Photoassimilate Partitioning of Main Shoot Leaves in Field-Grown Spring Barley[1]

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ABSTRACT

Premature tiller mortality could conceivably limit grain yield production in barley (*Hordeum vulgare* L.). Knowing photoassimilate partitioning patterns during the vegetative development phase of growth is important for understanding the causes of tiller mortality. A field experiment was conducted to ascertain the ^{14}C translocation patterns of individual main shoot leaf blades during the pre-anthesis period for three spring barley genotypes differing in tiller production and survival. One of the top three to five leaves was labelled with $^{14}CO_2$ on each date and aboveground plant parts were harvested for determining the distribution of ^{14}C after a 24 h translocation period. Also, for two of the leaves, labelled plants were allowed to translocate until anthesis or maturity before the distribution of radioactivity was measured. Most ^{14}C fixed by the first developed leaves on the main shoot was translocated to newly emerging main shoot leaves or to young tillers. The leaf subtending and the leaf above a particular tiller preferentially exported carbon to that tiller. During the early tiller production phase of growth, proportionately more ^{14}C was translocated to tillers of the higher tillering genotypes than for the lower tillering one. During the time when tiller mortality became evident, no differences in partitioning patterns were found between the high or low tiller mortality genotypes. Later formed leaves in all genotypes provided relatively large proportions of labelled photoassimilate to the main shoot stem and inflorescence. A sharp decline in the percentage of ^{14}C translocated to all tillers occurred when the main stem began rapid growth. We conclude that the shift in main shoot photoassimilate translocation away from tillers and to the main shoot stem contributes to the premature abortion of tillers in barley.

Additional index words: **Tillering, Translocation, *Hordeum vulgare* L.**

A KNOWLEDGE of leaf photoassimilate partitioning patterns is fundamental to a comprehensive understanding of barley (*Hordeum vulgare* L.) development. Most information regarding leaf partitioning in cereals has been obtained for wheat (*Triticum aestivum* L.) grown in a phytotron or greenhouse (Quinlan and Sagar, 1962; Doodson et al., 1964; Lupton and Pinthus, 1969; Rawson and Hofstra, 1969.)

Few studies of leaf partitioning patterns have been reported for barley. Felippe and Dale (1972) measured photoassimilate movement from the first leaf on a barley plant early in crop development. Anderson and Dale (1983) further studied the short-term quantitative contribution of carbon from various sources to growth of the second, third, and fourth leaves on spring barley plants cultured in a growth room.

Carbon assimilated early in barley development is translocated preferentially to the roots and newly emerging leaves (Felippe and Dale, 1972). Research with wheat has shown that the distribution of photoassimilate from main shoot leaves to tillers is high early in development, but decreases subsequently (Quinlan and Sagar, 1962; Lupton, 1966). Within the crop canopy the lower leaves transport proportionately more photoassimilate to roots and tillers than the upper leaves. Upper leaves export photoassimilate primarily to young expanding leaves, to the stem, and to the spike (Rawson and Hofstra, 1969; Quinlan and Sagar, 1962). A portion of the leaf photoassimilate initially transported to one plant part may subsequently be redistributed to another part (Austin et al., 1977; Bidinger et al., 1977).

Leaf partitioning patterns could vary from genotype to genotype, depending on their growth habit. One characteristic which likely influences partitioning early in development is the number of tillers produced and whether they subsequently survive. Carbon translocation patterns to tillers and the presence of genotypic variability have not been previously investigated.

The objective of this study was to describe the photoassimilate partitioning patterns for specific main shoot leaves of spring barley grown in the field, with major emphasis on the period of vegetative development. Also, ascertaining the partitioning patterns of photoassimilate to specific tillers was of interest. Ultimately we desired to establish whether shifts in leaf carbon partitioning patterns might help to explain the premature mortality of tillers commonly observed in barley crop communities.

MATERIALS AND METHODS

The study was conducted in 1982 at St. Paul, MN. The barley cultivars Dickson and Manker and the experimental genotype M72-269 were planted in a randomized complete block design with six replications. Dickson and M72-269 have intermediate to high tiller production capacity, whereas Manker tillers considerably less (Simmons et al., 1982). Dickson has a much lower percent tiller survival than the

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other genotypes (Fig. 1). A preliminary study in 1981 with two genotypes (not reported here) was used to develop labelling techniques and other background information.

