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# Carbon-14 Translocation in Three Warm-Season Grasses as Affected by Stage of Development

WALTER H. FICK AND LOWELL E. MOSER

**Highlight:** Radioactive carbon dioxide was utilized to trace carbohydrate translocation in blue grama, sideoats grama, and switchgrass. Tagged tillers retained 77% of their fixed carbon following a 24-hour translocation period. The roots were the strongest sink of assimilate, receiving 76.2% of the total  $^{14}\text{C}$  translocated. The pre-elongated and elongated tiller fractions received 16.3% and 7.5% of the  $^{14}\text{C}$  translocated, respectively. Major differences among the grasses became evident upon examination of relative total activity (RTA) ratios in elongated/pre-elongated tillers and root/shoot fractions. Switchgrass produced many more elongated tillers and had the highest elongated/pre-elongated RTA ratio. Blue grama had the greatest weight of pre-elongated tillers, a strong above-ground sink, and therefore had the lowest root/shoot RTA ratio. Sideoats grama had RTA ratios similar to those of blue grama.

Carbohydrate translocation and the relative partitioning of photosynthate is important since plant growth depends upon carbohydrates for energy production and as building blocks for storage and structural compounds. The distribution of carbohydrates is governed by a source-sink relationship which changes with the plant's growth stage. A carbohydrate sink is an area of carbohydrate storage or utilization, and the source is usually an area of photosynthate production, such as the leaves or any other green plant part. However, storage organs may become the source for carbohydrate when a strong above-ground sink and little leaf area exists. For example, storage organs serve as sources during spring growth of grasses.

Stem bases, stolons, roots and rhizomes represent the major storage organs for carbohydrate reserves of grasses (White 1973). Carbohydrate reserves are important in perennial plants for winter survival, early spring growth initiation, and initial regrowth following defoliation (White 1973). Nonstructural carbohydrates, such as glucose, fructose, sucrose, fructosan, and starch are the major types of carbohydrates stored. Structural carbohydrates, primarily cellulose and hemicellulose, are not used as reserve carbohydrates.

Begg and Wright (1964) suggested an order of priority for photosynthate utilization in vegetative reed canarygrass (*Phalaris arundinacea*) shoots. The first priority for photosynthate was for initiation and development of leaves; second, for an increase in dry weight of the shoot and elongation of internodes; and third, for the accumulation of root reserves.

St. Pierre and Wright (1972) studied translocation between tillers of timothy (*Phleum pratense*). The  $^{14}\text{C}$  tracer moved from the main shoots to all sinks at both the 3- and 5-leaf stages. Treated tillers consistently exported  $^{14}\text{C}$  to roots, but inconsistently sent  $^{14}\text{C}$  to the main shoot and sister tillers. More labeled assimilate moved from the top blades of the main shoot to elongating leaves above them, while with the basal leaves more assimilate moved to the tillers and roots.

The emergence and development of a seedhead in grasses constitutes a strong sink for carbohydrates. Carr and Wardlaw (1965) found 49% of the  $^{14}\text{C}$  assimilated by the flag leaf of wheat (*Triticum aestivum*) and up to 80% of  $^{14}\text{C}$  assimilated in the glumes to be translocated to the developing grain.

Dahlman and Kucera (1968) reported about 50% of  $^{14}\text{C}$  moved to the roots of less mature vegetation and as much as 85% moved to the roots of mature tallgrass prairie grasses 8 weeks after tagging. Singh and Coleman (1974) working with blue grama and buffalograss-dominated shortgrass prairie, reported that 67–76% of the roots at the 0–20 cm depth received  $^{14}\text{C}$  fed to leaves and 29–44% of the roots at greater depths received  $^{14}\text{C}$ . Stage of development had a significant effect on  $^{14}\text{C}$  distribution in the roots.

Carbohydrate translocation in grasses is a dynamic process and occurs toward centers of active growth and storage. Morphological changes cause the formation of new centers of carbohydrate utilization and storage in grasses.

Most research on carbohydrate translocation has been done with cool-season grasses or annual plants, such as cereal grains. Thus, a definite need exists for expanded research in the area of carbohydrate translocation in perennial plants, especially warm-season range grasses. This research was initiated to determine whether short-term photosynthate distribution was similar in blue grama (*Bouteloua gracilis*), sideoats grama (*Bouteloua curtipendula*), and switchgrass (*Panicum virgatum*). These three grasses were selected because of their relative abundance and importance in Nebraska rangelands and because a comparison of a short, a mid-height, and a tall grass was possible. The purpose of this study was to determine the relative carbon contribution made by a single tagged tiller to other parts of a single plant.

