrass.

The effects of stage of development (1 to 10 weeks after seedling emergence at weekly intervals) on net photosynthesis, dark respiration and distribution of ^{14}C -photosynthate were studied in Merion Kentucky bluegrass and Pennlawn red fescue (Festuca rubra L.). Lateral shoot development occurred after the fifth leaf stage in Kentucky bluegrass (3 to 4 weeks after seedling emergence) and after the third leaf stage in red fescue (3 weeks after seedling emergence). Tillering occurred in the axils of leaves below fully expanded leaves in both species. Tiller development preceded rhizome initiation in red fescue; whereas, tillers and rhizomes were not initiated preferentially to one another in Kentucky bluegrass. Enhanced photosynthesis, greater percent of leaf dry weight and raised dark respiration rates occurred during the initial weeks after seedling emergence (1 to 2 weeks). The percent distribution of ^{14}C -photosynthate shifted from the leaves to stems between the second and third weeks after seedling emergence in Kentucky bluegrass; whereas, this similar shift occurred between the third and fourth week after seedling emergence in red fescue. These developmental and physiological changes may signify critical changes in the developmental process.

The effects of reduced light intensity on net photosynthesis, dark respiration, root respiration, distribution of ^{14}C -photosynthate and relative rate of ^{14}C -photosynthate translocation were studied in six cool season turfgrass cultivars showing various degrees of shade tolerance. All the cultivars responded similarly to reduced light intensities in terms of net photosynthesis, dark respiration, root respiration, and relative rate of

^{14}C -photosynthate translocation. Enhanced accumulation of ^{14}C -photosynthate in the stem tissue in Nugget and A-34 Kentucky bluegrass occurred at the lowest light intensity. This response may be associated with a shade adaptive mechanism; however, further investigation is needed to elucidate this finding.

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To my wife, Kay

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TABLE OF CONTENTS

	Page
LIST OF TABLES	vi
LIST OF FIGURES	viii
INTRODUCTION	1
CHAPTER 1: THE EFFECT OF CUTTING HEIGHT AND MOWING FREQUENCY ON NET PHOTOSYNTHESIS, DARK RESPIRATION AND DIS- TRIBUTION OF ¹⁴ C-PHOTOSYNTHATE IN MERION KENTUCKY BLUEGRASS	
Abstract	4
Introduction	5
Materials and Methods	6
Results and Discussion	9
Literature Cited	15
CHAPTER 2: THE EFFECT OF STAGE OF DEVELOPMENT ON NET PHOTO- SYNTHESIS, DARK RESPIRATION AND DISTRIBUTION OF ¹⁴ C-PHOTOSYNTHATE IN MERION KENTUCKY BLUEGRASS AND PENNLAWN RED FESCUE	
Abstract	26
Introduction	27
Materials and Methods	28
Results and Discussion	29
Literature Cited	32
CHAPTER 3: THE EFFECT OF REDUCED LIGHT INTENSITY ON NET PHOTOSYNTHESIS, DARK RESPIRATION, AND DISTRI- BUTION OF ¹⁴ C-PHOTOSYNTHATE IN COOL SEASON TURFGRASSES	
Abstract	37

	Page
Introduction	38
Materials and Methods	40
Results and Discussion	43
Literature Cited	46
CONCLUSIONS	58
LIST OF REFERENCES	60

LIST OF TABLES

Table	Page
CHAPTER 1	
1. The flux of photosynthetically effective radiation in the bands $\lambda=425-475$ nm and $\lambda=650-700$ nm from a 400 watt Sylvania mercury vapor lamp (H 33)	17
2. The effect of mowing height and frequency on the distribution of dry weight in roots, stems, leaves, and rhizomes (rhiz) in Merion Kentucky bluegrass at 2, 4, and 6 weeks after treatment initiation	18
3. The effect of mowing height and frequency on net CO ₂ fixation capacity at 2, 4, and 6 weeks after clipping treatment initiation	19
4. The effect of mowing height and frequency on the number of lateral shoots in Merion Kentucky bluegrass at 2, 4, and 6 weeks after treatment initiation	20
5. The effect of mowing height and frequency on the net regrowth after mowing Merion Kentucky bluegrass at 2, 4, and 6 weeks after treatment	21
6. The effect of mowing height and frequency on net photosynthesis (P _N) and dark respiration (R _D) in Merion Kentucky bluegrass at 2, 4, and 6 weeks after treatment initiation	22
7. The effect of mowing height and frequency on the percent distribution of dry weight in roots, stems, leaves, and rhizomes (rhiz) in Merion Kentucky bluegrass at 2, 4, and 6 weeks after treatment initiation	23
8. The effects of mowing height and frequency on the percent distribution of ¹⁴ C-photosynthate in the roots, stems, leaves, and rhizomes (rhiz) in Merion Kentucky bluegrass at 2, 4, and 6 weeks after treatment initiation	24
CHAPTER 2	
1. The effect of stage of development on the percent distribution of dry weight in Merion Kentucky bluegrass and Pennlawn red fescue	34

Table	Page
2. The effect of stage of development on the net photosynthesis (P_N) and dark respiration (R_D) in Merion Kentucky bluegrass and Pennlawn red fescue	35
3. The effect of stage of development on the percent distribution of ^{14}C -photosynthate in Merion Kentucky bluegrass and Pennlawn red fescue	36
 CHAPTER 3	
1. The effect of three light intensities on the distribution of dry weight in the roots, stems, leaves, and rhizomes in six cool season turfgrasses after 8 weeks of growth at preconditioning light intensities	49
2. The effect of three light intensities on the percent distribution of dry weight in the roots, stems, leaves, and rhizomes in six cool season turfgrasses after 8 weeks of growth at preconditioning light intensities	50
3. The effect of three light intensities on the percent distribution of ^{14}C -photosynthate in the roots, stems, leaves, and rhizomes in six cool season turfgrasses after 8 weeks of growth at preconditioning light intensities	51
4. The effect of three light intensities on the relative rate of ^{14}C -photosynthate transport measured at $\frac{1}{2}$ and 2 hrs after labelling in the upper roots, lower roots, stems, and leaves in six cool season turfgrasses after 8 weeks of growth at preconditioning light intensities	52
5. The effect of three light intensities on the net photosynthetic and dark respiration rates in six cool season turfgrasses after 8 weeks of growth at preconditioning light intensities.	53
6. The effect of three light intensities on root respiration rates measured by two methods in six cool season turfgrasses after 8 weeks of growth at preconditioning light intensities.	54

LIST OF FIGURES

Figure	Page
CHAPTER 1	
1. The effect of mowing (2.5 cm cutting height) on dark respiration monitored over a 72 hr period in Merion Kentucky bluegrass	25
CHAPTER 3	
1. The relative rate of ^{14}C -assimilate translocation. (A) Plants, from left to right - Merion Kentucky bluegrass, Merion Kentucky bluegrass, Park Kentucky bluegrass, Park Kentucky bluegrass. (B) Radioautographs, from left to right - Merion Kentucky bluegrass $\frac{1}{2}$ hr after labelling, Merion Kentucky bluegrass 2 hr after labelling, Park Kentucky bluegrass $\frac{1}{2}$ hr after labelling, and Park Kentucky bluegrass 2 hr after labelling	55
2. The relative rate of ^{14}C -assimilate translocation. (A) Plants, from left to right - Nugget Kentucky bluegrass, Nugget Kentucky bluegrass, A-34 Kentucky bluegrass, A-34 Kentucky bluegrass. (B) Radioautographs, from left to right - Nugget Kentucky bluegrass $\frac{1}{2}$ hr after labelling, Nugget Kentucky bluegrass 2 hr after labelling, A-34 Kentucky bluegrass $\frac{1}{2}$ hr after labelling, and A-34 Kentucky bluegrass 2 hr after labelling	56
3. The relative rate of ^{14}C -assimilate translocation. (A) Plants, from left to right - Pennlawn red fescue, Pennlawn red fescue, Wintergreen chewings fescue, Wintergreen chewings fescue. (B) Radioautographs, from left to right - Pennlawn red fescue $\frac{1}{2}$ hr after labelling, Pennlawn red fescue 2 hr after labelling, Wintergreen chewings fescue $\frac{1}{2}$ hr after labelling, and Wintergreen chewings fescue 2 hr after labelling	57

INTRODUCTION

Net photosynthesis, dark respiration, and the distribution of photosynthate are key parameters in describing a plant's physiological status. Net photosynthetic measurements are determined by monitoring the incorporation of CO₂ into a plant system. Dark respiration measurements are determined by monitoring the evolution of CO₂ from plant leaves. The major portion of CO₂ given off by the plant results from decarboxylation reactions in the tricarboxylic acid cycle. These reactions result in reduced pyridine nucleotide (NADH and NADPH) formation which are oxidized via the electron transport chain in mitochondria to form the high energy ATP molecules. This measurement of dark respiration provides an estimation of the relative rate of energy use. Combining the rate of dark respiration with the total leaf area will provide an indication of the total energy requirements in the plant leaves. Both the photosynthetic and dark respiration measurements have been used extensively in the plant science as indicators of metabolic activity. The distribution pattern of photosynthate is directed by the relative location of assimilate demands within the plant (19). This pattern of distribution usually indicates areas of high metabolic activity associated with growth and/or assimilate storage. Monitoring these shifts in metabolic activity in the plant system is an important aspect of plant physiology.

The objectives of this investigation were to monitor net photosynthesis, dark respiration and distribution of ¹⁴C-photosynthate during mowing stress, developmental growth changes, and reduced light intensities in cool season

turfgrasses. These treatments were selected as being important management and environmental factors associated with turfgrass culture.

Mowing is the most widely used cultural practice common to all turfgrass species. Growth and morphological responses in turfgrass have been extensively investigated under mowing stress (8, 21, 22, 33). This research was designed to investigate the physiological responses of mowing stress. It is anticipated that this study will lead to more effective mowing practices. Merion Kentucky bluegrass (Poa pratensis L.) was selected for use in this study because of its wide dominant planting in the temperate climates.

Developmental changes associated with turfgrass seedling growth are important aspects of turfgrass culture. Rapid, successful turfgrass establishment is required for effective dust and erosion control. Investigation of the physiological and morphological responses associated with seedling establishment may indicate critical periods requiring intensified cultural management. Knowledge of these physiological changes may provide a greater understanding of turfgrass growth and development and lead to more effective establishment practices. Merion Kentucky bluegrass and Pennlawn red fescue (Festuca rubra L.) were selected for use in this study. Both species are widely grown in the temperate climates.

Considerable difficulty can be experienced in the culture of turfgrass under shaded conditions. Various components of the microenvironment are adversely altered under shade. An obvious and detrimental effect of shade is reduced light intensity. Red fescue has been reported as a dominant shade tolerant cool season turfgrass (8). Past investigations have shown poor shade tolerance in Kentucky bluegrass (58, 59). Recently, two cultivars of Kentucky bluegrass (Nugget and A-34) have shown excellent shade tolerance. This investigation of the physiological responses associated

with shade tolerant and intolerant cultivars of Kentucky bluegrass and fescue species may elucidate possible shade adaptive mechanisms. Knowledge of these shade adaptations may be helpful in selection of additional turfgrass varieties for use in the shade.

