Photoassimilate Partitioning by Tillers and Individual Tiller Leaves in Field-Grown Spring Barley

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ABSTRACT

A large proportion of initiated tillers on field-grown barley (*Hordeum vulgare* L.) plants does not survive to bear grain. Increasing the percentage of tillers that survive has been hypothesized as an approach for increasing yield. The objective of this study was to determine photoassimilate translocation patterns of surviving and nonsurviving tillers in barley and to begin assessing the consequences of premature tiller senescence on grain yield. Field experiments were conducted in 1983 and 1984 at St. Paul, MN, on a Waukegan silt loam soil (Typic Hapludoll) using a replicated, randomized complete block design. Entire shoots, as well as individual tiller leaves, were labeled with $^{14}CO_2$ in separate experiments. Following a 24-h translocation period, the three genotypes evaluated did not differ in their fundamental tiller photoassimilate partitioning patterns. Nonsurviving tillers allocated proportionately more photoassimilate to the main shoot than surviving tillers, with the main shoot stem and emerging leaves receiving most of the photoassimilate. After onset of stem elongation, surviving tillers translocated proportionately less photoassimilate to the main shoot. During this time, the tiller stem received most of the photoassimilate fixed by a surviving tiller. From these experiments, we conclude that tillers, and especially nonsurviving tillers, may contribute appreciable quantities of current photoassimilate to the main shoot during early stem elongation, a factor that should be considered in assessing the agronomic value of tillers in barley.

Additional Index Words: **Carbon-14, *Hordeum vulgare* L., Senescence, Tiller survival, Translocation, Source-sink relations.**

THE MANNER in which cereal plants partition photoassimilate at various growth stages is a fundamental aspect of understanding plant growth and development. Photoassimilate partitioning patterns for individual leaves on main shoots of barley were previously determined (Gordon et al., 1980, 1982; Anderson and Dale, 1983; Felippe and Dale, 1972; Lauer and Simmons, 1985). Similarly, whole shoot photoassimilate partitioning patterns were studied for the main shoot and higher order tillers of greenhouse-grown (potted) barley plants (Anderson-Taylor and Marshall, 1983; Khalifa et al., 1982). However, partitioning patterns of tillers have not been reported for barley plants field-grown in a crop community. This study was undertaken to determine the partitioning patterns for individual tiller leaves and whole shoots grown under field community conditions. Since a large proportion of the tillers initiated under such conditions does not survive to produce grain-bearing spikes, an associated objective of our study was to compare photoassimilate partitioning patterns for tillers that survived with those that did not. Some researchers have hypothesized that nonsurviving tillers are counter-productive in cereals since they utilize plant and environmental resources without contributing directly to grain yield (Donald, 1968; Kirby and Jones, 1977). Thus, more detailed information on photoassimilate exchange between shoots will help to resolve this question of the agronomic contribution of nonsurviving tillers.

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MATERIALS AND METHODS

Crop Culture

The cultivars 'Dickson' and 'Morex' and the experimental genotype M72-269 were grown on a Waukegan silt loam soil at St. Paul, MN, in 1983 and 1984. Dickson and M72-269 were previously shown to have very different tiller survival properties (Simmons et al., 1982). Dickson is consistently low in tiller survival and M72-269 is high. Morex expresses intermediate tiller survival. Experiments were fertilized in accordance with soil test recommendations for a grain productivity goal of 3.2 Mg/ha. A plant population of 330 plants/m^2 was established by overseeding with subsequent thinning. Plots were 3 m long with rows 18 cm apart. No pesticides were applied to the plots, and weeds were controlled by hand cultivation.

In 1983 plots were 18 rows wide. The experiment was replicated three times in a randomized complete block design. The crop was sown on 27 April and emerged 7 May.

In 1984, the number of rows per plot was reduced to nine. This experiment was replicated four times in a randomized complete block design with a split-plot restriction on the randomization. Main plots were dates of sampling and the subplots were assigned to genotypes. The crop was sown on 17 April and emerged 3 May.

Labeling Procedures

Individual tiller leaves or whole shoots, depending on the experiment, were labeled using $^{14}CO_2$ between 1000 and 1600 h at 3- to 9-d intervals from early tillering through early grain filling. In the 1983 and 1984 experiments, radioactive CO_2 was supplied to one tiller leaf blade per plant (numbered from the base of the tiller). In a second labeling experiment in 1984, entire shoots were exposed to $^{14}CO_2$ (one shoot per plant). These were the main shoot (MS) as well as the primary tillers that formed in the axils of the first and second leaves on the MS (identified as T1 and T2, respectively).

