Translocation and Storage of ^{14}C-labled Total Nonstructural Carbohydrates in Honey Mesquite

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Abstract

Translocation of total nonstructural carbohydrates (TNC) in mature honey mesquite *(Prosopis glandulosa* var. *glandulosa)* trees was studied by photosynthetically incorporating $^{14}CO_2$ on eight dates during the summer of 1975. Several plant parts were analyzed for TNC and relative total activity (RTA) to determine direction of translocation and sink strength. Stem and twig TNC fluctuated more than basal bud TNC in response to phenological development. Pods were generally the strongest TNC sink except during initial pod formation (June 25), when bidirectional translocation occurred and all plant parts sampled contained equal concentrations of the ^{14}C label. A RTA/TNC ratio used in conjunction with RTA and TNC suggested that increased TNC concentrations in the pods and stems may not always be due to increased import of TNC but caused by a reduction in growth with constant importation. Greatest translocation of TNC to the basal buds occurred between the phenological stages of green flower spikes (June 10) and pod formation (June 25) and during pod maturation (August 4 to August 19).

Honey mesquite *(Prosopis glandulosa* var. *glandulosa)* is the most widely spread "pest" plant in Texas and now occupies more than 22.7 million ha of grassland. The distribution of honey mesquite increased by 506,000 ha between 1948 and 1963 (Smith and Rechenthin 1964). Many mechanical and chemical control methods are beneficial, but none prevent reestablishment of honey mesquite.

Dormant buds, located in the crown area of the underground stem, allow honey mesquite to resprout and become reestablished. Any foliar applied herbicide must be translocated to the crown area and accumulate at toxic levels in order to kill honey mesquite.

Translocation of organic food materials from the leaves to other plant parts has been associated with the movement of 2,4-D (2,4-dichlorophenoxyacetic acid) (Mitchell and Brown 1946). Greatest translocation of 2,4,5-T (2,4,5-trichlorophenoxyacetic acid) occurred when there was a moderate to rapid movement of sugars to the roots of honey mesquite (Fisher et al. 1956). Thus, carbohydrate translocation can be studied to determine the probable distribution of foliar applied systemic herbicides indirectly.

Previous studies have examined root and stem carbohydrates in relation to season of the year (Fisher et al. 1956) and total available carbohydrates in honey mesquite roots in relation to phenological development and reproductive potential (Wilson et al. 1975). These studies used carbohydrate concentrations as an indication of direction of translocation. This study examined total nonstructural carbohydrates (TNC) in several parts of honey mesquite during the growing season and the distribution of radioactive labeled TNC. Specific objectives of the study were to determine nonstructural carbohydrate sinks and better establish direction of translocation as affected by phenological development.

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Experimental Procedures

The site for this study was on the Texas Tech University campus in Lubbock. Level topography characterizes the area and the soil is an Amarillo fine sandy loam (an Alfisol). Blue grama *(Bouteloua gracilis)* and buffalograss *(Buchloe dactyloides)* are the dominant grasses. Major forb species are horseweed *(Conyza canadensis),* kochia *(Kochia scoparia),* and broom snakeweed *(Xanthocephalum sarothrae),* whereas honey mesquite is the dominant shrub.

Radioactive carbon dioxide was generated in the field by mixing a 10% HCl solution with aqueous sodium bicarbonate ($NaH^{14}CO_3$) solution. The generation occurred in a closed system into which $^{14}CO_2$ was pumped and circulated for 10 min. The system consisted of a plexiglass chamber placed on the terminal branch of the mesquite tree. A total of 32 trees were randomly selected and exposed to 2 μc of the ^{14}C-label on eight treatment dates between May 20 and September 8, 1975.

Samples collected 1 week after tagging included the tagged leaves, tagged twig, stem below the tagged twig, a portion of the basal bud zone, and pods. Tagged tissues refer to those actually exposed to $^{14}CO_2$. The below-ground sample was collected by mechanically removing the soil around a tree to a depth of 0.6 m and cutting the taproot approximately 0.3 m below the crown buds. A hatchet was used to chip an adequate sample (5 to 10 g) from the bud zone. Once collected, all samples were immediately placed under dry ice to stop enzyme activity. Samples were dried in a forced-air oven at 55° C for a minimum of 48 hr and ground in a Wiley Mill to pass a 0.5-mm screen. Phenological development was described on each sampling date.

All samples were analyzed for TNC by extracting a 500 mg sample of plant material using acid (0.2N HCl) hydrolysis as described by Smith et al. (1964). Carbohydrate concentration was determined using anthrone reagent and spectrophotometry (Murphy 1958) with glucose as the standard. Once extracted, a 2-ml aliquot of the aqueous solution was added to 10 ml of a dioxane based counting solution which was prepared by adding 4 g PPO (2,5-diphenyloxazole), 300 mg POPOP (p-bis[2-(5-phenyloxazolyl)]-benzene), and 100 g naphthalene to 1,000 ml 1,4-dioxane. The amount of radioactivity in a sample was determined using a liquid scintillation counter. Results are reported as relative total activity (RTA) which is the disintegrations per minute (dpm) in a plant fraction divided by the total dpm recovered from the entire plant multiplied by 100.

Within a treatment date, TNC, RTA, and RTA/TNC data were analyzed using a nested classification. A completely randomized design with subsampling was used to analyze across treatment dates and within a plant part. Means were separated by Duncan's multiple range test.