The Waukegan silt loam soil (fine-silty, over sandy, mixed, mesic Typic Hapludolls) on which the study was conducted was fertilized in accordance with soil test procedures in eastern Minnesota for a grain yield goal of 3.2 Mg ha^{-1}. Plots were each nine rows wide and 6 m long with 18 cm row spacings. Plant density was approximately 330 plants m^{-2}. These culture conditions approximate those used in commercial spring barley production in Minnesota. No pesticides were used, and weeds were removed by hand.

Single leaf blades on the main shoot of selected plants were exposed to $^{14}CO_2$ (37 000Bq) for 5 min in a plexiglass chamber with a Propafilm window. The chamber was connected to a pump and a test tube in which $^{14}CO_2$ was generated by adding lactic acid to $Na_2{}^{14}CO_3$ (New England Nuclear, Boston, MA)[3]. Labelling dates were spaced at 4 to 11 day intervals beginning when the main shoot apex was at the double ridge stage (about 14 days after plant emergence) and ending at early grain filling (Fig. 1). Altogether the top three to five leaf positions were exposed to $^{14}CO_2$ on any single date (one leaf labelled per plant). These represented the major leaves exporting photosynthate on each date. Labelled plants were permitted to translocate for 24 h. Export of radioactive carbon from labelled barley leaves is slow after 24 h (Anderson and Dale, 1983). Longer-term partitioning patterns were assessed by labelling the fourth and fifth leaves of Manker just after they were fully emerged (28 to 34 days after emergence). These plants were not harvested until anthesis or crop maturity.

Aboveground plant parts were harvested, immediately subdivided, and dried at 70°C. The main shoot was separated into the labelled leaf and leaf sheath, emerging leaves and sheaths, fully emerged leaves and sheaths, the main stem, and the main shoot inflorescence. Leaves were considered fully emerged if their auricles were visible. Primary tillers formed in the axils of the first, second, and third leaves on the main shoot were designated T1, T2, and T3, respectively. These tillers were the only ones to develop consistently at the plant populations used in this study. All plant parts were oxidized using a Packard Tricarb Oxidizer (Model B0306). Radioactivity was trapped using Carbosorb II and Permafluor V (Packard-Instruments, Inc., Downers Grove, IL), and quantified using a Beckman (Model LS 8000) Liquid Scintillation Counter.

Radioactivity distribution to each plant part after the translocation period was expressed as percentage of total radioactivity remaining in the aboveground portions of the plant (excluding the labelled leaf). Differential respiratory losses among the various plant parts during the translocation period could slightly influence the apparent carbon distribution patterns, but such differences were assumed to be small. Relative specific activity, as defined by Mor and Halevy (1980), is the ratio of the radioactivity distribution in a plant part to its relative dry matter contribution. Thus, relative specific activity can be used as an indicator of current growth by plant parts. A relative specific activity of one indicates that current (labelled) photoassimilate is imported by the plant part in the same relative proportion as it previously accumulated dry matter. A relative specific activity value above one for a plant part indicates accelerated carbon import relative to its previous dry matter accumulation.

[3] Mention of a vendor or proprietary products does not constitute a guarantee or a warranty of the vendor or product by the Univ. of Minnesota, and does not imply its approval to the exclusion of other vendors or products that may also be suitable.

Table 1. Yield characteristics of Dickson, Manker, and M72-269 barley in 1982.

Genotype	Grain yield†	Biological yield‡	Mass per kernel	Spikes	Kernels
	g m^{-2}		mg	no. m^{-2}	
Dickson	379	913	25	329	13 592
Manker	399	931	26	337	15 758
M72-269	389	895	24	433	16 395
$LSD_{0.05}$	NS	NS	1	55	NS

† Grain yield at 0% moisture.
‡ Biological yield = grain yield + straw yield at maturity.