## Materials and Methods

Excess seed of Nebraska 28 switchgrass, Nebraska 58 blue grama, and Trailway sideoats grama were germinated in February in the greenhouse at Lincoln, Nebraska. The natural photoperiod, which ranged from 12 to 14 hours, was extended to 14 hours with low intensity incandescent light ( $110 \mu \text{ einsteins m}^{-2} \text{ sec}^{-1}$ ,  $\lambda = 400 - 700 \text{ nm}$ ). Maximum daytime temperature ranged from 30 to 35°C. Four seedlings were transplanted to 20 cm × 20 cm plastic pots and

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each pot was thinned to one healthy plant after the seedlings reached the 3-leaf stage. Plants were watered as needed and fertilized with 45 kg/ha N (ammonium nitrate, 34-0-0) and 34 kg/ha P (triple superphosphate, 0-46-0) on March 27 and again with 14 kg/ha N on April 26. The potted plants were put outside on May 8 and received natural light only.

Radioactive barium carbonate served as the  $^{14}\text{C}$  source. Radioactive carbon dioxide was generated by treating  $\text{Ba}^{14}\text{CO}_3$  with lactic acid and trapping the gas in sodium hydroxide until the  $^{14}\text{CO}_2$  was released at the time plants were tagged.

Tagging refers to the photosynthetic incorporation of  $^{14}\text{CO}_2$  into the plant. Tagging occurred outside and in full sunlight between 10:00 a.m. and 2:00 p.m. to coincide with the time of maximum irradiance. Four plexiglass assimilation chambers, 20 cm long  $\times$  8 cm wide  $\times$  7 cm deep, were used for tagging. The inside edges of the chambers were lined with an adhesive plastic foam tape to provide a tight seal while preventing crushing of the culms or leaves. Two syringes were inserted into a serum vial containing the NaOH with the trapped  $^{14}\text{CO}_2$  through a rubber stopper. Excess 3N  $\text{H}_2\text{SO}_4$  was injected with one syringe to release  $^{14}\text{CO}_2$ . The released gas was then drawn into the second syringe and injected into an assimilation chamber through a rubber stoppered porthole in the top of the chamber. A complete tiller or the three uppermost leaves were tagged. The tiller in each chamber was allowed to assimilate  $^{14}\text{CO}_2$  for 30 minutes.

Four tiller stages were selected on the same date for labeling. These stages were the 2- to 3-leaf stage, a 4-leaf pre-elongated stage, an elongated stem prior to boot, and a tiller with a seedhead near anthesis. All phenological stages within a grass were tagged on the same day. Blue grama, sideoats grama, and switchgrass were tagged on May 15, May 26, and June 5, 1974, respectively. Plants remained outside after labeling and a 24-hour period was allowed for translocation of assimilated  $^{14}\text{CO}_2$ . After 24 hours the soil was washed from the roots, and plants were dried for 24 hours in a forced-air oven at 75°C. Dried plants were separated into four plant parts: roots and rhizomes, pre-elongated tillers, elongated tillers, and the tagged tiller. The oven-dry weight was obtained for each part before grinding the samples in a Wiley mill to pass a 1-mm screen.

Approximately 300 mg of oven-dried material of each sample was pelleted in tissue paper prior to oxidation. Oxidation was accomplished using a Packard Tri-Carb Sample Oxidizer, Model 306. Packard's Carbo-Sorb, and organic amine, was used as the  $^{14}\text{CO}_2$  absorber; and a prepared counting solution, Permafluor V, was used as the scintillation medium. The counting solution and  $\text{CO}_2$  absorber were collected in a scintillation counter to determine radioactivity present. The samples were counted for 10 minutes or 40,000 counts. A channels ratio quench correction curve was utilized for determining counting efficiency. The counts per minute recorded by the instrument, divided by the counting efficiency, equals the actual number of nuclear disintegrations per minute (dpm) which occurred. Data for each fraction was expressed in terms of dpm/mg, a measure of specific activity. The amount of radioactivity in a plant fraction was also recorded as relative total activity (RTA), where  $\text{RTA} = \text{dpm in plant fraction} / \text{total dpm recovered} \times 100$ . The amount of assimilated  $^{14}\text{CO}_2$  translocated was determined by subtracting the amount retained by the tagged tiller from 100%.

Percentage figures were transformed using  $(\arcsin) (\%)^{1/2}$  to allow statistical analysis. A split plot design with four replications was used to analyze the overall effects of phenological stage. Retention by the tagged tiller, percent RTA in the elongated/pre-elongated tillers ratio, and root/shoot ratio were analyzed for the three grasses and four tiller stages using a factorial arrangement in a completely randomized design. Duncan's multiple range test was used to determine significant differences ( $P = 0.05$ ) between treatment means.

