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 14 C-photosynthate and relative rate of 14 C-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 14 C-photosynthate incorporation in the stem fractions and reduced movement of labelled assimilates out of the leaves. The relative rate of 14 C-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 14 C-photosynthate translocation. The high accumulation of 14 C-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 (<u>Festuca rubra</u> L.) is a shade adaptive cool season turfgrass species (5, 29). Past investigations have usually reported poor shade tolerance for Kentucky bluegrass (<u>Poa pratensis</u> 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 ¹⁴C-labelled assimilates to be differentially stimulated by selected spectrums of light quality. Nelson (24) showed greater transport of ¹⁴C-assimilates from shoots to roots in <u>Pinus</u> 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, Pennlawn 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 μ E M⁻² 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 μ Ci ¹⁴C). 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 $\mu E M^{-2} sec^{-1}$) only. This light treatment was selected as a means of indicating possible similarities or trends among shade tolerant cultivars. Labelling (5 μ Ci of 14 CO₂ for 15 min) was conducted according to procedures previously described (22). Plants were returned to the growth chamber (110 μ E M⁻² 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 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 CO_2 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 CO_2 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 μ E M⁻²sec⁻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 ¹⁴C-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 $^{14} ext{C-}$ 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 ¹⁴C-labelling, however no marked similarities or differences were measured among shade tolerant and intolerant cultivars. Pennlawn showed significantly greater movement of ¹⁴C-photosynthate out of the leaf fraction 2 hours after 14 C-labelling and was associated with an enhanced accumulation in the stem The relative rates of assimilate translocation at reduced light fraction. 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 respiraton tended to decline slightly (Table 5). Larger reductions in net photosynthesis occurred between plants grown at 1200 μ E M⁻² sec⁻¹ and 300 μ E M⁻² 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 <u>et al</u>. (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 CO₂ 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.

		Distribution of dry weight*				
Cultivar	Light Radiation	Roots	Stems	Leaves	Rhizomes	
	μΕ M-2 sec-1		M	[g		
Merion	1200	388 d	300 ef			
	300	213 c	166 c	120 d	27 с	
	110	50 a	27 a	26 a	0 a	
Park	1200	486 e	360 g	473 j	27 с	
	300	110 Ъ	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	
11 34	300	111 Ъ	90 Ъ	65 bc	23 bc	
	110	56 a	41 a	24 a	0 a	
Penn1awn	1200	508 e	331 fg	271 h	11 a	
I CHILDWIN	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	
wincergreen	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.

		Percen	t distributi	ion of dry	vweight*
	Light			_	
Cultivar	Radiation	Roots	Stems	Leaves	Rhizomes
	µE M-2 sec-1		%-		
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 Ъ
	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 Ъс
	110	46 efgh	34 de	20 ab	0 a
Pennlawn	1200	46 efgh	30 abcd	23 Ъс	<1 a
I CIMILAWI	300	46 efgh		26 c	0 a
	110	53 h	31 abcd	16 a	0 a
Wintergreen	1200	48 fgh	28 abcd	23 bc	0 a
ariter Precen	300	41 abcdef		25 bc	0 a
	110	44 defg		25 Ъс	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 ¹⁴C-photosynthate in the roots, stems, leaves, and rhizomes in six cool season turfgrasses after 8 weeks of growth at preconditioning light intensities.

	Ticht	<u>Percent di</u>	stribution of	ofC-pho	otosynthate
Cultivars	Light Radiation	Roots	Stems	Leaves	Rhizomes
	μE M-2 sec-1		%·		
Nomion	1200	28 aba**	48 efg	23 f	1 a
Merion	300	25 a.	55 gh		
	110	40 efg			0 a
Park	1200	44 fgh	39 abc	15 cd	2 ab
IUIK	300	30 abcd			5 cd
	110	43 fgh	-		0 a
Nugget	1200	27 ab	50 fgh	22 ef	
	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 Ъс
	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	
	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
"THEEL BLEEN	300	44 fgh		23 f	0 a
	110	40 efg	_	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 ¹⁴C-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.