The individual leaf or shoot was exposed to $^{14}CO_2$ in a polyethylene bag assimilation chamber (Ziploc,® Dow Chemical, Midland, MI). Attached to the outside of the bag was a vial containing $Na_2{}^{14}CO_3$ (Research Products Int., Mt. Prospect, IL) into which lactic acid (250 g lactic acid/L H_2O) was injected through a serum stopper to generate $^{14}CO_2$. After a 24-h translocation period, the aboveground parts of the labeled plants were harvested and subdivided.

In 1983, individual tiller leaf blades were exposed to 111 mBq $^{14}CO_2$ for 30 min in a 13- × 20-cm polyethylene bag assimilation chamber. The same labeling treatment was applied to three plants within each plot. Plants labeled in 1983 were predicted to have a surviving T1 and a nonsurviving T2 tiller. Labeling dates began 18 d after crop emergence

Table 1. Percentage distribution of radioactivity exported from individual barley tiller leaf blades to other plant parts at various stages of plant development in 1983. On these plants, tiller T1 survived while T2 did not. Values are averaged over three genotypes.

Days after emergence	Shoot	Labeled leaf†	Plant part: Main shoot EL‡	Main shoot FEL	Main shoot S	Main shoot I	Tiller of labeled leaf EL	Tiller of labeled leaf FEL	Tiller of labeled leaf S	Tiller of labeled leaf I	Other tillers T1	Other tillers T2	Other tillers MT
			%										
18	T1	1	15	5	3	–§	64	–	6	–	–	6	1
25	T1	1	23	8	5	–	43	11	8	–	–	2	0
	T1	2	21	7	5	–	45	6	13	–	–	2	0
	T2	1	38	7	9	–	34	–	8	–	5	–	0
	LSD (0.05)		13	NS	2	–	NS	NS	3	–	–	NS	0
33	T1	1	–	13	9	0	37	5	33	1	–	2	0
	T1	2	–	8	5	0	39	3	42	2	–	1	0
	T1	3	–	4	3	0	32	2	57	1	–	1	0
	T2	1	–	31	30	1	13	–	7	–	17	–	0
	LSD (0.05)		–	6	6	0	10	NS	8	0	–	NS	NS
40	T1	3	–	2	1	0	10	4	74	8	–	1	1
	T1	4	–	1	1	0	7	5	68	16	–	2	0
	T1	5	–	1	0	0	14	3	56	25	–	1	0
	LSD (0.05)		–	1	NS	NS	NS	NS	6	6	–	1	NS
47	T1	4	–	1	2	1	–	3	82	12	–	0	0
	T1	5	–	1	1	0	–	3	71	23	–	0	2
	T1	6	–	1	0	0	–	1	60	38	–	0	0
	LSD (0.05)		–	NS	1	NS	–	1	9	8	–	NS	NS

† Leaves are numbered acropetally from the base of the tiller.
‡ EL = emerging leaves; FEL = fully emerged leaves; S = stem; I = inflorescence; T1 = tiller formed in axil of the first leaf on main shoot; T2 = tiller formed in axil at second leaf on main shoot; MT = other primary and secondary tillers.
§ Indicates radioactivity was not measured.

Table 2. Percentage distribution of radioactivity exported from individual barley tiller leaf blades to other plant parts at various stages of crop development in 1984. On these plants both tillers T1 and T2 survived. Values are averaged over three genotypes.

Days after emergence	Shoot	Labeled leaf†	Plant part: Main shoot L‡	Main shoot S	Tiller of labeled leaf L	Tiller of labeled leaf S	Tiller of labeled leaf I	Other tillers T1	Other tillers T2
			%						
19	T1	1	13	3	69	10	–§	–	6
22	T1	1	14	4	66	11	–	–	5
		2	13	4	66	12	–	–	6
	T2	1	30	9	42	11	–	8	–
	LSD (0.05)		8	3	11	NS	–	–	NS
26	T1	1	16	3	60	15	–	–	6
		2	15	3	48	27	–	–	6
	T2	1	27	9	46	11	–	7	–
		2	25	8	44	14	–	9	–
	LSD (0.05)		NS	4	13	8	–	NS	NS
30	T1	1	36	7	33	18	–	–	6
		2	22	9	30	32	–	–	6
		3	11	6	32	46	–	–	5
	T2	1	22	12	38	21	–	7	–
		2	18	14	27	32	–	8	–
	LSD (0.05)		18	NS	NS	14	–	NS	NS
38	T1	3	15¶		8	59	7	–	11
		4	4		16	53	24	–	11
		5	5		11	45	37	–	11
	T2	2	9		30	48	8	13	–
		3	3		29	46	19	4	–
		4	3		29	46	19	4	–
	LSD (0.05)		7		11	NS	9	NS	NS
47	T2	4	6		4	67	18	5	–
		5	4		6	45	40	5	–
		6	7		10	37	39	7	–
	LSD (0.05)		NS		NS	17	14	NS	NS

