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 eleviate 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 turfgrass 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 $\mu E\ M^{-2}\ sec^{-1}$. 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 cyclindrical 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 $\mu E\ M^{-2}\ sec^{-1}$ was maintained at the plant surface. The entire system was located in a Puffer Hubbard UNI-THERM refrigerator for constant temperature (23 ± 1 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 $^{14}CO_2$ 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 $Na^{14}CO_3$ solution ($Na^{14}CO_3$ in H_2O) reaction with 5 ml of 45% lactic acid. The $^{14}CO_2$ 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 $^{14}CO_2$ 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 $^{14}CO_2$ 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 CO_2 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 CO_2 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 attendent 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 λ = 425-475 nm and λ = 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 CO_2 fixation capacity at 2, 4, and 6 weeks after clipping treatment initiation.

Cutting height	Mowing frequency	Net CO_2 fixation*		
		2 weeks	4 weeks	6 weeks
(cm)	(weeks)	--------------- $mgCO_2\ hr^{-1}$	---------------	---------------
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	Mowing frequency	Lateral shoots*/plant		
		2 weeks	4 weeks	6 weeks
(cm)	(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.

		Dry Weight*		
Cutting height	Mowing frequency	2 weeks	4 weeks	6 weeks
(cm)	(weeks)	---mg---		
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	Mowing frequency	P_N* 2 weeks	P_N* 4 weeks	P_N* 6 weeks	R_D 2 weeks	R_D 4 weeks	R_D 6 weeks
(cm)	(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.

		Percent distribution of dry weight*											
		2 weeks				4 weeks				6 weeks			
Cutting height	Mowing frequency	Roots	Stems	Leaves	Rhiz	Roots	Stems	Leaves	Rhiz	Roots	Stems	Leaves	Rhiz
(cm)	(weeks)	%											
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.

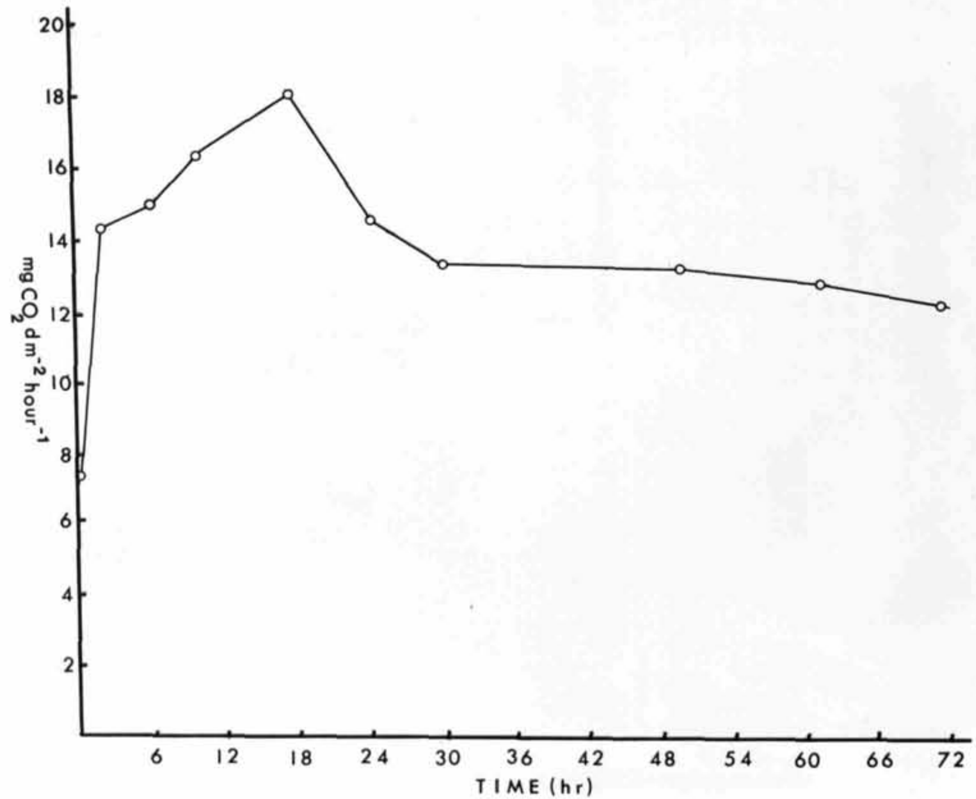
Table 8. The effects of mowing height and frequency on the percent distribution of ^{14}C-photosynthate in the roots, stems, leaves, and rhizomes (rhiz) in Merion Kentucky bluegrass at 2, 4, and 6 weeks after treatment initiation.

		Percent distribution of ^{14}C-photosynthate*											
		2 weeks				4 weeks				6 weeks			
Cutting height	Mowing frequency	Roots	Stems	Leaves	Rhiz	Roots	Stems	Leaves	Rhiz	Roots	Stems	Leaves	Rhiz
(cm)	(weeks)	%											
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.