The research presented in this investigation was divided into three separate studies. Each study will be handled as an individual research project and will be discussed accordingly. The three areas of investigation included the effects of a) mowing stress, b) developmental changes, and c) reduced light intensity on net photosynthesis, dark respiration, and distribution of ^{14}C -photosynthate in cool season turfgrass species.

CHAPTER 1

THE EFFECT OF CUTTING HEIGHT AND MOWING FREQUENCY ON NET PHOTOSYNTHESIS, DARK RESPIRATION, AND DISTRIBUTION OF ^{14}C -PHOTOSYNTHATE IN MERION KENTUCKY BLUEGRASS (POA PRATENSIS L.)

Abstract

This study evaluated the effects of cutting height (2.5 cm, 6.25 cm, and not mowed) and mowing frequency (semi-weekly, weekly, and biweekly) on net photosynthesis, dark respiration, and distribution of ^{14}C -photosynthate in Merion Kentucky bluegrass (Poa pratensis L.). Root production declined, shoot growth decreased, net photosynthesis increased and dark respiration rates increased as mowing frequency increased and cutting heights decreased. The percent of ^{14}C -photosynthate incorporation in the root and stem fractions increased as mowing frequency increased only. The trends in photosynthesis and percent distribution of ^{14}C -photosynthate followed the relative changes in assimilate supply and demand as created by the degree of leaf defoliation. The results did not reflect on the growth responses associated with mowing stress.

The effect of accelerated dark respiration and severe defoliation of leaf area are suggested as the major contributing factors associated with mowing stress. Proper mowing frequency (>semi-weekly) and cutting height (6.25 cm) may help alleviate mowing stress and improve turfgrass quality in Kentucky bluegrass.

Introduction

Mowing is the most widely used cultural practice common to all turfgrass species. The grasses used in turfs evolved under the selective grazing pressures of animals. They adapted by developing a stem apex located near the soil and a basal type leaf growth (2). This evolutionary development does not indicate mowing is advantageous. Actually, it is detrimental due to the removal of photosynthetically active leaf tissue and frequent wounding. The loss of leaf area has been generally accepted as the major cause of mowing stress in turfs (2, 12). Wounding has been shown to significantly increase respiration in dicotyledons (9, 10, 18). However, this response has not been reported as a contributing factor relating to mowing stress. The rise in respiratory activity associated with wounded plant tissue gradually increases to a maximum within one to two days and declines thereafter to the levels originally observed before injury (19). This accelerated respiration has been prevented by actinomycin D and puromycin applications and appears to be dependent on RNA and protein synthesis (1, 22).

Numerous investigators have reported on the effects of mowing stress on various physiological, morphological, and developmental responses of turfgrasses. As mowing height is moderately lowered and mowing frequency increased, turfgrass plants exhibit reduced carbohydrate synthesis and storage (5, 6, 17); increased shoot density (11, 14, 15); decreased leaf width (12, 21); increased succulence (14); and decreased root production (7, 14, 15).

The photosynthetic-respiratory balance can be an important factor in plant survival and recuperation from stress. Madison (12) suggested that photosynthesis may be reduced during mowing stress. However, net photosynthetic

and dark respiration rates have not been reported under mowing stress differential. Photosynthate distribution patterns usually indicate sites of major metabolic activity. The pattern of distribution during mowing stress may provide a better understanding of the mechanism causing severe root reduction.

In this investigation, net photosynthesis, dark respiration, and distribution of ^{14}C -photosynthate were measured to determine the effects of cutting height and mowing frequency as mowing stress factors on turf-grass growth. In addition, the major associated morphological and growth responses were monitored.

Materials and Methods

Treatments included three cutting heights (2.5 cm, 6.25 cm, and not mowed) and three mowing frequencies (semi-weekly, weekly, and bi-weekly). Mowing frequencies were applied in a factorial design on the 2.5 and 6.25 cm mowing heights. Individual plants of Merion Kentucky bluegrass (Poa pratensis L.) were grown from seed in 5 cm diameter by 15 cm deep plastic containers filled with washed silica sand. A nutrient solution drench (8) was applied every third day and plants were irrigated with tap water on alternate days. Containers were perforated to allow free drainage. Plants were grown in an environmental growth chamber at 23 C day and 16 C night temperatures. The light radiation was $1000 \mu\text{E M}^{-2} \text{sec}^{-1}$. The relative humidity was $70 \pm 5\%$ and the photoperiod was 14 hours.

Plants were grown for 8 weeks prior to initiation of mowing treatments. This time period allowed the plants to reach a suitable level of maturity. All newly initiated tillers and rhizomes were removed at the crown surface during this initial growth period. This was done to facilitate evaluation

of the effects of mowing stress on tiller and rhizome development from a single crown. Once mowing treatments were initiated, the clippings were collected from all treatments, frozen, and freeze dried.

Photosynthesis, dark respiration, distribution of ^{14}C -photosynthate, and number of lateral shoots were measured at 2, 4, and 6 week intervals after mowing treatments were applied. These time intervals between measurements were selected to monitor the initial and prolonged effects of mowing stress. Photosynthetic and dark respiration rates were measured by monitoring the rate of change in CO_2 concentration between 270 and 330 ppm in a closed CO_2 exchange system.

This system consisted of a Beckman Model 215 infrared gas analyzer, a FMI Model RRP piston pump for air circulation, a Sargent Model SR strip chart recorder, a Drierite column, and a cylindrical assimilation chamber (internal volume 0.22 liters). The flow rate was 500 ml/min and total volume of the system was 0.313 liters. The connecting lines were constructed primarily of 0.63 cm diameter copper tubing with short lengths of tygon tubing to aid in flexibility. A 400 watt Sylvania mercury vapor lamp (Table 1) was placed above the assimilation chamber. The light was passed through a water bath to reduce heat reaching the assimilation chamber. A radiation level of $850 \mu\text{E M}^{-2} \text{sec}^{-1}$ was maintained at the plant surface. The entire system was located in a Puffer Hubbard UNI-THERM refrigerator for constant temperature ($23 \pm 1 \text{ C}$). A bulb thermometer was inserted into the chamber for monitoring temperature. Soil respiration was eliminated by flooding the container with distilled water to a depth of 0.5 to 1.0 cm above the sand surface. Photosynthetic and dark respiration rates were measured 4 hours after initiation of the light period. Dark respiration was monitored first, followed by photosynthetic measurements.

Plants were treated with 1 μCi of $^{14}\text{CO}_2$ for the purpose of measuring photosynthate distribution. Labelling was done by diverting the air stream within the CO_2 exchange system into a reaction flask containing 0.2 ml (1 μCi) of $\text{Na}^{14}\text{CO}_3$ solution ($\text{Na}^{14}\text{CO}_3$ in H_2O) reaction with 5 ml of 45% lactic acid. The $^{14}\text{CO}_2$ evolved was continually circulated around the grass leaves for 30 min during which time the plant reached its CO_2 compensation concentration. The plants were returned to the environmental growth chambers after labelling for a 24 hr period and were then harvested by washing the root system free of sand, immediately frozen, and stored. Plants were subsequently sectioned into leaf, root, stem, and rhizome fractions and freeze dried.

The leaf fraction consisted of leaf tissue located above the collar. The crown and leaf sheath were included in the stem fraction. Root segments were removed below and immediately adjacent to the crown. The rhizome fraction consisted of subsurface secondary lateral shoots that developed extravaginally and extended horizontally. Only those rhizomes which did not reach the soil surface were included in this fraction. Rhizomes which had emerged into the light and formed photosynthetically active leaves were separated into leaf and stem fractions.

Each plant segment was weighed and a sub-sample (50 to 100 mg) taken for a determination of the amount of $^{14}\text{CO}_2$ incorporation. The amount of radioactivity was measured by combusting plant samples in a sealed 1000 ml Erlenmeyer flask containing an oxygen pure atmosphere. The radioactive $^{14}\text{CO}_2$ which evolved was captured in 20 ml of ethanol-ethanolamine (2:1). A 5 ml aliquot was combined with 10 ml of scintillation solution [0.3 g of dimethyl POPOP (1,4-bis 2-(4-methyl-5-phenyloxazolyl)-benzene, 5.0 g of PPO (2,5-diphenyloxazole) per liter of toluene] and radioassayed by liquid

scintillation spectrometry. Counting efficiency was determined by channel ratios and ranged between 70 to 75%. Net radioactive incorporation was measured in disintegrations per minute (dpm).

Leaf area was determined with a LI-COR, Model LI-3000 portable area meter using a sub-sample of fresh leaf blades (5 to 10). Leaf area was measured at each treatment and sampling period. A leaf area:weight ratio was used to estimate the total leaf area.

Each mowing treatment was replicated three times in a completely randomized block design. Differences between treatment means were tested statistically using Duncan's Multiple Range Test. Orthogonal comparisons were used to statistically evaluate the main effects of mowing height and frequency.

Results and Discussion

The net distribution of dry weight in the root, stem, leaf, and rhizome fractions decreased under lower cutting heights and increased mowing frequencies (Table 2). This decrease in dry weight measured in the leaf and stem fraction is an obvious reflection of the degree of defoliation. The decline in root mass associated with the lower cutting heights and increased mowing frequencies is a well documented effect of mowing stress (7, 14, 15). Lower cutting heights and increased mowing frequencies resulted in reduced net CO₂ fixation capacity (Table 3). This relationship is mainly associated with the loss of photosynthetically active leaf area (Table 2). Reduced leaf area during mowing is generally accepted as the major cause of decreased root production (2, 12). No differences in net CO₂ fixation capacity were measured at 6 weeks after treatment initiation (6.25 cm cutting

height) as mowing frequency decreased. This trend was associated with abnormally low photosynthetic measurements resulting from excessive interleaf shading (Table 6).

Shoot density, as measured by the total number of primary and secondary lateral shoots, was greater at the 6.25 cm cutting height than the 2.5 cm or not mowed treatments (Table 4). These findings agree with reports showing stimulation of shoot density under moderate defoliation (11, 14, 15). The 2.5 cm cutting height is excessively low for Kentucky bluegrass (2) and may have inhibited shoot initiation. Vaartnou (25) showed similar restrictions in lateral shoot development in Agrostis L. when mowed excessively low. Shoot density increased at the 6.25 cm and 2.5 cm height as mowing frequency decreased at 2 and 4 weeks after treatment initiation (Table 4). However, at 6 weeks after treatment initiation, no differences were measured and a reversed numerical trend was indicated at the 6.25 cm cutting height. Madison (13) reported greater shoot density at moderate cutting heights as mowing frequency was increased in creeping bentgrass (Agrostis palustris Huds.)

Net growth after mowing increased under higher mowing heights and decreased mowing frequencies (Table 5). Similar trends in the regrowth rate following defoliation have been reported for grasses mowed at moderate heights and frequencies (11, 12, 13, 14). Madison (12) suggested that the regrowth after mowing is reduced on frequently mowed turf because of a decline in photosynthesis and attendant loss of leaf surface.