† Leaves were numbered acropetally from the base of the shoot.
‡ L = leaves; S = stem; I = inflorescence; T1 and T2 = tillers formed in the axils of the first and second leaves of the main shoot, respectively.
§ Indicates radioactivity was not measured.
¶ After 38 DAE, the main shoot was not subdivided.

(DAE) and continued at 7- to 8-d intervals until early grain filling. The top 1 to 3 leaves were labeled on each date.

In 1984 individual tiller leaf blades were exposed to 185 mBq $^{14}CO_2$ for 10 min in a 26- × 28-cm polyethylene bag assimilation chamber. Plants selected for labeling were those on which T1 and T2 were predicted to survive. Labeling dates began 19 DAE and continued at 3- to 9-d intervals until early grain filling.

In the whole shoot labeling study conducted in 1984, entire T1 or T2 tillers and main shoots were exposed (one per plant) to 185 mBq $^{14}CO_2$ for 10 min in a 26- × 28-cm polyethylene bag assimilation chamber. On 41 DAE only, shoots were enclosed in a 33- × 45-cm chamber. Labeling dates were spaced at 3- to 9-d intervals beginning 14 DAE and ending during early grain filling.

Predicting Tiller Survival

In order to compare partitioning patterns for surviving and nonsurviving tillers, it was necessary to predict which shoots were likely to die even before visible signs of senescence, such as chlorosis, were evident. This was accomplished by monitoring leaf emergence for plants to be labeled using the system of Haun (1973). Tillers that were more advanced relative to the main shoot on the basis of their leaf development were those judged most likely to survive (Ong, 1978). Each plant selected for labeling had tiller survival patterns that fell into one of three categories. (i) both tillers T1 and T2 survived, (ii) T1 survived and T2 did not, and (iii) both T1 and T2 were nonsurviving.

Monitoring of Radioactivity

When an entire shoot was labeled, the plant was subsequently subdivided into the main shoot, T1, and T2, and each part was monitored for radioactivity. Other tillers were seldom present and were not monitored. When an individual leaf blade was labeled on a tiller, the labeled leaf and sheath, other leaves and sheaths, stem, and inflorescence

were separated and analyzed for radioactivity. Also, the stem and leaves on the main shoot were subdivided and monitored. The T1 or T2 tiller not exposed to $^{14}CO_2$ on each plant was analyzed intact without subdividing.

All plant parts were oven-dried at 70°C. Samples were ground and combusted using a Packard Tricarb oxidizer, absorbing the CO_2 in Carbosorb® and measuring the ^{14}C by scintillation counting in Permafluor® (Packard Instrument Co., Downers Grove, IL).

The amount of radioactivity within each plant part was expressed as a percentage of total radioactivity in the aboveground portions of the plant (excluding the labeled leaf). Losses of radioactivity to roots and by respiration in the 24 h between labeling and harvest were not estimated. Analysis of variance was calculated for each labeling date, and mean comparisons were made using least significant difference when F values were significant ($P \leq 0.05$).

RESULTS

Background on Crop Development

Crop development, environmental conditions, and agronomic performance were similar in 1983 and 1984. Grain yields averaged 3.5 Mg/ha and did not differ significantly among the genotypes. Tiller production and survival characteristics were consistent with the characterization for these genotypes provided elsewhere (Simmons et al., 1982). In both years main shoot spike differentiation (double ridge) began 13 to 14 DAE, and spikes attained the awn initials stage by 24 to 25 DAE. Main shoot stem elongation also began about 25 DAE. Flag leaf emergence on the main shoot occurred 35 to 37 DAE, and anthesis was 45 to 46 DAE.