## Results and Discussion

Blue grama, sideoats grama, and switchgrass averaged 70, 54, and 13 tillers per plant, respectively, at the time of tagging. Following a 24-hour translocation period, 7.4, 9.2, and 10.3% of the released  $^{14}\text{C}_2$  was recovered in blue grama, sideoats

**Table 1. Average percent retention of  $^{14}\text{C}$  by the tagged tillers of three grasses.**

Phenological stage when labeled	Grasses		
	Blue grama	Sideoats grama	Switchgrass
2- to 3-leaf	69.1 b <sup>1</sup>	80.3 ab	76.3 a
4-leaf	80.5 ab	68.9 b	60.3 b
Stem elongation	76.7 ab	82.0 a	75.5 a
Seedhead	86.7 a	86.4 a	79.3 a

<sup>1</sup> Within each column, numbers followed by the same letter are not different at the 0.05 level of significance.

grama, and switchgrass, respectively. Tagged tillers retained an average of 76.8% of their fixed carbon after 24 hours of translocation (Tables 1, 2). This retention is comparable to the 69 to 86% retention reported by Marshall and Sager (1968) when whole tillers of Italian ryegrass (*Lolium multiflorum*) were tagged. Tagged blue grama tillers with seedheads retained more  $^{14}\text{C}$  than those at the 2- to 3-leaf tiller stage. Tillers with seedheads in sideoats grama and switchgrass retained more  $^{14}\text{C}$  than tillers at the 4-leaf pre-elongation stage. The developing seedhead has been shown to constitute a strong carbohydrate sink (Sosebee and Wiebe 1973). No differences in retention of  $^{14}\text{C}$  by the tagged tiller were detected among the three grasses (Table 2).

**Table 2. Average percent relative total activity (RTA) in four plant parts of three grasses when labeled at four phenological stages.**

Plant part	Grasses			
	Blue grama	Sideoats grama	Switchgrass	Mean
Pre-elongated tillers	5.8 c <sup>1</sup>	3.5 c	2.6 c	4.0 c
Elongated tillers	0.9 d	1.8 c	2.4 c	1.7 d
Roots	15.1 b	15.4 b	22.1 b	17.5 b
Tagged tillers	78.2 a	79.3 a	72.9 a	76.8 a

<sup>1</sup> Within each column, numbers followed by the same letter are not different at the 0.05 level of significance.

The greatest amount of  $^{14}\text{C}$  remained in the tagged tillers and roots had the next highest level of  $^{14}\text{C}$ . In blue grama the elongated tiller fraction had the least amount of  $^{14}\text{C}$ . However, in sideoats grama and switchgrass the pre-elongated and elongated tiller fractions did not differ in RTA (Table 2). Averaged over the four stages of maturity, less than 6% of the RTA was located in tillers other than the tagged tiller. Since there was a limited movement of  $^{14}\text{C}$  to other tillers, the tillers on these three grasses are largely, but not completely independent of each other under conditions of this experiment. The elongated tillers of blue grama exhibited the most independence by receiving the least amount of  $^{14}\text{C}$ . Marshall and Sager (1968) obtained similar results with Italian ryegrass. In their study, the roots received most of the translocated  $^{14}\text{C}$  when whole tillers were tagged and the oldest daughter tiller of the main shoot was the most independent.

Less  $^{14}\text{C}$  was translocated from a tagged 4-leaf tiller to elongated tillers compared to pre-elongated tillers. A tiller labeled with  $^{14}\text{C}$  at the 2- to 3-leaf stage, stem elongation stage, or seedhead stage, translocated equal amounts to the pre-elongated and elongated tillers (Table 3). Differences among the grasses occurred at the 4-leaf stage because the tagged 4-leaf tiller of switchgrass had a lower retention of  $^{14}\text{C}$  compared with other tagged tillers, whereas, blue grama and sideoats grama retained similar amounts of  $^{14}\text{C}$  in at least two of the different tagged tiller stages (Table 1).

**Table 3. Average percent relative total activity (RTA) in four plant parts at four phenological stages for three grasses.**

Plant part	Tiller stage			
	2-3 leaf	4-leaf	Stem elongation	Seedhead
Pre-elongated tillers	3.7 c <sup>1</sup>	6.9 c	3.3 c	1.8 c
Elongated tillers	1.4 c	2.8 d	1.3 c	1.2 c
Roots	19.7 b	20.4 b	17.3 b	12.9 b
Tagged tiller	75.2 a	69.9 a	78.1 a	84.1 a

<sup>1</sup> Within each column, numbers followed by the same letter are not different at the 0.05 level of significance.

Roots were the strongest sink for translocated <sup>14</sup>C in the three grasses at every stage of development, followed by the pre-elongated and elongated tiller fractions in blue and sideoats grama (Table 4). Switchgrass tillers translocated equal amounts of <sup>14</sup>C to the pre-elongated and elongated tiller fractions.