Net photosynthetic rates tended to increase as cutting heights were lowered and mowing frequencies increased (Table 6). Statistical comparisons of cutting heights pooled across mowing frequencies revealed significantly higher net photosynthetic rates in the order of 2.5 cm > 6.25 cm > not mowed for all sampling periods.

A statistical comparison of mowing frequency on net photosynthesis resulted in the semi-weekly frequency being significantly greater than the biweekly treatment both at the 2.5 cm and 6.25 cm cutting heights.

High photosynthetic rates measured at 2 and 4 (2.5 cm cutting height; semi-weekly and weekly frequencies) after treatment initiation are interpreted in terms of supply and demand for photosynthate. Reduced cutting heights and increased mowing frequencies resulted in greater proportion of sink (roots plus stems) to source (leaves) (Table 7). This relationship caused by defoliation resulted in greater assimilate demand on the photosynthetically active leaf area. Vanden Driessche (26) and Maggs (16) reported greater photosynthetic rates after partial defoliation of leaves of dicotyledons. Both attributed this response to increased assimilate demand on the remaining photosynthetic area. Thorne (23) increased net assimilation in sugar beets (Beta vulgaris) by grafting larger roots to similar tops. This increase in assimilation was interpreted as a high assimilate demand on the existing leaves. The above results (16, 23, 26) and the findings of this study suggest a "feedback" mechanism in which the demand for photosynthates regulates the rate of photosynthesis.

Lower photosynthetic rates were measured at 4 and 6 weeks after treatment initiation in grass mowed at 2.5 cm (biweekly frequency), 6.25 cm (weekly and biweekly frequencies) and not mowed treatments (Table 6). These trends in photosynthesis are attributed in part to excessive interleaf shading.

Enhanced rhizome development at the higher cutting heights and reduced frequencies indicate greater assimilate demand in these treatments. This trend may indicate higher photosynthetic measurements based on effect of

assimilate demand. However, this effect was not observed and may have been negated by excessive interleaf shading.

Photosynthetic rates appeared to decline from the second through sixth week following treatment initiations. This trend is attributed to greater interleaf shading and reduced sink to source ratios, as shoot density increased.

Dark respiration rates were higher in grass mowed at the semi-weekly frequency both at the 2.5 cm and the 6.25 cm cutting heights for all sampling periods (Table 6). This trend in respiration is associated in part to a wounding and accelerated growth response (Figure 1). Dark respiration was periodically monitored for 72 hours after mowing. Respiration rates increased more than twofold following cutting. Dark respiration reached a maximum 20 hours after cutting, declined slightly and leveled off to values noticeably greater than that measured before cutting. The initial rise in respiration (0 to 2 hrs) is attributed mainly to wound respiration. The continued rise and elevated rates thereafter may be related to enhanced lateral shoot initiation caused by defoliation. This effect of mowing turfs has not been reported previously and may be an important factor contributing to mowing stress.

A trend in reduced dark respiration rates were measured from the second to fourth sampling periods in all treatments (Table 6). This relationship may indicate an adjustment by plants to frequent wounding.

The methods used in severing the turf during mowing may influence wound respiration. A tearing or ripping of the leaf tissue (rotary mowers) may increase the wound response compared to a clean cutting action (reel mowers). This aspect of mowing requires further investigation and may be an important factor associated with cutting methods.

The relative location of assimilate demands in plant systems are attributed as the major driving force in photosynthate distribution (4). High accumulation of ^{14}C -photosynthate was measured in the root and stem fractions in plants mowed at increased frequencies (Table 8). This trend corresponded with enhanced movement of labelled photosynthate out of the leaves. An exception was at 4 weeks after treatment initiation where the stem fraction showed no significant differences among mowing frequencies. A statistical comparison of cutting heights revealed few differences in the percent distribution of ^{14}C -photosynthate within the root, stem and leaf fractions. Increased cutting frequencies resulted in a greater proportion of sink (root plus stem) to source (leaves) two weeks after treatment initiation (Table 7). This relationship caused by defoliation resulted in greater assimilate demand on the photosynthetically active leaf area. High percent incorporation of ^{14}C -photosynthate in the root and stem fraction and increased movement of labelled photosynthate out of the leaves is attributed in part to the direct effects of defoliation.

The distribution pattern of labelled photosynthate at 4 and 6 weeks after treatment initiation may be related to different rhizome development (Table 7). Increased rhizome development occurred under higher cutting heights and decreased mowing frequency. This trend results in increased assimilate demand on the leaf fraction. This relationship is suggested as the major driving force resulting in enhanced percent of ^{14}C -photosynthate movement out of the leaves. The reduction in the percent of incorporation of labelled photosynthate in the root fraction may be related to the greater sink capacity associated with rhizome development. The relationship of relative sink capacity between roots and rhizomes may indicate rhizome development occurs at the expense of root production (Table 8).

The pattern of ^{14}C -photosynthate distribution and high photosynthetic rates do not accurately reflect on the reduction in total root mass or decline in turfgrass vigor associated with excessively low cutting heights and frequent mowing. The effect of accelerated dark respiration and severe defoliation of leaf area are suggested as the major contributing factors associated with mowing stress. Proper mowing frequency (>semi-weekly) and cutting height (6.25 cm) may help alleviate mowing stress and improve turfgrass quality in Kentucky bluegrass.

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Table 1. The flux of photosynthetically effective radiation in the bands $\lambda = 425-475$ nm and $\lambda = 650-700$ nm from a 400 watt Sylvania mercury vapor lamp (H 33).

Band	Flux of radiation
nm	micro watts cm^{-2}
425-475	1221
650-700	2376

Table 2. The effect of mowing height and frequency on the distribution of dry weight in roots, stems, leaves and rhizomes (rhiz) in Merion Kentucky bluegrass at 2, 4, and 6 weeks after treatment initiation.

		Distribution of dry weight*											
		2 weeks				4 weeks				6 weeks			
Cutting height (cm)	Mowing frequency (weeks)	Roots	Stems	Leaves	Rhiz	Roots	Stems	Leaves	Rhiz	Roots	Stems	Leaves	Rhiz
		-----mg-----											
2.5	1/2	23a	22a	10	0a	29a	30a	20a	0a	64a	76a	39a	3a
	1	25a	26ab	20b	0a	37b	45b	47b	0a	74a	85a	81b	6a
	2	37b	34c	42c	0a	76c	69c	96d	5b	205b	181b	247c	30b
6.25	1/2	39bc	34c	33d	0a	75c	69c	80c	0a	220b	196bc	212c	33b
	1	44c	31bc	37cd	0a	93d	82d	121e	6b	267d	223c	244c	35b
	2	53d	45d	67e	3b	148e	125f	225g	20c	248c	269c	360d	81c
not mowed		75e	63e	81f	5b	127f	113e	187f	15c	288e	233cd	335d	83c

*Means within columns with common lettera are not significantly different at the 5% level by the Duncan's Multiple Range Test.

Table 3. The effect of mowing height and frequency on the net CO₂ fixation capacity at 2, 4, and 6 weeks after clipping treatment initiation.

Cutting height (cm)	Mowing frequency (weeks)	Net CO ₂ fixation*		
		2 weeks	4 weeks	6 weeks
2.5	1/2	362 a	633 a	939 a
	1	649 b	1090 ab	1633 b
	2	1026 c	1479 b	1984 b
6.25	1/2	733 b	1559 b	2181 b
	1	731 b	1582 b	2169 b
	2	1381 d	2589 c	2084 b
not mowed		1369 d	2340 c	2167 b

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

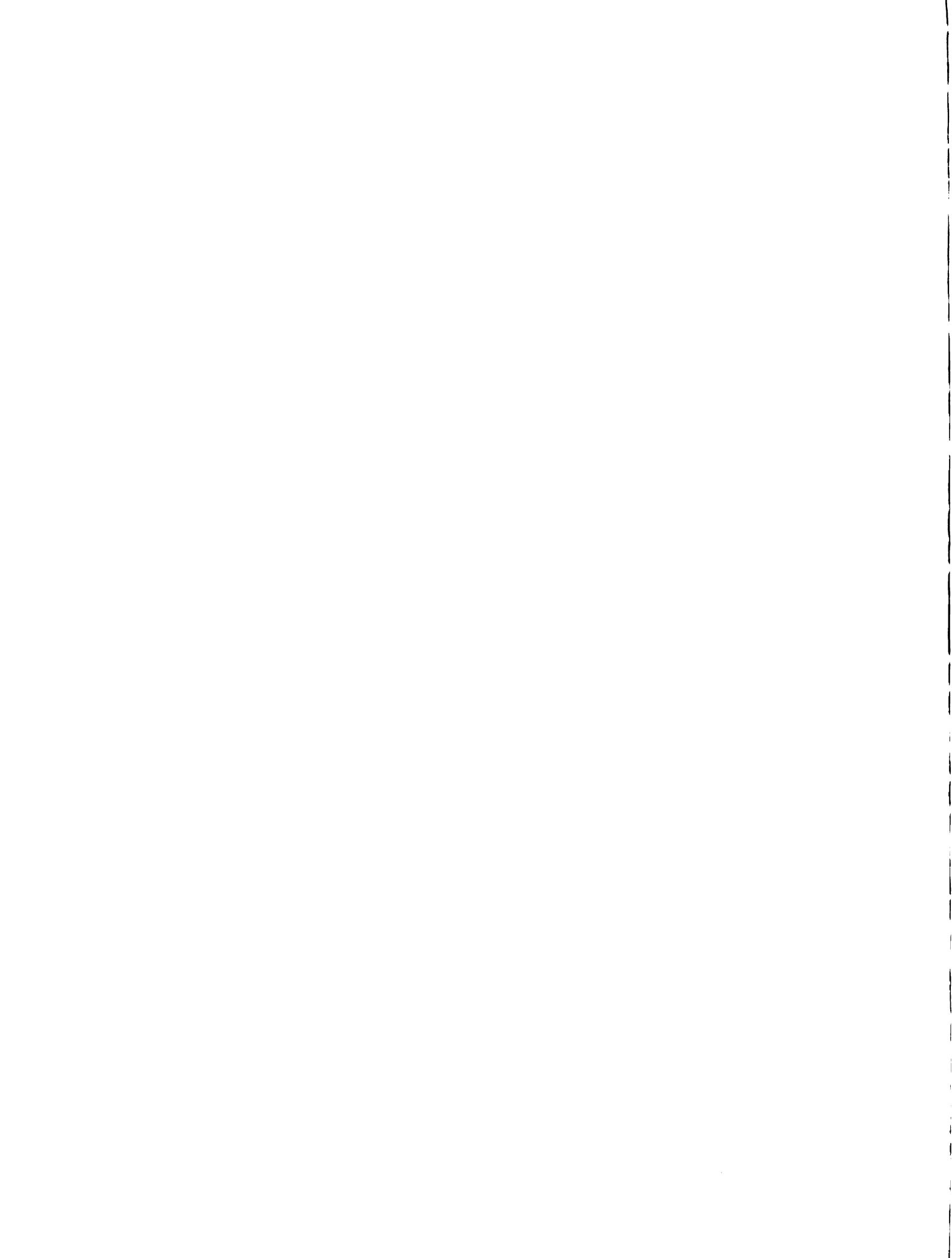


Table 4. The effect of mowing height and frequency on the number of lateral shoots in Merion Kentucky bluegrass at 2, 4, and 6 weeks after treatment initiation.