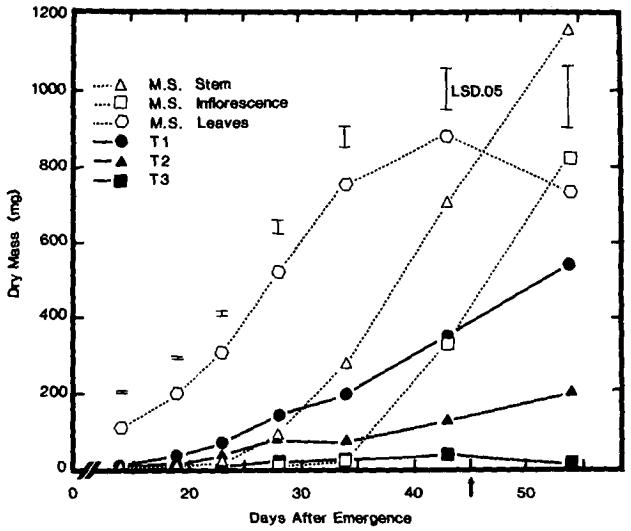

Fig. 1. Shoot production in 1982 for Dickson, Manker, and M72-269 barley. Dates of ^{14}C labelling are shown by arrows along the horizontal axis. Asterisks on shoot number curves identify anthesis dates for each genotype. Vertical bars indicate $LSD_{0.05}$.

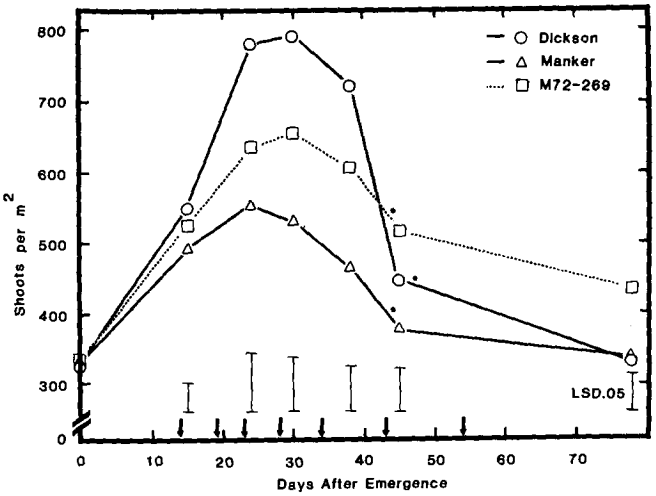

Fig. 2. Dry mass of barley main shoot stem, inflorescence, and leaves as well as the individual T1, T2, and T3 tillers during the study period. The arrow indicates the average date of anthesis for three genotypes. Vertical bars indicate $LSD_{0.05}$.

RESULTS AND DISCUSSION

Development and Performance

The genotypes each had similar grain and biological yields. The genotype M72-269 had significantly more spikes m^{-2} than the other genotypes (Table 1). This higher spike number for M72-269 was the consequence of greater tillering capacity compared with Manker and a lower tiller mortality in comparison with Dickson (Fig. 1). Manker was more advanced in development than the other genotypes and reached anthesis slightly earlier (Fig. 1).

General Partitioning Patterns

Overall, pre-anthesis main shoot leaf partitioning patterns for barley in a field community generally agree with patterns previously described for wheat (Quinlan and Sagar, 1962; Lupton, 1966; Rawson and Hofstra, 1969).

On the first three labelling dates (14 to 23 days after emergence) the emerging leaves received, on average, 54 to 59% of the exported ^{14}C (Table 2). Between 23 and 34 days after emergence the distribution of radioactivity to the younger leaves declined while that exported to the main shoot stem increased to 60%. On subsequent sampling dates the percentage of radioactivity translocated to the main shoot inflorescence increased. These partitioning patterns do not necessarily reflect changes in the absolute supply of photoassimilate available to a particular organ. They do, however, provide an indication of the qualitative, proportional distributions of photoassimilate among the various organs. Significant genotype × labelled leaf position interactions were few; thus, data in Table 2 are averaged over all three genotypes.

Shifts in radioactivity distribution to the various plant parts (Table 2) should be interpreted in relation to their corresponding mass accumulation trends (Fig. 2). Relative specific activities, shown in Table 3, help describe such relationships. As an example, consider the dry matter and average relative specific activity values for the main shoot stem (Fig. 2 and Table 3). Growth of the stem accelerated between 19 and 28 days after emergence. During this time its relative specific activity tended to increase. By about 35 days after emergence dry matter accumulation by the stem was proceeding in a linear manner. At about this time, the relative specific activity began to decline, ultimately to values not significantly different from one. Growth of tillers can be interpreted in a similar fashion. Each tiller displayed a high average relative specific activity followed by a decline as tiller dry matter accumulation accelerated (Table 3 and Fig. 2).