**Table 4. Percent translocated <sup>14</sup>C recovered in three plant parts for three grasses averaged over four phenological stages.**

Plant part	Grasses			
	Blue grama	Sideoats grama	Switchgrass	Mean
Pre-elongated tillers	25.7 b <sup>1</sup>	17.3 b	5.9 b	16.3 b
Elongated tillers	4.6 c	8.0 c	9.8 b	7.5 c
Roots	69.7 a	74.7 a	84.3 a	76.2 a

<sup>1</sup> Within a column, numbers followed by the same letter are not different at the 0.05 level of significance.

A ratio of the RTA in the elongated/pre-elongated tillers indicated which of the two fractions was the strongest sink and whether differences existed among the grasses or tiller stages in translocating <sup>14</sup>C to the above-ground sinks. No differences were detected among the tiller stages when averaged over the three grasses, but the grasses differed significantly. The elongated/pre-elongated ratio of RTA in switchgrass was significantly higher than that found in blue grama and sideoats grama (Table 5). Blue grama and sideoats grama had similar ratios except at the 4-leaf stage, where sideoats grama has a higher elongated/pre-elongated RTA ratio because of greater numbers of elongated tillers. Comparing both the RTA and weight ratios, pre-elongated tillers of blue and sideoats grama were shown to be strong sinks since the elongated/pre-elongated tiller RTA ratios were considerably less than the weight ratios (Table 6). In switchgrass the few non-elongated tillers that were present did not represent a strong sink.

The root/shoot ratio of RTA allows comparison of the above- and below-ground sinks. The tagged tiller was not included in the shoot fraction. Generally, switchgrass had the highest root/

shoot RTA ratio (Table 5). Sideoats grama had the highest ratio at the 4-leaf stage because of a more actively growing root system compared to the other grasses. Comparing the RTA and weight ratios for roots and shoots, the roots of all three grasses were shown to be strong sinks since the RTA ratios exceed the weight ratios (Table 6). Switchgrass had the fewest number of tillers of the three grasses and the large majority of them were elongated. Apparently, switchgrass did not have as strong an above-ground sink as the other grasses. Consequently, the roots of switchgrass received most of the translocated <sup>14</sup>C. A large percentage of the above-ground sinks of blue grama were pre-elongated tillers. A larger amount of <sup>14</sup>C was translocated to the tillers of blue grama compared to those of switchgrass. Sideoats grama had an intermediate ratio of RTA in the root/shoot fractions. The above-ground sinks of sideoats grama were mostly elongated tillers and the roots were relatively less developed than the roots of switchgrass (Table 6).

**Table 6. Ratios of relative total activity (RTA) and weight in elongated/pre-elongated tillers and root/shoot fractions of three grasses.<sup>1</sup>**

Grass	Root/shoot		Elongated/pre-elongated	
	RTA	Weight	RTA	Weight
Switchgrass	8.14 a <sup>2</sup>	0.74 a	9.05 a	6.00 a
Sideoats grama	5.40 b	0.59 b	0.67 b	3.60 b
Blue grama	3.04 b	0.62 b	0.29 b	1.60 c

<sup>1</sup> The tagged tiller was not included in any of the ratios.

<sup>2</sup> Within a column, numbers followed by the same letter are not different at the 0.05 level of significance.

Differences among a short, a mid-height, and a tall grass in translocating carbon were closely related to plant growth and development. Blue grama, which produced many unelongated tillers, allocated relatively more carbon to aerial plant parts than did sideoats grama or switchgrass which produced fewer tillers. Under unclipped conditions there is evidence that there is a considerable amount of independence between tillers, but some carbon compounds do move between them in the 24-hour time span measured by this study.

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**Table 5. Ratio of the relative total activity (RTA) in the root/shoot fractions and in the elongated/pre-elongated tillers of three grasses.<sup>1</sup>**

Phenological stage when labeled	Grasses					
	Blue grama		Sideoats grama		Switchgrass	
	Root/shoot RTA	Elongated/pre-elongated RTA	Root/shoot RTA	Elongated/pre-elongated RTA	Root/shoot RTA	Elongated/pre-elongated RTA
2- to 3-leaf	3.58 b <sup>2</sup>	0.14 b	3.75 b	0.19 b	11.07 a	11.60 a
4-leaf	1.99 b	0.41 c	10.45 a	1.41 b	5.38 b	4.15 a
Stem elongation	2.10 b	0.08 b	4.24 b	0.43 b	9.84 a	7.25 a
Seedhead	4.50 a	0.54 b	3.16 a	0.66 b	6.29 a	13.19 a
Mean	3.04 b	0.29 b	5.40 b	0.67 b	8.14 a	9.05 a

<sup>1</sup> The tagged tiller was not included in the ratio.

<sup>2</sup> Within a tiller stage and a parameter numbers followed by the same letter are not different at the 0.05 level of significance.

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