Cutting height (cm)	Mowing frequency (weeks)	Lateral shoots*/plant		
		2 weeks	4 weeks	6 weeks
2.5	1/2	5 ab	7 a	24 a
	1	5 ab	9 ab	22 a
	2	8 cd	12 b	28 ab
6.25	1/2	4 a	11 b	33 b
	1	7 bc	12 b	26 ab
	2	9 cd	16 c	28 ab
not mowed		10 d	11 b	22 a

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

Table 5. The effect of mowing and frequency on the net regrowth after mowing 'Merion' Kentucky bluegrass at 2, 4, and 6 weeks after treatment initiation.

Cutting height (cm)	Mowing frequency (weeks)	Dry Weight*		
		2 weeks	4 weeks	6 weeks
2.5	1/2	18.2 a**	32.5 a	68.7 a
	1	27.2 a	57.0 b	122.1 b
	2	45.5 b	99.5 c	247.6 c
6.25	1/2	46.6 b	102.3 c	260.0 cd
	1	42.9 b	121.1 d	285.6 d
	2	67.8 c	225.0 e	360.3 e
not mowed		81.3 d	186.6 f	335.0 e

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

**Values representing the net sum of dry weight from growth for two week intervals between sampling periods.

Table 6. The effect of mowing height and frequency on net photosynthesis (P_N) and dark respiration (R_D) in Merion Kentucky bluegrass at 2, 4, and 6 weeks after treatment initiation.

Cutting height (cm)	Mowing frequency (weeks)	P_N^*			R_D		
		2 weeks	4 weeks	6 weeks	2 weeks	4 weeks	6 weeks
-----mgCO ₂ dm ⁻² hr ⁻¹ -----							
2.5	1/2	37.2 d	31.0 c	24.3 e	16.4 c	8.1 b	9.2 c
	1	32.0 c	23.3 b	20.0 d	6.6 ab	5.6 a	4.6 a
	2	22.5 b	15.3 a	8.0 b	7.4 ab	5.8 a	4.6 a
6.25	1/2	22.0 b	19.6 b	13.6 c	8.4 b	6.5 ab	5.3 ab
	1	17.9 ab	12.9 a	8.9 b	6.6 ab	4.7 a	4.0 a
	2	20.4 ab	11.5 a	5.8 a	5.7 a	4.9 a	4.2 a
not mowed		17.0 a	12.5 a	5.0 a	5.6 a	4.7 a	3.7 a

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

Table 7. The effect of mowing height and frequency on the percent distribution of dry weight in roots, stems, leaves, and rhizomes (rhiz) in Merion Kentucky bluegrass at 2, 4, and 6 weeks after treatment initiation.

Cutting height (cm)	Mowing frequency (weeks)	Percent distribution of dry weight*											
		2 weeks			4 weeks			6 weeks					
		Roots	Stems	Leaves	Rhiz	Roots	Stems	Leaves	Rhiz	Roots	Stems	Leaves	Rhiz
2.5	1/2	42 d**	40 d	18 a	0 a	37 c	38 cd	25 a	0 a	35 c	42 e	21 a	2 a
	1	35 bc	36 c	28 b	0 a	29 a	35 c	36 bc	0 a	30 b	34 d	33 b	2 a
	2	33 ab	30 ab	37 c	0 a	28 a	26 ab	37 bc	2 b	30 b	27 abc	38 c	5 b
6.25	1/2	37 c	32 bc	31 b	0 a	34 b	30 bc	30 b	0 a	33 bc	29 c	32 b	5 b
	1	39 cd	38 cd	33 bc	0 a	31 ab	27 ab	40 cd	2 b	35 c	30 c	32 b	4 b
	2	31 a	27 a	40 d	2 a	28 a	24 a	43 d	4 c	26 a	28 bc	38 c	8 c
not mowed		34 bc	28 ab	36 c	2 a	29 a	26 ab	43 d	1 ab	31 b	25 a	36 c	7 c

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

**Values represent percent based on total dry weight.

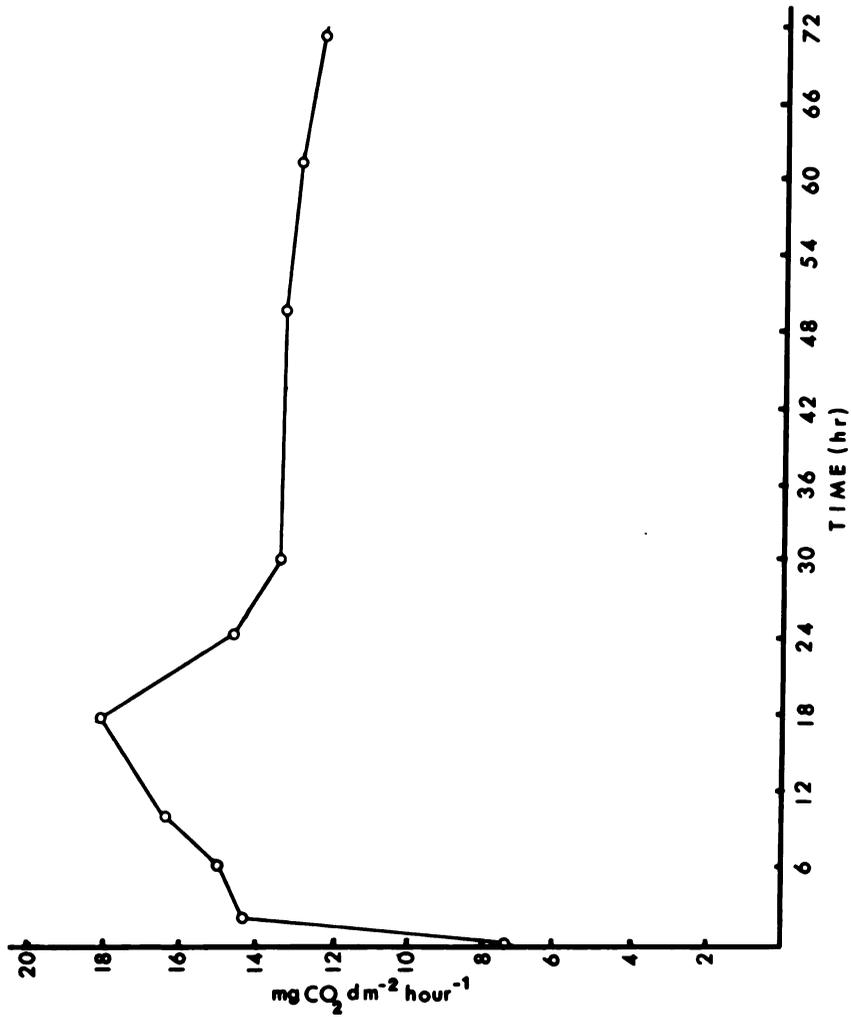
Table 8. The effects of mowing height and frequency on the percent distribution of ¹⁴C-photosynthate in the roots, stems, leaves, and rhizomes (rhiz) in Merion Kentucky bluegrass at 2, 4, and 6 weeks after treatment initiation.

		Percent distribution of ¹⁴ C-photosynthate*											
Cutting height (cm)	Mowing frequency (weeks)	2 weeks			4 weeks			6 weeks			Rhiz	Rhiz	
		Roots	Stems	Leaves	Rhiz	Roots	Stems	Leaves	Rhiz	Roots			Stems
2.5	1/2	15 ab**	63 a	22 a	0 a	19 a	52 a	29 a	0 a	17 a	56 a	26 a	1 a
	1	12 ac	52 bc	36 b	0 a	15 ab	51 a	34 b	0 a	14 ab	47 b	37 b	1 a
	2	8 d	49 b	43 c	0 a	9 d	50 a	38 bc	3 a	10 b	43 b	40 b	7 c
6.25	1/2	13 ac	54 c	33 b	0 a	18 a	53 ab	29 a	0 a	14 ab	46 b	35 b	5 bc
	1	10 cd	49 b	38 b	0 a	13 abc	48 b	37 bc	2 a	9 b	44 b	44 bc	3 b
	2	10 cd	50 b	39 bc	2 b	9 d	44 bc	38 bc	7 c	10 b	43 b	41 b	6 b
not mowed		8 d	50 b	39 b	2 b	11 cd	47 b	39 c	2 a	15 ab	40 bc	42 b	3 a

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

**Values represent the percent of total radioactivity incorporation.

Figure 1. The effect of mowing (2.5 cm cutting height) on dark respiration monitored over a 72 hr period in Merion Kentucky bluegrass.*



*Mowing treatment was initiated at 0 hrs.

**Values represent the mean of three replications.

CHAPTER 2

THE EFFECT OF STAGE OF DEVELOPMENT ON PHOTOSYNTHESIS, DARK RESPIRATION, AND DISTRIBUTION OF ^{14}C -PHOTOSYNTHATE IN MERION KENTUCKY BLUEGRASS (POA PRATENSIS L.) AND PENNLAWN RED FESCUE (FESTUCA RUBRA L.)

Abstract

The effects of stage of development on net photosynthesis, dark respiration and distribution of ^{14}C -photosynthate in Merion Kentucky bluegrass (Poa pratensis L.) and Pennlawn red fescue (Festuca rubra L.) were evaluated. Lateral shoot development occurred after the third (3 weeks after seedling emergence) and fifth leaf stage (3 to 4 weeks after seedling emergence) in Pennlawn red fescue and Merion Kentucky bluegrass, respectively. Tillers were initiated in the axils of leaves below fully expanded leaves in both species. Tiller development preceded rhizome initiation in red fescue; whereas, tillers and rhizomes were not initiated preferentially to one another in Merion Kentucky bluegrass. High dark respiration rates and a large percentage of leaf dry weight occurred at the first sampling period. The percent distribution of ^{14}C -photosynthate shifted from the leaves to stems between the second and third week after seedling emergence in Kentucky bluegrass; whereas, this shift occurred between the third and fourth week after seedling emergence in red fescue. The stem fractions were the dominant sinks for photosynthate after the second and third week following seedling emergence in Pennlawn red fescue and Merion Kentucky bluegrass, respectively.

The changes in these morphological and physiological responses during seedling growth may indicate critical developmental periods.

Introduction

Effective turfgrass management requires knowledge of the physiological and morphological changes associated with its growth and development. Rapid, successful turfgrass establishment is required for effective dust and erosion control. Delays in establishment will increase the likelihood of soil loss by erosion.

Few turfgrass investigations have described the physiological plant responses associated with growth and development. DeFrance and Simmons (7) briefly characterized the relative growth patterns of three cool season turfgrasses during seedling development. Tiller and rhizome development has been correlated with the early stages of turfgrass growth and shown to be dependent on species and environmental conditions (3, 4, 11).