The mass accumulation trends shown in Fig. 2 for each tiller were different since T_2 and T_3 prematurely aborted with a greater frequency than T_1. The relative specific activity trends and peak values were, however, similar among these shoots (Table 3). The sequence of initiation of the tillers (T_1 preceding T_2 followed by T_3) is evident in their relative specific activity trends. Although T_3 never achieved the same level of dry matter accumulation as the other tillers it still displayed the same transitory, relative specific activity peak. The highest relative specific activity for each tiller occurred just after it emerged from its subtending leaf sheath.

As the proportional distribution of radioactivity to the main shoot stem rose between 19 and 34 days after emergence, the percent of radioactivity translocated to tillers declined (Table 2). This shift in partitioning occurred when awn primordia on the main shoot apex were initiated, which corresponded to the time when the main shoot stem began rapid dry matter accumulation. Thus, the onset of stem growth is pivotal in the shoot production and mortality patterns for spring barley. It occurs when later developing primary and secondary tillers are still enclosed within their subtending leaf sheaths and are heavily dependent on the main shoot for photoassimilate. Therefore, spring barley plants grown under com-

Table 2. Radioactivity distribution from individual main shoot leaves to main shoot plant parts and individual tillers at successive stages of development for barley. Values are means averaged over three genotypes.

Days after emergence	Labelled leaf position†	Plant part‡							
		EL	FEL	S	I	T1	T2	T3	AT
		% exported radioactivity							
14	1	51	4	4	–	35	3	–	41
	2	68	2	5	–	19	6	–	25
	$LSD_{0.05}$	8	1	NS	–	11	2	–	9
	Mean	59	3	5	–	27	4	–	33
19	1	56	14	6	–	18	7	0§	25
	2	50	5	7	–	15	21	1	38
	3	60	2	6	–	12	17	3	32
	$LSD_{0.05}$	8	1	NS	–	NS	7	NS	8
	Mean	55	7	6	–	15	15	1	31
23	2	45	8	11	–	18	17	10	36
	3	55	4	12	–	8	18	3	29
	4	61	2	21	–	6	7	3	17
	$LSD_{0.05}$	9	1	5	–	6	9	NS	11
	Mean	54	5	15	–	10	14	2	27
28	3	32	10	31	1	11	10	5	26
	4	47	5	35	1	6	4	1	11
	5	38	2	52	1	2	3	2	7
	$LSD_{0.05}$	8	3	9	NS	NS	NS	3	12
	Mean	39	6	40	1	6	6	3	15
34	4	14	15	49	1	9	5	7	21
	5	21	4	63	3	8	1	0	9
	6	22	2	67	6	2	0	1	3
	$LSD_{0.05}$	5	3	8	1	6	NS	1	10
	Mean	19	7	60	3	6	2	3	11
43	4/5¶	–	17	54	5	10	2	7	24
	5/6	–	10	67	7	3	1	5	16
	6/7	–	5	62	19	6	0	3	14
	7/8	–	3	50	42	1	0	2	5
	8/9	–	1	44	54	1	0	0	1
	$LSD_{0.05}$	–	3	11	6	2	2	NS	12
	Mean	–	7	55	25	4	1	3	12
54	6/7	–	4	63	19	6	4	0	13
	7/8	–	2	49	35	1	4	1	14
	8/9	–	1	26	70	1	1	0	3
	$LSD_{0.05}$	–	1	11	6	4	NS	NS	3
	Mean	–	2	46	41	2	3	0	10

† Leaves are designated numerically from the base of the plant.

‡ EL = emerging leaves; FEL = emerged leaves; S = main shoot stem; I = main shoot inflorescence; T1, T2, T3 = tillers in axils of first, second and third main shoot leaves, respectively; AT = includes all emerged primary and secondary tillers.

§ 0 indicates trace amounts of radioactivity detected (less than 0.5%).

¶ Manker produced eight leaves total and Dickson and M72-269 each formed nine. On 43 and 54 days after emergence leaves were statistically analyzed from the top leaf down.

Table 3. Relative specific activity of labelled photoassimilate from individual main shoot leaves to main shoot plant parts and individual tillers at successive stages of development for barley. Values are means averaged over three genotypes.