		Percent distribution of ¹⁴ C-photosynthate*				
	Translocation	Upper	Lower			
Cultivars	Period	Root	Root	Stems	Leaves	
	-hr-			-%		
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 с	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 е	
	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.

		Net*	Dark
Cultivar	Radiation	Photosynthesis	Respiraton
· · · · · · · · · · · · · · · · · · ·	µЕ <u>M</u> -2 sec-1	mgCO ₂	dm-2 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
00	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
Penn1awn	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.

	Light	
Cultivar	Radiation	Root respiration
	$\mu E M^{-2} sec^{-1}$	Root respiration -mgCO ₂ gm ⁻¹ 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
00	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

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.

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

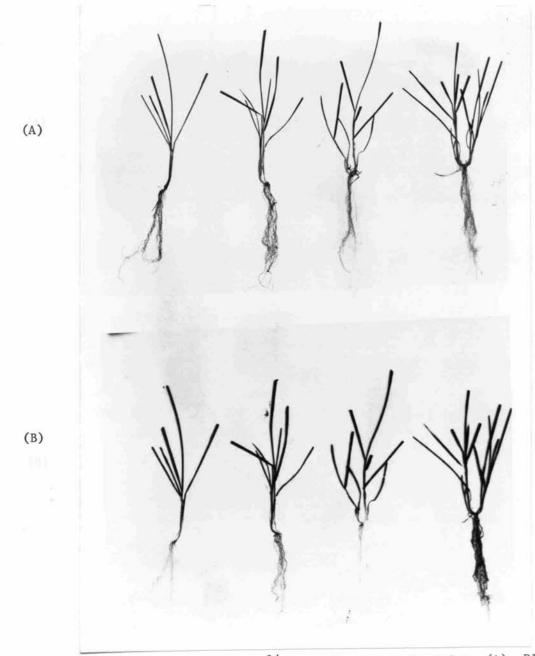
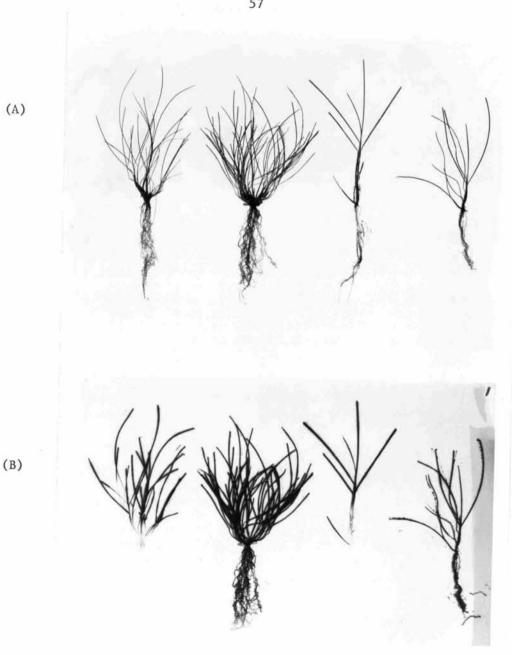


Figure 1. The relative rate of ¹⁴C-assimlate translocation. (A) Plants from left to right--Merion Kentucky bluegrass, Merion Kentucky bluegrass, Park Kentucky bluegrass, Park Kentucky bluegrass. (B) Radioautographs, from left to right--Merion Kentucky bluegrass 1/2 hr after ¹⁴C-labelling, Merion Kentucky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

56 (A) (B)

Figure 2. The relative rate of ¹⁴C-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 ¹⁴C-labelling, Nugget Kentucky bluegrass 2 hr after ¹⁴C-labelling, A-34 Kentucky bluegrass 1/2 hr after ¹⁴C-labelling, and A-34 Kentucky bluegrass 2 hr after ¹⁴C-labelling.



The relative rate of ¹⁴C-assimilate translocation. (A) Plants, Figure 3. 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 ¹⁴C-labelling, Pennlawn red fescue 2 hr after 14C-labelling, Wintergreen chewings fescue 1/2 hr after 14Clabelling, and Wintergreen chewings fescue 2 hr after 14Clabelling.