The photosynthetic-respiratory balance can be a critical factor during plant growth and development. Net photosynthesis and dark respiration have been reported to vary independently from the stage of plant maturity (5, 9, 17).

Photosynthate distribution depends on assimilate supply and demand and usually reflects areas of active metabolism (5, 6, 14). Carpenter (5) measured photosynthate distribution during seedling growth in dicotyledons and reported a gradual shifting of metabolic activity from leaves to stems and finally to roots. Nyahoza (12) reported enhanced movement of photosynthate into developing rhizomes during seedling growth in Kentucky bluegrass.

The objectives of this study were to investigate the morphological and physiological changes occurring during seedling development in turfgrass. Net photosynthesis, dark respiration, and distribution of ^{14}C -photosynthate were measured in order to estimate the energy balance and monitor shifts

in metabolic activity within the plant. Plant age, leaf stage, and leaf positioning were also measured during the various phases of lateral shoot development. This information could provide insight into more effective establishment practices and an understanding of the development patterns associated with turfgrass growth.

Materials and Methods

Cultivars of Merion Kentucky bluegrass and Pennlawn red fescue were selected based on their dominant use in temperate regions. Plants of each species were grown from seed in 5 cm diameter by 15 cm deep plastic containers filled with washed silica sand and having perforated bases for free drainage. Each species was seeded at 15 to 20 seeds per pot and the seedlings thinned gradually to one plant per pot at the end of 4 weeks. The higher plant density provided sufficient plant material for accurate sub-sampling during the early growth stages. Later thinning was done to minimize competition and reduce interleaf shading during photosynthetic measurements.

The germinated seedlings were grown in an environmental growth chamber at 23 C day and 16 C night temperatures. Light radiation level was 1000 $\mu\text{E M}^{-2} \text{ sec}^{-1}$. Relative humidity ranged between 65 to 75% and the photoperiod was 14 hours. A nutrient solution drench (8) was applied every third day and plants irrigated with tap water on alternate days. Weekly clipping was initiated 4 weeks after seedling emergence at a height of 7.6 cm.

Photosynthesis, dark respiration, and distribution of ^{14}C -photosynthate were measured using methods previously described (10). The plants were returned to the environmental growth chambers after labelling for a 24 hour period. The root system was washed free of sand, immediately frozen with dry ice, and stored in a -10 C freezer. Plants were subsequently sectioned into leaf, root, stem, and rhizome fractions and freeze dried.

The leaf fraction consisted of leaf tissue located above the collar. The crown and leaf sheath were included in the stem fraction. Root segments were removed from below and immediately adjacent to the crown. The rhizome fraction consisted of subsurface secondary lateral shoots that developed extravaginally and extended horizontally. Only those rhizomes that emerged into the light and formed photosynthetically active leaf tissue were separated into leaf and stem fractions.

Leaf area measurements were made with a LI-COR, Model LI-3000 portable area meter using a subsample of fresh leaf blades (5 to 10). Measurements were taken weekly and a leaf area : leaf weight ratio was determined for calculation of total leaf area.

Each measurement was replicated three times on separate plants and a completely randomized block analysis of variance used. Differences between treatment means were tested statistically using Duncan's Multiple Range Test.

Results and Discussion

Pennlawn red fescue initiated lateral shoots only after the third leaf stage of development (approximately 3 weeks after seedling emergence). Merion Kentucky bluegrass initiated lateral shoots after the fifth leaf stage (approximately 3 to 4 weeks after seedling emergence). These results indicate that a specific level of maturity or developmental stage is required before lateral shoot development can occur. Soper (16) also reported distinct levels in maturity at which tillers were initiated in perennial ryegrass (Lolium perenne L.)

Tiller development in both species occurred only in the axils of leaves below fully expanded leaves. Similar leaf positioning has been reported in other grasses undergoing tiller development (13). Tiller development in red fescue preceded rhizome initiation in all observations. However, in Merion Kentucky bluegrass, neither tillers nor rhizomes were initiated preferentially to one another.

The percent distribution of dry weight during turfgrass seedling development is shown in Table 1. Both species showed similar distribution patterns. The percent distribution of dry weight in the root fraction tended to increase from the initial sampling to 3 weeks after seedling emergence. The leaf fraction showed enhanced percent dry weight accumulation during the first 2 weeks. This trend was followed by some slight differences, however, these variations did not follow a noticeable trend in either species. The proportion of dry weight in the stem fraction in Merion Kentucky bluegrass increased gradually from the second sampling period to the eighth week of development. The percent of stem dry weight dropped at the last sampling period and corresponds to a significant increase in rhizome growth. These changes in the percent dry weight distribution reflect inherent shifts in the developmental growth pattern. This type of information should provide a greater understanding of turfgrass growth and development.

Variations in net photosynthate and dark respiration during the ten week sampling period were similar for both species (Table 2). Higher photosynthetic rates occurred at the initial sampling period only. Dark respiration rates were accelerated 1 and 2 weeks after seedling emergence. Rates were greatest one week after emergence and declined to one-half the original level at the second sampling period. This initial acceleration in respiration may indicate a time sequence of high energy demands. Heightened photosynthetic

rate at the initial sampling period corresponded with a high percent leaf dry weight and may indicate a plant response designed for high photosynthate output.

The percent distribution of photosynthate shifted significantly from the leaves to the stems in both species (Table 3). This shift occurred between the third and fourth sampling periods in Pennlawn red fescue and second and third sampling periods in Merion Kentucky bluegrass. Rhizome development followed 1 week after and this shift in distribution may be a factor related to the initiation of secondary lateral shoot development. The percent distribution of ^{14}C -photosynthate in the root fraction declined during rhizome development in both Merion Kentucky bluegrass and Pennlawn red fescue. Rhizome development has been shown to act as a noticeably strong sink within plant systems and alters photosynthate distribution (6, 12). The relationship between rhizome development and decline in percent accumulation of photosynthate in the roots may indicate that rhizome development occurs at the expense of root growth. The stem fraction showed a high percentage of ^{14}C -photosynthate accumulation. Stem tissue has been reported as a major region of carbohydrate storage in grasses (1, 2, 15).

Proper selection of planting dates for optimal environmental growth conditions (15-20 C) and cultural practices for adequate moisture and nutrient availability during these marked changes in seedling development may be an important key to rapid and successful turfgrass establishment.

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Table 1. The effect of stage of development on the percent distribution of dry weight in Pennlawn red fescue and Merion Kentucky bluegrass.

Species	Plant Tissue	Percent distribution of dry weight*									
		1	2	3	4	5	6	7	8	10	
Pennlawn red fescue	Roots	19 a**	29 b	36 cd	33 bcd	35 cd	33 bcd	34 bcd	30 bc	32 bcd	
	Stems	24 a	18 b	18 b	21 ab	26 a	23 ab	21 ab	25 a	24 a	
	Leaves	57 a	53 a	46 b	46 b	38 c	43 bc	44 bc	44 bc	42 bc	
	Rhizomes	0 a	0 a	0 a	0 a	1 a	1 a	1 a	1 a	4 b	
Merion Kentucky bluegrass	Roots	21 a	27 b	34 c	30 bc	30 bc	35 c	32 bc	30 bc	29 bc	
	Stems	20 ab	17 a	20 ab	22 b	27 cd	28 cd	28 cd	30 d	24 bc	
	Leaves	59 a	56 a	46 b	47 b	40 c	36 c	37 c	37 c	41 c	
	Rhizomes	0 a	0 a	0 a	1 a	2 a	2 a	3 b	3 b	6 c	

* Values represent the percent dry weight based on total plant weight.

**Means within rows (across) with common letters are not significantly different at the 5% level by the Duncan's Multiple Range Test.

Table 2. The effect of stage of development on the net photosynthetic (P_N) and dark respiration (R_D) in Merion Kentucky bluegrass and Pennlawn red fescue.

Species	Plant measurement	Net photosynthesis and dark respiration*								
		1	2	3	4	5	6	7	8	10
		-----MgCO ₂ dm ⁻² hr ⁻¹ -----								
Pennlawn red fescue	P_N	41 a	23 bc	22 bc	26 b	20 bc	21 bc	20 bc	20 bc	17 c
	R_D	13 a	7 b	5 c	4 c	4 c	4 c	5 c	5 c	4 c
Merion Kentucky bluegrass	P_N	34 a	15 b	16 b	17 b	16 b	18 b	15 b	14 b	14 b
	R_D	16 a	8 b	5 c	5 c	4 c	4 c	5 c	4 c	5 c

*Means within rows (across) with common letters are not significantly different at the 5% level by the Duncan's Multiple Range Test.

Table 3. The effect of stage of development on the percent distribution of ^{14}C -photosynthate in Pennlawn red fescue and Merion Kentucky bluegrass.

		Percent distribution of ^{14}C -photosynthate*								
Species	Plant tissue	Sampling period (wk)								
		1	2	3	4	5	6	7	8	10
Pennlawn red fescue	Roots	27 a**	20 b	21 ab	19 b	16 bcd	17 bc	12 cd	10 d	10 d
	Stems	26 a	25 a	32 ab	49 bc	53 bcd	51 bc	48 bc	55 cd	59 d
	Leaves	47 a	55 b	47 a	32 de	30 de	31 de	40 cd	33 de	40 de
	Rhizomes	0 a	0 a	0 a	0 a	1 a	1 a	1 a	2 a	2 a
Merion Kentucky bluegrass	Roots	18 a	16 a	17 a	14 ab	16 a	9 c	7 c	10 bc	8 c
	Stems	20 a	22 a	50 b	50 b	53 b	51 b	51 b	51 b	47 bc
	Leaves	62 a	62 a	33 de	35 cd	30 e	36 cd	38 cd	37 cd	40 c
	Rhizomes	0 a	0 a	0 a	1 a	1 a	4 b	4 b	3 b	5 c

* Values represent the percent radioactivity based on total ^{14}C -incorporation per plant.

**Means within rows (across) with common letters are not significantly different at the 5% level by Duncan's Multiple Range Test.

CHAPTER 3

THE EFFECT OF REDUCED LIGHT INTENSITY ON NET PHOTOSYNTHESIS, DARK RESPIRATION, ROOT RESPIRATION, DISTRIBUTION OF ¹⁴C-PHOTOSYNTHATE AND RELATIVE RATE OF ¹⁴C-PHOTOSYNTHATE TRANSLOCATION IN SIX COOL SEASON TURFGRASSES

Abstract

The effects of reduced light on net photosynthesis, dark respiration, root respiration, distribution of ¹⁴C-photosynthate and relative rate of ¹⁴C-photosynthate translocation were initiated in six cool season turfgrasses showing several degrees of shade tolerance. All cultivars, except Wintergreen showed a high percentage of root dry weight at the lowest light intensity. Net photosynthetic rates declined as light intensity was decreased in all species. No significant differences in dark respiration rates occurred among cultivars as light intensities decreased. However, Pennlawn and Wintergreen tended to decline as light intensities were lowered. Root respiration rates increased as light intensity decreased in all cultivars determined with washed root samples. Nugget and A-34 showed a high percentage of ¹⁴C-photosynthate incorporation in the stem fractions and reduced movement of labelled assimilates out of the leaves. The relative rate of ¹⁴C-photosynthate translocation was variable depending on species tested.