Days after emergence	Labelled leaf position†	Plant part‡						
		EL	FEL	S	I	T1	T2	T3
14	1	0.8	0.2	2.7	–	6.6	1.6	–
	2	1.1	0.1	3.0	–	2.4	3.7	–
	$LSD_{0.05}$	0.1	0.1	NS	–	3.4	1.7	–
	Mean	0.9	0.1	2.8	–	4.5	2.7	–
19	1	1.3	0.4	2.6	–	1.2	0.9	0.0§
	2	1.1	0.1	3.2	–	1.0	9.4	1.6
	3	1.2	0.1	2.6	–	0.7	2.5	4.1
	$LSD_{0.05}$	0.1	0.0	NS	–	0.3	NS	3.2
	Mean	1.2	0.2	2.8	–	0.9	4.3	1.9
23	2	1.4	0.2	3.3	–	0.8	2.0	1.5
	3	1.9	0.1	2.6	–	0.3	1.8	5.6
	4	1.8	0.1	3.9	–	0.3	0.8	2.6
	$LSD_{0.05}$	NS	0.0	0.9	–	0.3	NS	NS
	Mean	1.7	0.1	3.3	–	0.5	1.5	3.2
28	3	1.3	0.3	2.6	3.9	0.5	1.4	9.6
	4	1.9	0.2	3.4	4.0	0.3	0.3	4.7
	5	1.4	0.1	4.8	6.1	0.1	0.3	1.4
	$LSD_{0.05}$	0.2	0.1	0.6	NS	NS	NS	6.3
	Mean	1.5	0.2	3.6	4.7	0.3	0.7	5.2
34	4	0.7	0.5	2.1	0.4	0.5	0.4	3.8
	5	1.0	0.1	2.8	2.9	0.3	0.3	1.0
	6	1.1	0.1	2.8	4.0	0.1	0.0	0.5
	$LSD_{0.05}$	NS	0.1	0.3	0.8	0.2	NS	2.4
	Mean	0.9	0.2	2.6	2.4	0.3	0.2	1.8
43	4/5¶	–	0.5	1.7	0.3	0.6	0.4	1.6
	5/6	–	0.3	2.0	0.6	0.1	0.1	1.2
	6/7	–	0.2	1.9	1.7	0.2	0.1	0.8
	7/8	–	0.1	1.6	3.5	0.1	0.1	0.2
	8/9	–	0.0	1.4	4.2	0.0	0.0	0.1
	$LSD_{0.05}$	–	0.1	0.4	0.9	0.2	NS	NS
	Mean	–	0.2	1.7	2.1	0.2	0.1	0.8
54	6/7	–	0.3	1.7	0.7	1.0	0.8	0.2
	7/8	–	0.1	1.4	1.2	0.3	1.3	1.2
	8/9	–	0.0	0.8	3.0	0.0	0.1	0.0
	$LSD_{0.05}$	–	0.0	0.4	0.4	NS	NS	NS
	Mean	–	0.1	1.3	1.6	0.3	0.7	0.5

† Leaves are designated numerically from the base of the plant.
‡ EL = emerging leaves; FEL = emerged leaves; S = main shoot stem; I = main shoot inflorescence; T1, T2, T3 = tillers in axils of first, second and third main shoot leaves, respectively.
§ 0 indicates trace amounts of radioactivity detected (less than 0.5%).
¶ Manker produced 8 leaves total and Dickson and M72-269 each formed 9. On 43 and 54 days after emergence, leaves were statistically analyzed from the top leaf down.

mercial crop conditions undergo a period of about 2 weeks duration when competition for photoassimilate between the main shoot emerging leaves, stems, and tillers is intense. We conclude that this competition, coupled with increased shading of tillers positioned in the lower crop canopy as the main stem elongates, plays a role in premature mortality of tillers.

Leaf Partitioning Patterns

The largest proportion of radioactivity exported from a specific leaf was translocated to actively growing plant parts near that leaf (Table 2). The first developed leaves supplied photoassimilate to the newly emerging leaves on the main shoot. The first, second, and third leaves also partitioned extensively to tillers, especially T_1 and T_2. The leaves subtending and immediately above a tiller translocated their photoassimilate preferentially to that tiller. This pattern is clear for tillers T_1 and T_2. The stem received photoassimilate preferentially from leaves four through nine. The inflorescence began rapid growth 34 days after emergence (Fig. 2) and received photoassimilate preferentially from the top two to three leaves on the plant (Table 2). Individual leaves often changed their relative partitioning patterns as development progressed. For example, the proportionate amount of carbon partitioned to the stem by leaves three, four, and five became greater as stem growth increased (Table 2).