Partitioning Patterns Following Tiller Leaf Labeling

Leaf partitioning patterns for surviving tillers resembled the patterns previously described for main shoot leaves of barley (Lauer and Simmons, 1985). All genotypes partitioned photoassimilate similarly. Early in development (18–22 DAE), the emerging leaves of tillers were a strong sink for photoassimilate (Tables 1 and 2). By 30 to 33 DAE, the first three leaves each allocated comparable percentages of photoassimilate (30–39%) to leaves, and the proportion translocated to the tiller stem by leaves 1, 2, and 3 was similar to or greater than that partitioned to leaves (Tables 1 and 2). Thereafter, the stem became the major sink for photoassimilate exported from leaves 2 through 6. The tiller inflorescence became a predominant sink following 38 DAE.

The main shoot received substantial proportions of the tiller photoassimilate until about 33 to 38 DAE (Tables 1 and 2). Sixteen to 43% of the photoassimilate exported from surviving tiller leaves was translocated to the main shoot during this period. The main shoot emerging leaves received most tiller-exported photoassimilate. Even after main stem elongation began, tiller leaves continued to send a substantial percentage of their exported photoassimilate to the main shoot (Tables 1 and 2). Proportionately more of the radioactivity exported by upper leaves on a surviving T1 or T2 tiller was retained by that tiller rather than being sent to the main shoot. Relatively little radioactivity was exported by a labeled tiller to adjacent tillers, except in the case of a nonsurviving T2 tiller translocating to a surviving T1 tiller as shown for 33 DAE in Table 1.

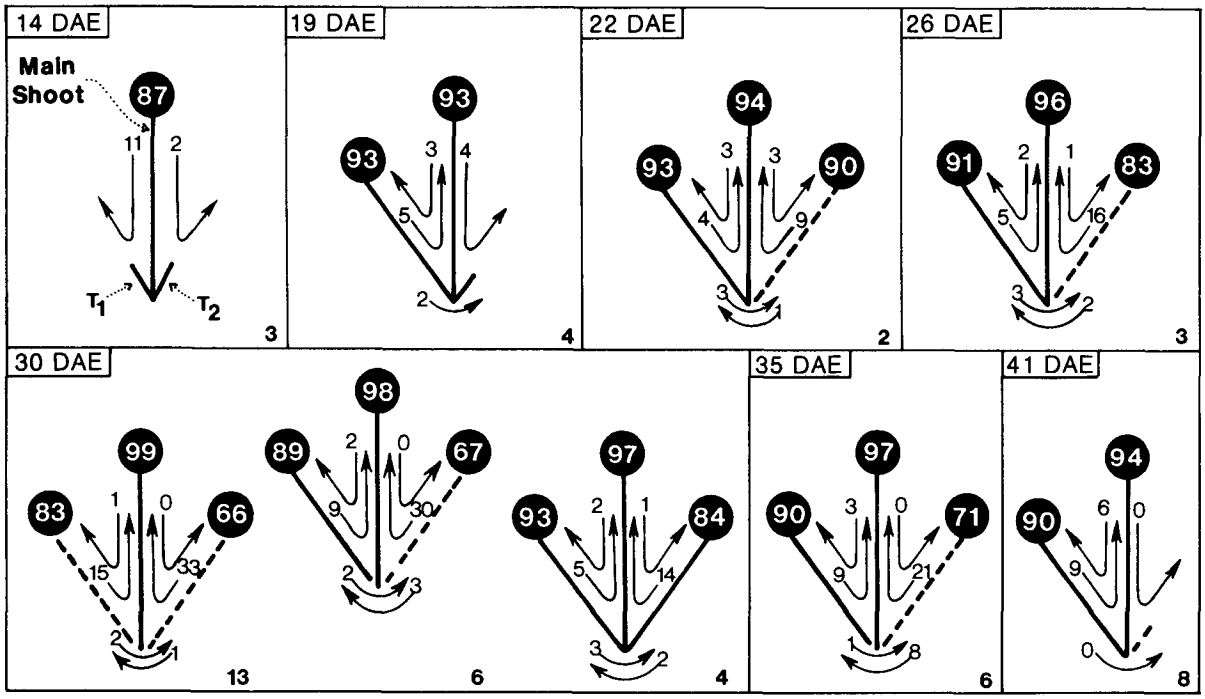

Fig. 1. Plant schematics showing percentage distribution of radioactivity among shoots on barley plants between 14 and 41 DAE in 1984. Values are averaged over three genotypes. Dashed lines indicate nonsurviving tillers and solid lines represent surviving shoots. Values within circles are percentages of the radioactivity retained by each shoot. The other values show the percentage of radioactivity translocated to other shoots as indicated by the arrows. On 30 DAE, plants selected for labeling were of three types: no surviving tillers, tiller T1 only surviving, and tillers T1 and T2 surviving. The LSD (0.05) is shown below each plant diagram and may be used when comparing any two values in that diagram.