All cultivars responded similarly or lacked definite trends at reduced light intensities in terms of net photosynthesis, dark respiration, root respiration and relative rate of ¹⁴C-photosynthate translocation. The high accumulation of ¹⁴C-photosynthate in the stem tissue in Nugget and

A-34 Kentucky bluegrass at the lowest light intensity may be associated with a shade adaptive mechanism. This study did not reveal conclusive trends or similarities between cultivars indicative of possible shade adaptive mechanisms.

Introduction

Red fescue (Festuca rubra L.) is a shade adaptive cool season turfgrass species (5, 29). Past investigations have usually reported poor shade tolerance for Kentucky bluegrass (Poa pratensis L.) (4, 29, 30). Recently, two improved cultivars of Kentucky bluegrass (Nugget and A-34) have shown excellent shade tolerance under field conditions (6).

Shade adversely alters the microenvironment for turfgrass growth and development. The most obvious effect of shade is reduced light intensity. Low light levels have been reported to reduce net photosynthesis, dark respiration, light compensation points, and light saturation levels (3, 8, 9, 10, 11, 12, 13). Higher light saturation levels and light compensation points have been used to classify plants as "sun" or "shade" species (12). Wilkinson, Beard, and Krans (30) recently investigated these responses at reduced light intensity in Pennlawn red fescue and Merion Kentucky bluegrass. They showed no significant differences in the net photosynthetic rates, light compensation points, or light saturation levels between species. However, dark respiration was significantly lower in Pennlawn compared to Merion at the lowest light level (2.7 Klux). They concluded that a more favorable photosynthetic-respiratory balance which may contribute to the persistence of Pennlawn in shade.

Root respiration rates have been shown to vary in creeping bentgrass (Agrostis palustris Huds.) depending on the strains tested and temperature (21).

The degree of root respiration may be a significant factor influencing the photosynthetic-respiratory balance. Shade adaptation of several species has been related to an improved photosynthetic-respiratory balance (11, 13).

The close interrelationship between assimilate translocation and light intensity is well established (13, 16, 24, 27, 28). Crafts (16) indicated that the influence of light on assimilate translocation is indirectly related to photosynthesis by the "supply of osmotically active solutes which drive the osmotic pumps." Hartt (17) has proposed that the translocation of assimilates is directly controlled by light which may not involve pressure flow. She (18) reported the translocation of ^{14}C -labelled assimilates to be differentially stimulated by selected spectrums of light quality. Nelson (24) showed greater transport of ^{14}C -assimilates from shoots to roots in Pinus seedling grown in full sunlight versus plants under lower light levels (6% full sunlight). This effect was not observed in plants grown at full sunlight prior to sampling at reduced light intensities. This relationship may indicate that the influence of light on translocation is indirectly related to light intensity.

Greater translocation of assimilates usually occurs during the light (15, 18, 26) period. However, investigators using different plant species showed greater movement of assimilates into the root systems during the dark (20, 23, 25) period. Brady (13) reported that the effect of reduced light intensity on the distribution of foliar applied 2,4,5-T varied depending on the species tested.

The objectives of this study were to measure net photosynthesis, dark respiration, root respiration, distribution of ^{14}C -photosynthate and relative rate of ^{14}C -photosynthate transport at reduced light intensities in shade adapted and unadapted turfgrasses. This information may further elucidate mechanisms of shade adaptation in turfgrasses and prove useful in the selection of improved turfgrasses suitable for growth in the shade.

Materials and Methods

Turfgrass cultivars used in this study were selected on the basis of evaluation trials conducted under a dense shade tree canopy at Michigan State University (6). Four turfgrass cultivars showing shade tolerance [Nugget Kentucky bluegrass, A-34 Kentucky bluegrass, Penmlawn red fescue, and Wintergreen chewings fescue (*Festuca rubra* var. *commutata* Gaud.)] and two shade intolerant cultivars (Merion Kentucky bluegrass and Park Kentucky bluegrass) were grown from seed in 5 cm diameter by 15 cm deep plastic containers filled with washed silica sand. Each cultivar was seeded at 5 plants per pot and thinned to one plant following emergence. Preconditioning light intensities of 1200, 300, and 110 $\mu\text{E M}^{-2} \text{ sec}^{-1}$ (43.0, 10.0, and 3.0 Klux, respectively) were initiated in separate growth chambers upon seedling emergence. Temperatures within growth chambers were maintained at 23 C day and 16 C night temperatures. A photoperiod of 14 hr and relative humidity of 70+5% was maintained in the growth chambers throughout the study. Plants were mowed weekly at 6.75 cm beginning at the fourth week following emergence. A nutrient solution drench (19) was applied every third day and plants irrigated with tap water on alternate days. Containers were perforated to provide free drainage.

Light intensity treatments were selected on the bases of previous research (29). Light radiation levels were measured with a Lambda LI-170 radiometer. Light treatments were established by adjusting the relative proportions of fluorescent to incandescent bulbs and raising or lowering the chamber shelves. Light quality was monitored with an ISCO Model SR spectroradiometer. Only slight differences in light quality were observed among growth chambers throughout the study. Plants were grown under each light intensity for 8 weeks prior to sampling. Variations in confounding



factors such as light quality, soil moisture, soil temperature, and disease were controlled or eliminated during the study.

Photosynthesis, dark respiration, and distribution of ^{14}C -photosynthate were measured according to methods and conditions previously described (22). Net photosynthetic rates were measured at the preconditioning light intensity. Total radioactive plant incorporation was similar among cultivars ($1\ \mu\text{Ci } ^{14}\text{C}$). The relative rates of assimilate transport were determined by monitoring the degree of radioactive movement at 0.5 and 2 hour intervals following labelling. The relative rate of translocation was determined at the lowest light level ($110\ \mu\text{E M}^{-2}\ \text{sec}^{-1}$) only. This light treatment was selected as a means of indicating possible similarities or trends among shade tolerant cultivars. Labelling ($5\ \mu\text{Ci}$ of $^{14}\text{CO}_2$ for 15 min) was conducted according to procedures previously described (22). Plants were returned to the growth chamber ($110\ \mu\text{E M}^{-2}\ \text{sec}^{-1}$) for the specified time interval (0.5 or 2 hours) before harvesting. The amount of labelled photosynthate incorporation into the root, stem, leaf, and rhizome fractions was determined by combustion methods previously described (22). The rate of photosynthate transport was also monitored by radioautography.

Plant materials were prepared for determination of distribution patterns and rate of transport of ^{14}C -photosynthate by washing the root system free of sand, immediately freezing with dry ice and storing in a $-10\ \text{C}$ freezer. Plants used for combustion analysis were separated into root, stem, leaf, and rhizome fractions and freeze dried. Plants used for determining the rate of translocation were further subdivided into an upper and lower root fraction. The upper fractions consisted of roots immediately below the crown and downward to a distance of $1/2$ the total root length. The lower fraction included the remaining roots. The leaf fraction consisted

of leaf tissue located above the collar. The crown and leaf sheath were included in the stem fraction. Root segments were removed below and immediately adjacent to the crown. The rhizome fraction consisted of subsurface secondary lateral shoots that developed extravaginally and extended horizontally. Only those rhizomes which emerged into the light and formed a photosynthetically active leaf area were separated into leaf and stem fractions.

Root respiration rates were estimated by two methods. Root respiration measurements were made on plants prior to harvesting for determining the distribution of labelled photosynthate. Plants were defoliated at the surface of the sand. The container of sand plus roots was placed in the CO₂ exchange system and the rate of CO₂ evolution monitored. Following this measurement, roots were washed from the sand. The container with sand only was allowed to drain free for 24 hours, and then placed in the CO₂ exchange system for determining the rate of CO₂ evolution. The washed roots were placed in the CO₂ exchange system and their rate of respiration measured. The rate of CO₂ evolved from the sand plus roots minus the sand provided another estimation of root respiration. Measurements of CO₂ evolution were made over a 15 min time interval for both sampling methods. The rate of CO₂ evolution was measured 3 minutes after the system was closed. This time coincided with an initial linear portion of the root respiration response.

Leaf area measurements were made with a LI-COR, Model LI-3000 portable area meter using a sub-sample (5 to 10) of fresh leaf blades. A leaf area: leaf weight ratio was determined for calculation of the total area.

Each measurement was replicated three times on separate plants and a factorial analysis of variance used. Differences between treatment

means and main effects of light intensity and cultivar were tested statistically using Duncan's Multiple Range Test.

Results and Discussion

Total dry weight accumulation in the root, stem, and leaf fractions declined as light intensity decreased in all cultivars (Table 1). No noticeable differences were measured in the stem and leaf dry weight fractions among cultivars at the three light intensities. The greater root development in both fescue cultivars may indicate a more extensive root system for nutrient and moisture uptake at reduced light intensities. Rhizome development tended to decline as light intensities decreased in all rhizomatous grasses. A-34 Kentucky bluegrass showed significantly greater rhizome development at the highest light intensity. Park and A-34 Kentucky bluegrasses showed higher total dry weight accumulation at the $1200 \mu\text{E M}^{-2}\text{sec}^{-1}$ light level compared to the other Kentucky bluegrasses. This may be related to reports indicating a rapid seedling establishment rate for Park and A-34 (6).

No consistent trends or similarities in the percent distribution of dry weight were found among species at the three light intensities in the stem and leaf fractions (Table 2). Merion, Park, and A-34 showed a high percentage of dry weight accumulation at the intermediate light intensity in the rhizome fraction. These cultivars have been shown to be vigorous sod formers (7). There were no noticeable trends in the distribution pattern of dry weight at the three light intensities between Kentucky bluegrass and fescue or among Kentucky bluegrass cultivars that would indicate a morphological response associated with a shade adaptive mechanism.

The percent distribution of ^{14}C -photosynthate did not follow consistent trends as light intensity decreased in the root, stem, and leaf fractions (Table 3). Pennlawn showed the greatest proportion of ^{14}C -photosynthate accumulation in the root fraction at the lowest light intensity. Nugget and A-34 showed a high percent incorporation of labelled photosynthate in the stem fractions at the lowest light intensity. This trend was associated with increased movement of ^{14}C -photosynthate out of the leaf fraction. The stem tissue has been shown to be dominant region of carbohydrate storage in grasses (1, 2). This relationship between the stem tissue as an area of carbohydrate storage and high assimilate accumulation at low light intensities may be a response unique to these shade tolerant cultivars.