Table 4. Radioactivity distribution of Manker for labelled photoassimilate from main shoot leaves four and five after 24 h and longer-term translocation periods. Leaves four and five were the uppermost leaves at 23 and 28 days after emergence. At 34 days after emergence leaf six was the uppermost leaf.

Labelled leaf position†	Date of labelling (days after emergence)	Harvest time	Plant part‡				
			L	S	I	T1	T2
			% exported radioactivity				
4	23	Labelling + 24 h	58	35	–	2	–
		Anthesis	52	40	4	5	0§
		Maturity	52	31	12	4	5
5	28	Labelling + 24 h	34	60	2	2	2
		Anthesis	29	61	5	3	1
		Maturity	29	48	20	1	1
5	34	Labelling + 24 h	17	72	4	7	0
		Anthesis	15	77	9	0	0
		Maturity	21	65	18	2	0
$LSD_{0.05}$			5	5	3	NS	NS

† Leaves are designated numerically from the base of the plant. Manker produced a total of eight leaves.
‡ L = main shoot leaves excluding labelled leaf; S = main shoot stem; I = main shoot inflorescence; T1, T2 = tillers in axils of first and second main shoot leaves, respectively.
§ 0 indicates trace amounts of radioactivity detected (< 0.5%).

Most attention in this study has been given to translocation of ^{14}C within the initial 24 h after labelling. The proportion of radioactivity detected in the main shoot leaves, stem, or tillers after a longer-term translocation period resembled the pattern seen at 24 h (Table 4). Most radioactivity from leaves four or five was present in the stem or other leaves. Initially, less radioactivity was found in the main shoot inflorescence, but levels in this plant part became greater by maturity. This was attributed to the influence of secondary ^{14}C mobilization to the inflorescence from other organs where ^{14}C was originally translocated. The longer-term translocation patterns may also have been influenced by differences in respiratory ^{14}C losses among plant parts, although such differences were not measured and were assumed to be minor.

Genotype Partitioning Comparisons

Early in development the genotypes partitioned radioactivity similarly to various main shoot plant parts (data not shown). Beginning about 19 days after emergence, the higher tillering genotypes Dickson and M72-269 partitioned proportionately more photoassimilate to tillers than Manker (Table 5). Tillers began to show visible signs of aborting 28 days after crop emergence. However, differences in photoassimilate partitioning among genotypes at this time did not explain their differential tiller mortality characteristics.

Table 5. Radioactivity distribution from main shoot leaves to individual tillers for Dickson, Manker, and M72-269 barley at successive stages of development. Values are means averaged over all leaf positions labelled on each date.

Plant part	Genotype	Days after emergence						
		14	19	23	28	34	43	54
		% exported radioactivity						
T_1	Dickson	28	16	18	5	9	2	4
	Manker	25	11	8	8	4	6	1
	M72-269	28	18	6	6	7	5	2
	$LSD_{0.05}$	NS	5	7	NS	NS	NS	NS
T_2	Dickson	10	24	14	9	4	1	3
	Manker	1	7	14	2	2	1	0†
	M72-269	2	14	15	6	0	1	6
	$LSD_{0.05}$	5	8	NS	2	1	NS	1
T_3	Dickson	–	3	4	5	1	0	0
	Manker	–	0	1	1	6	6	0
	M72-269	–	0	2	2	2	4	1
	$LSD_{0.05}$	–	2	NS	NS	NS	NS	NS
All tillers‡	Dickson	37	43	30	18	13	4	7
	Manker	31	18	18	11	12	14	4
	M72-269	31	33	33	14	9	18	19
	$LSD_{0.05}$	NS	10	NS	NS	NS	11	13

† 0 indicates trace amounts of radioactivity detected (< 0.5%)
‡ "All tillers" includes all emerged primary and secondary tillers.

Anderson and Dale (1983) recently provided data quantifying carbon exchanges among the earlier formed leaves of barley under controlled environment conditions. Our study measured relative partitioning patterns. Absolute quantities of photoassimilate translocated from leaves to various plant parts, including tillers, during the preanthesis period in barley remain to be assessed.

ACKNOWLEDGMENTS

We thank Dr. D.C. Rasmusson for providing the genotypes used in this study, and Mr. Ken Meyers for technical assistance.

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