Partitioning Patterns Following Whole Shoot Labeling

The main shoot initially retained 87% of its photoassimilate (14 DAE in Fig. 1), and this increased to a maximum of about 98% at 30 DAE, at which time main shoot stem growth was increasing. A surviving T1 tiller retained 93% of its photoassimilate initially and this was essentially maintained during the remainder of the study. The proportion retained by a nonsurviving T2 was initially high (90%) but subsequently declined markedly.

Photoassimilate partitioning from whole tillers to the main shoot increased to a maximum shortly after jointing. A nonsurviving T2 partitioned a larger percentage of its photoassimilate to the main shoot than a surviving T1 (e.g., 26 DAE in Fig. 1). Little photoassimilate was translocated by a tiller to an adjacent tiller, except during the stem elongation phase of T1 on 35 DAE when the nonsurviving T2 partitioned 8% of its radioactivity to T1.

Translocation percentages for plants displaying all three tiller survival patterns are shown for 30 DAE in Fig. 1. A surviving tiller always retained a higher proportion of its photoassimilate than a nonsurviving tiller. Regardless of the tiller, the most prominent sink for its exported photoassimilate was the main shoot.

DISCUSSION

Tillers were presumed to be entirely dependent on the main shoot for photoassimilate and nutrients prior to the time that they emerged (Felippe and Dale, 1972). Between tiller emergence and flag leaf appearance, a large proportion of the radiocarbon fixed by tillers was observed to be translocated to the main shoot. The highest percentage of photoassimilate exported to the main shoot from either a surviving or nonsurviving tiller occurred shortly after the onset of main stem elongation (26 DAE). Translocation of photoassimilate from tiller leaves to the main shoot virtually ceased by the time of flag leaf appearance on the main shoot.

Specific partitioning patterns for leaves on surviving tillers were similar to those previously reported for main shoot leaves (Lauer and Simmons, 1985). Initially, photoassimilate was translocated from fully emerged leaves to emerging leaves. Later, the stem and finally the inflorescence became dominant sinks.

Partitioning patterns of leaves on nonsurviving tillers differed from those on surviving tillers. Prior to the time of main stem elongation, nonsurviving and surviving tillers partitioned their photoassimilate similarly. However, after main stem elongation began, nonsurviving tillers partitioned a larger percentage of their photoassimilate to the main shoot. Accordingly, the proportion translocated to the tiller's own emerging leaves declined, which agrees with the observation that slow leaf growth is one of the first indications of impending tiller death (Kirby and Riggs, 1978). In winter wheat (*Triticum aestivum* L.), Thorne and Wood (1987) observed that as much as 70% of the photoassimilate fixed by nonsurviving tillers was translocated to other plant parts as the tillers senesced.

Photoassimilate exported from leaves on either surviving or nonsurviving tillers was always translocated preferentially to the main shoot in our study. Photoassimilate partitioning patterns following labeling of whole shoots agreed with the patterns described for individual leaves.

It has been estimated for barley that about 5% of the current shoot photoassimilate is translocated to the root system (Anderson-Taylor and Marshall, 1983). Thus, the aboveground partitioning patterns presented in this study would not likely have been greatly different even if the roots had been monitored.

In conclusion, we have shown that a substantial proportion of the current photoassimilate exported by tillers, and particularly nonsurviving tillers, was translocated to the main shoot. Thus, tillers are a source of photoassimilate, especially for the stem of the main shoot. Thus, it may be that nonsurviving T1 and T2 tillers translocate quantitatively more photoassimilate to the main shoot than is initially invested in them. It has been proposed (Kirby and Jones, 1977; Thorne and Wood, 1987) that nonsurviving tillers in cereals compete with the main shoot and reduce yield. However, the value of nonsurviving tillers as a source of current assimilate for other plant parts has not been previously addressed and is a factor that should be considered in resolving the question of the agronomic value of tillers.

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ERRATA

The paper "Photoassimilate Partitioning by Tillers and Individual Tiller Leaves in Field-Grown Spring Barley" by J.G. Lauer and S.R. Simmons in *Crop Science* 28:279–282 contains errors. On page 279, line 57, 111 mBq should be 1.11×10^5 Bq, and on page 280 line 4 and 11, 185 mBq should be 1.85×10^5 Bq.