The relative rate of ^{14}C -photosynthate transport measured at the lowest light intensity was variable depending on the cultivar tested (Table 4, Figures 1, 2, and 3). Pennlawn, Wintergreen and A-34 tended to show reduced incorporation of ^{14}C -photosynthate in the upper root fraction 1/2 hour after labelling. Nugget showed the high incorporation of ^{14}C -photosynthate into the upper root fraction 1/2 hour after labelling. Translocation of labelled photosynthate into the roots was noticeably higher in Pennlawn and Wintergreen 2 hours after labelling. The Kentucky bluegrasses showed increased translocation of ^{14}C -photosynthate into roots 2 hours after ^{14}C -labelling, however no marked similarities or differences were measured among shade tolerant and intolerant cultivars. Pennlawn showed significantly greater movement of ^{14}C -photosynthate out of the leaf fraction 2 hours after ^{14}C -labelling and was associated with an enhanced accumulation in the stem fraction. The relative rates of assimilate translocation at reduced light intensity did not reflect trends among shade tolerant or intolerant cultivars.

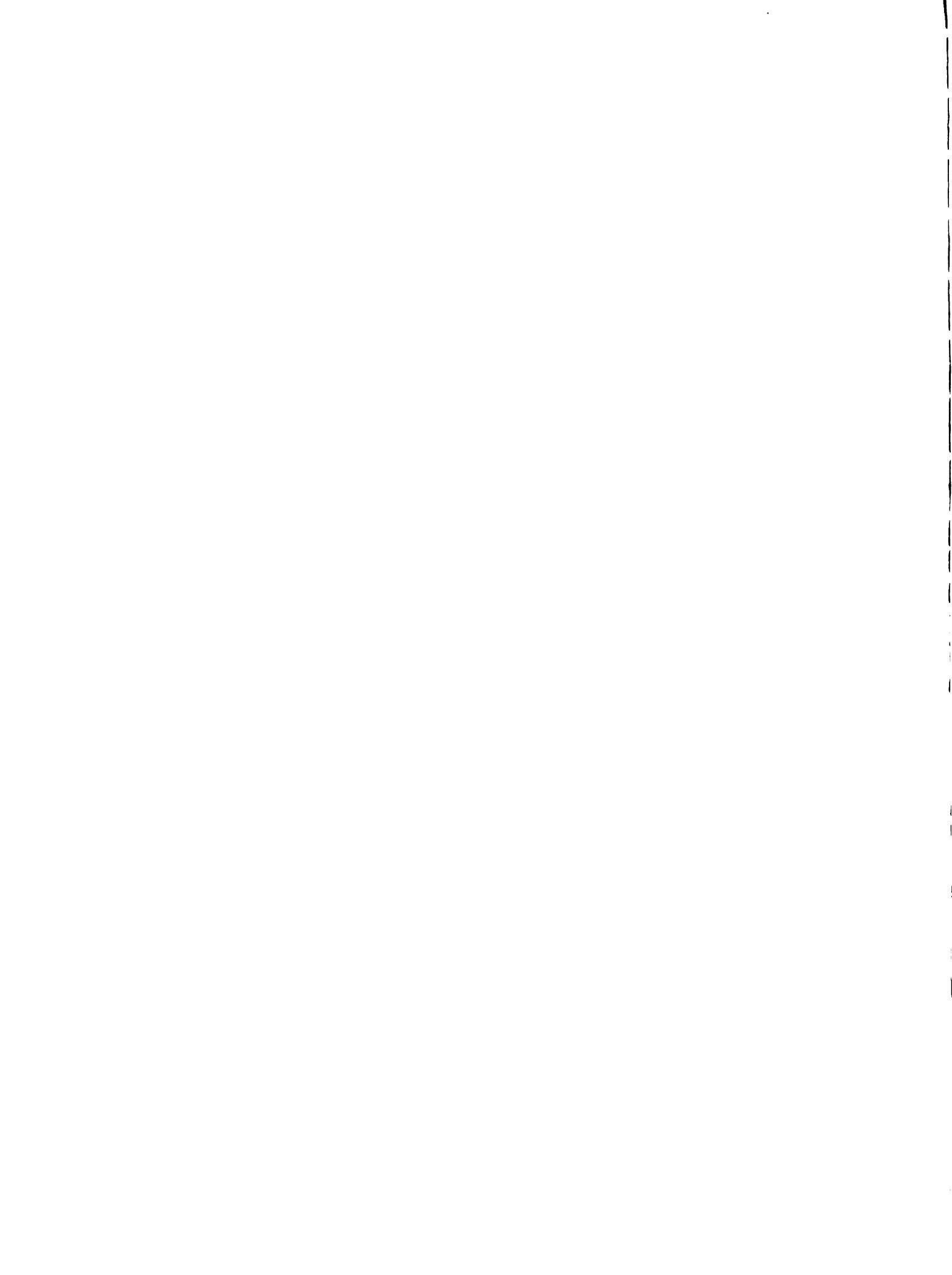
Net photosynthetic rates declined as light intensity decreased in all six cultivars; whereas, dark respiration tended to decline slightly (Table 5). Larger reductions in net photosynthesis occurred between plants grown at $1200 \mu\text{E M}^{-2} \text{ sec}^{-1}$ and $300 \mu\text{E M}^{-2} \text{ sec}^{-1}$. There were no significant differences in the net photosynthetic and dark respiration rates among shade tolerant or intolerant cultivars at the three light intensities; however, dark respiration rates tended to decline in both fescue cultivars. Wilkinson *et al.* (30) measured significant reductions in the dark respiration rates in Pennlawn at reduced light intensities for individual plants, but not in swards. This difference in dark respiration rates between swards and individual plants was in part attributed to greater CO_2 diffusion resistance in the canopy. The apparent cause of this inconsistency between studies is unknown and requires further investigation.

Root respiration rates determined with washed root samples tended to increase as light intensity decreased in all cultivars (Table 6). There were no consistent trends among cultivars in root respiration measurements taken from root plus sand samples at the three light intensities. Neither method showed differences in the root respiration among cultivars which could attribute a more favorable photosynthetic-respiratory balance.

The results of this study provides new information surrounding possible mechanisms of shade adaptation in turfgrasses. Conclusive evidence relating directly to shade tolerance was not revealed, however, specific trends were monitored which may lead to further investigations of shade adaptive mechanisms.

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Table 1. The effect of three light intensities on the distribution of dry weight in the roots, stems, leaves, and rhizomes in six cool season turfgrasses after 8 weeks of growth at preconditioning light intensities.

Cultivar	Light Radiation $\mu\text{E M}^{-2} \text{ sec}^{-1}$	Distribution of dry weight*			
		Roots	Stems	Leaves	Rhizomes
		-----Mg-----			
Merion	1200	388 d	300 ef	215 fg	12 abc
	300	213 c	166 c	120 d	27 c
	110	50 a	27 a	26 a	0 a
Park	1200	486 e	360 g	473 j	27 c
	300	110 b	93 b	97 cd	15 abc
	110	43 a	29 a	20 a	0 a
Nugget	1200	355 d	243 d	308 i	12 abc
	300	162 c	147 c	164 e	5 ab
	110	39 a	33 a	19 a	0 a
A-34	1200	490 e	432 h	272 h	91 d
	300	111 b	90 b	65 bc	23 bc
	110	56 a	41 a	24 a	0 a
Pennlawn	1200	508 e	331 fg	271 h	11 a
	300	344 d	209 d	194 ef	0 a
	110	85 ab	50 ab	28 a	0 a
Wintergreen	1200	492 e	284 e	241 gh	0 a
	300	179 c	150 c	113 d	0 a
	110	76 ab	52 ab	44 ab	0 a

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

Table 2. The effect of three light intensities on the percent distribution of dry weight in the roots, stems, leaves, and rhizomes in six cool season turfgrasses after 8 weeks of growth at preconditioning light intensities.

Cultivar	Light Radiation $\mu\text{E M}^{-2} \text{ sec}^{-1}$	Percent distribution of dry weight*			
		Roots	Stems	Leaves	Rhizomes
Merion	1200	**42 bcdefg	33 bcde	24 bc	1 a
	300	41 abcdef	31 abcde	23 bc	5 b
	110	49 gh	26 a	25 bc	0 a
Park	1200	36 abc	27 ab	35 d	2 a
	300	35 ab	29 abcd	31 d	5 b
	110	47 fgh	32 abcde	21 abc	0 a
Nugget	1200	39 abcde	27 ab	33 d	1 a
	300	34 a	30 abcd	35 d	1 a
	110	43 cdefg	37 e	21 abc	0 a
A-34	1200	38 abcd	34 cde	21 abc	7 bc
	300	39 abcde	31 abcd	23 bc	7 bc
	110	46 efgh	34 de	20 ab	0 a
Pennlawn	1200	46 efgh	30 abcd	23 bc	<1 a
	300	46 efgh	28 abc	26 c	0 a
	110	53 h	31 abcd	16 a	0 a
Wintergreen	1200	48 fgh	28 abcd	23 bc	0 a
	300	41 abcdef	34 cde	25 bc	0 a
	110	44 defg	30 abcd	25 bc	0 a

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

**Values represent the percent of the total dry weight.

Table 3. The effect of three light intensities on the percent distribution of ^{14}C -photosynthate in the roots, stems, leaves, and rhizomes in six cool season turfgrasses after 8 weeks of growth at preconditioning light intensities.

Cultivars	Light Radiation $\mu\text{E M}^{-2} \text{ sec}^{-1}$	Percent distribution of ^{14}C -photosynthate*			
		Roots	Stems	Leaves	Rhizomes
Merion	1200	28 abc**	48 efg	23 f	1 a
	300	25 a	55 gh	18 def	2 ab
	110	40 efg	49 efg	11 bc	0 a
Park	1200	44 fgh	39 abc	15 cd	2 ab
	300	30 abcd	50 fgh	15 cd	5 cd
	110	43 fgh	46 def	11 bc	0 a
Nugget	1200	27 ab	50 fgh	22 ef	1 a
	300	36 def	41 bcde	20 def	3 abc
	110	28 abc	62 i	8 a	0 a
A-34	1200	26 ab	51 fgh	19 def	4 bc
	300	35 cde	43 cdef	15 cd	7 de
	110	34 bcd	58 hi	8 a	0 a
Pennlawn	1200	45 gh	37 abc	18 def	1 a
	300	47 ghi	37 abc	14 bcd	2 ab
	110	53 i	31 a	16 cd	0 a
Wintergreen	1200	51 hi	34 ab	14 cd	0 a
	300	44 fgh	33 a	23 f	0 a
	110	40 efg	43 cdef	17 cde	0 a

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

**Values represent the percent of total radioactivity incorporated.

Table 4. The effect of three light intensities on the relative rate of ^{14}C -photosynthate transport measured at 1/2 and 2 hrs after labelling in the upper roots, lower roots, stems, and leaves in six cool season turfgrasses after 8 weeks of growth at preconditioning light intensities.

Cultivars	Translocation Period	Percent distribution of ^{14}C -photosynthate*			
		Upper Root	Lower Root	Stems	Leaves
-----%-----					
Merion	1/2	1.8 ab**	0.9 ab	15.7 bc	81.6 bcde
	2	2.0 b	1.5 abc	16.3 bcd	80.2 bcde
Park	1/2	1.7 ab	0.8 a	14.1 abc	83.4 cde
	1	3.1 c	2.0 bc	17.1 bcd	77.8 bcd
Nugget	1/2	2.4 bc	1.4 abc	16.3 bcd	79.9 bcde
	2	3.2 c	2.4 cd	21.6 de	72.8 b
A-34	1/2	1.0 a	0.6 a	12.8 ab	85.6 de
	2	2.8 bc	1.5 abc	19.7 cde	76.0 bc
Pennlawn	1/2	1.1 a	0.5 a	13.0 ab	85.4 de
	2	8.5 e	5.0 e	24.0 e	62.5 a
Wintergreen	1/2	1.2 a	0.5 a	9.5 a	88.8 e
	2	7.0 d	3.5 d	15.5 bc	74.0 b

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

**Values represent the percent of total radioactivity incorporated.

Table 5. The effect of three light intensities on the net photosynthetic and dark respiration rates in six cool season turfgrasses after 8 weeks of growth at preconditioning light intensities.

Cultivar	Radiation $\mu\text{E M}^{-2} \text{ sec}^{-1}$	Net*	Dark
		Photosynthesis ----- mgCO_2	Respiration $\text{dm}^{-2} \text{ hr}^{-1}$ -----
Merion	1200	18.4 gh	4.6 b
	300	5.2 cd	4.1 ab
	110	2.1 a	4.0 ab
Park	1200	16.5 fg	5.2 bc
	300	6.0 de	4.4 ab
	110	1.9 a	4.1 ab
Nugget	1200	17.7 fg	4.7 b
	300	4.9 c	4.3 ab
	110	2.6 ab	3.9 ab
A-34	1200	15.9 f	5.7 bc
	300	5.7 cd	4.2 ab
	110	2.3 a	4.0 ab
Pennlawn	1200	18.0 gh	4.3 ab
	300	6.0 de	3.2 a
	110	2.7 ab	3.0 a
Wintergreen	1200	17.6 fgh	4.1 ab
	300	4.8 c	3.1 a
	110	2.8 ab	2.9 a

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

Table 6. The effect of three light intensities on root respiration rates measured with washed roots in six cool season turfgrasses after 8 weeks of growth at preconditioning light intensities.

Cultivar	Light	Root respiration
	Radiation	
	$\mu\text{E M}^{-2} \text{sec}^{-1}$	$-\text{mgCO}_2 \text{ gm}^{-1} \text{hr}^{-1}$
Merion	1200	5.1 ab
	300	5.8 ab
	110	5.3 ab
Park	1200	4.3 ab
	300	6.0 ab
	110	6.5 ab
Nugget	1200	4.6 ab
	300	6.0 ab
	110	7.0 ab
A-34	1200	3.9 a
	300	7.9 b
	110	7.8 b
Pennlawn	1200	4.9 ab
	300	5.1 ab
	110	8.1 b
Wintergreen	1200	5.2 ab
	300	8.2 b
	110	8.1 b

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

(A)



(B)



Figure 1. The relative rate of ^{14}C -assimilate translocation. (A) Plants from left to right--Merion Kentucky bluegrass, Merion Kentucky bluegrass, Park Kentucky bluegrass, Park Kentucky bluegrass. (B) Radioautographs, from left to right--Merion Kentucky bluegrass 1/2 hr after ^{14}C -labelling, Merion Kentucky bluegrass 2 hr after ^{14}C -labelling, Park Kentucky bluegrass 1/2 hr after ^{14}C -labelling, and Park Kentucky bluegrass 2 hr after ^{14}C -labelling.

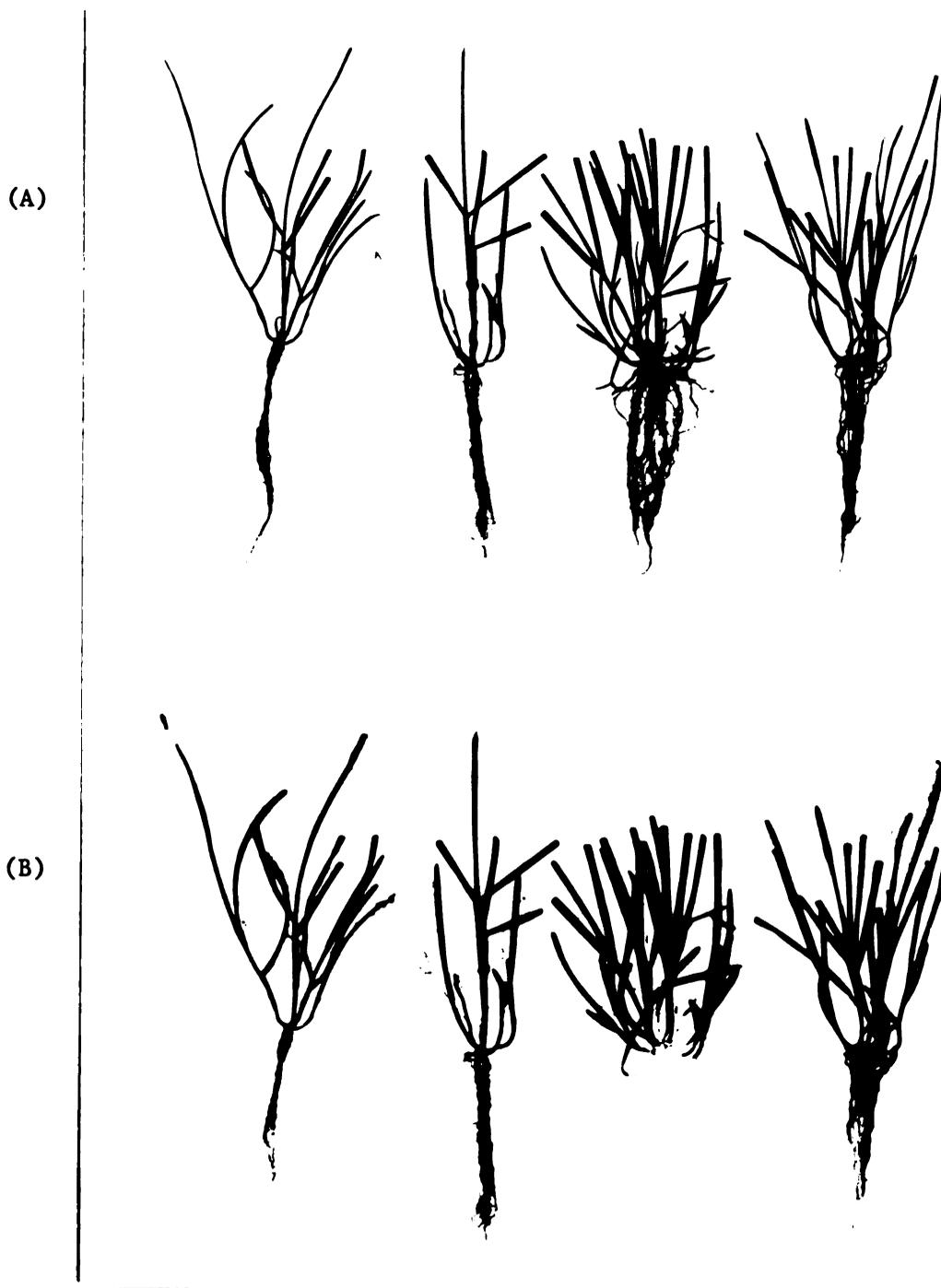


Figure 2. The relative rate of ^{14}C -assimilate translocation. (A) Plants, from left to right--Nugget Kentucky bluegrass, Nugget Kentucky bluegrass, A-34 Kentucky bluegrass, A-34 Kentucky bluegrass. (B) Radioautograph, from left to right--Nugget Kentucky bluegrass, 1/2 hr after ^{14}C -labelling, Nugget Kentucky bluegrass 2 hr after ^{14}C -labelling, A-34 Kentucky bluegrass 1/2 hr after ^{14}C -labelling, and A-34 Kentucky bluegrass 2 hr after ^{14}C -labelling.

(A)



(B)



Figure 3. The relative rate of ^{14}C -assimilate translocation. (A) Plants, from left to right--Pennlawn red fescue, Pennlawn red fescue, Wintergreen chewings fescue, Wintergreen chewings fescue. (B) Radioautographs, from left to right--Pennlawn red fescue 1/2 hr after ^{14}C -labelling, Pennlawn red fescue 2 hr after ^{14}C -labelling, Wintergreen chewings fescue 1/2 hr after ^{14}C -labelling, and Wintergreen chewings fescue 2 hr after ^{14}C -labelling.

CONCLUSIONS

1. Lower cutting heights and increased mowing frequencies resulted in reduced root production, decreased shoot growth, increased net photosynthesis, and increased dark respiration.
2. High percent incorporation of ^{14}C -photosynthate occurred in the root and stem fractions and lower accumulation of percent labelled photosynthate resulted in the leaf fraction as mowing frequencies increased.
3. High dark respiration rates were associated with a wounding respiration and accelerated lateral shoot growth.
4. The effect of mowing on accelerated dark respiration and defoliation of leaf area are suggested as the major contributing factors associated with mowing stress.
5. Lateral shoot development occurred after the third leaf stage in Kentucky bluegrass and after the fifth leaf stage in red fescue.
6. Tiller development preceded rhizome initiation in red fescue; whereas, tillers and rhizomes were not initiated preferentially to one another in Kentucky bluegrass.
7. Tillering occurred in the axils of leaves below fully expanded leaves in both species.
8. High photosynthetic rates, greater percent of leaf dry weight and high dark respiration rates occurred during the initial weeks after seedling emergence.
9. The developmental and physiological changes associated with seedling growth may signify critical changes in plant metabolism.

10. All cultivars investigated at reduced light intensities responded similarly or lacked definite trends in terms of net photosynthesis, dark respiration, root respiration and relative rate of ^{14}C -photosynthate translocation.
11. Pennlawn red fescue and Wintergreen chewings fescue tended to show a decreasing trend in dark respiration as light intensity was lowered.
12. The incorporation of ^{14}C -photosynthate was high in the stem fractions in Nugget and A-34 Kentucky bluegrass at the lowest light intensity. This trend may be associated with a shade adaptive mechanism within Kentucky bluegrasses.

The results of this investigation revealed new information concerning turf growth and development, mowing stress, and shade tolerance. Understanding these aspects of turf culture allows the turf professional to implement and adjust cultural practices to improve the level of turfgrass quality. Further investigations into these areas of research will promote the understanding and general knowledge associated with turfgrass management.

Further investigations may include: a) elucidation of wounding as a contributing factor in mowing stress; b) investigation of various environmental and nutritional factors associated with lateral shoot development; c) the significance of the shift in ^{14}C -photosynthate from the leaves to stems during seedling growth; d) investigation of the trend in reduced dark respiration as light intensities decreased in Pennlawn red fescue and Wintergreen chewings fescue; and 3) the relationship of high ^{14}C -photosynthate incorporation into the stem fraction in Nugget and A-34 Kentucky bluegrass grown under reduced light intensities to a possible shade adaptive mechanism.

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