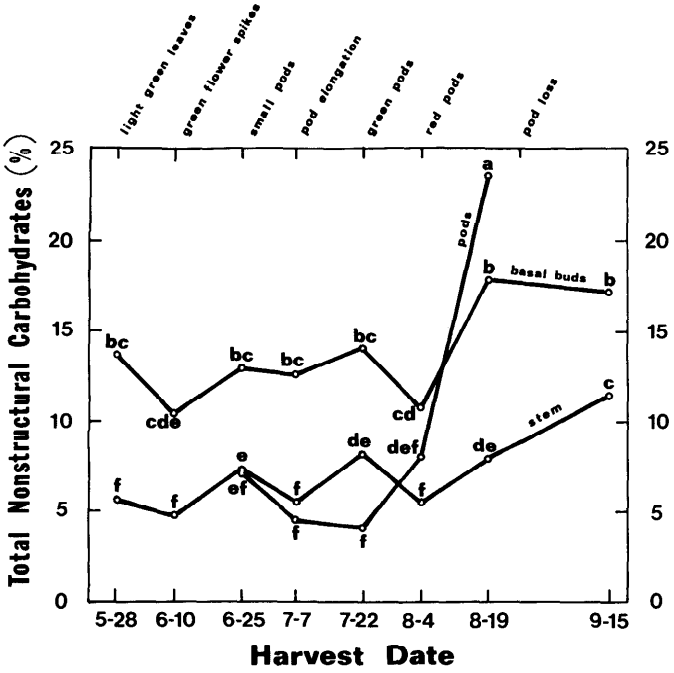

Fig. 1. *Total nonstructural carbohydrates in the basal buds, stems, and pods of honey mesquite trees harvested between May 28 and September 15, 1975. Phenological development is also indicated. TNC levels not followed by a similar letter differ significantly at the 5% level.*

Results and Discussion

The distribution of ^{14}C to the various plant parts of honey mesquite 1 week after exposure should be closely related to herbicide translocation. Most of the label would reasonably be expected to be present in the plant since Bamberg et al. (1973) recovered 98% of the fixed ^{14}C from *Ambrosia dumosa* 1 week after tagging. In the current study, 2.5% of the ^{14}C was recovered in the TNC fraction of honey mesquite samples 1 week after exposure. Mesquite trees sampled in this study had a high reproductive load (50 to 60% of their potential).

Total Nonstructural Carbohydrates

Minimum basal bud TNC was measured on June 10, 1975, when the trees had dark green leaves and green flower spikes (Fig. 1). Between June 10 and August 19, basal buds increased from 10.4 to 17.8% TNC. Most of this increase occurred during pod maturation (August 4 to August 19). During this same period (June 10 to August 19), stem TNC fluctuated greatly. Between the development of green flower spikes (June 10) and small pods (June 25) stems increased from 4.7 to 7.4% TNC indicating downward translocation of carbohydrates. Twigs (June 10 to June 25) also increased in TNC (Table 1) substantiating outward translocation of TNC from the leaves. During pod elongation (June 25 to July 7) stems (Fig. 1), twigs, and leaves (Table 1) declined in TNC suggesting possible translocation to the pods. Wilson et al. (1974) suggested that stored carbohydrate reserves were used during maximum dry matter accumulation by pods since current photosynthate was not adequate to meet the organic matter needs of the pods. Between cessation of pod elongation (July 7) and immature green pods (July 22), stems (Fig. 1) and twigs (Table 1) increased in TNC. Pod TNC (Fig. 1) remained low (4.5 to 8.0%) when the stems and leaves were fluctuating in TNC. Imported TNC by the pods was probably rapidly converted to structural material. After the pods turned red around August 4, their TNC content increased rapidly reaching 23.5% on August 19 (Fig. 1). Pods were importing TNC during this period but basipetal translocation was also occurring as the stems and basal buds (Fig. 1) began increasing TNC after pods began to mature (August 4).

Root mortality of honey mesquite using foliar applied herbicides generally increases when root TNC increases and declines when root TNC is depleted (Dyer and Dahl 1975). Thus, best root kills are obtained when honey mesquite is sprayed between the cessation of flowering and pod maturation. However, direction of translocation cannot be determined by measuring TNC concentration in the roots alone. In this study, fluctuating TNC levels in the stems and small twigs of honey mesquite more closely indicated direction of carbohydrate translocation from the photosynthetic source. George and McKell (1978) measured similar responses in the TNC storage organs of snowberry *(Symphoricarpus oreophilus).* Proximity of the leaves, twigs, and stems to elongating honey mesquite pods between June 25 and July 7 resulted in decreased TNC concentrations in these plant parts. The TNC level in the basal buds remained unchanged during this stage of phenological development. Depletion of TNC in a plant part indicates outward translocation or utilization. A radioactive tracer can be used to determine the TNC sink.

Table 1. Storage of total nonstructural carbohydrates (%) in the twigs and leaves of honey mesquite trees harvested between May 28 and September 15, 1975.

	Plant fraction		
Harvest date	Twigs	Leaves	Phenological stage
May 28	6.3 bcd[1]	6.6 bc	light green leaves
June 10	4.7 d	5.4 cd	green flower spikes
June 25	8.1 ab	6.4 bc	small pods
July 7	4.6 d	3.8 d	pod elongation
July 22	6.8 bc	5.4 cd	green pods
August 4	5.6 cd	5.6 cd	red pods
August 19	7.0 bc	5.0 cd	mature pods
September 15	9.7 a	4.5 a	no pods

[1]Values not followed by a similar letter differ significantly at the 5% level.

Table 2. Relative total activity (%) in plant fractions of honey mesquite 1 week after exposure to $^{14}CO_2$ on eight treatment dates.[1]

	Plant fraction					
	^{14}C-labeled tissues					
Harvest date	Leaves	Twig	Basal buds	Stem	Pods	Phenological stage
May 28	87.6 a[2]	10.0b	1.2 c	1.2 c		light green leaves
June 10	77.2 a	18.6 b	0.7 c	3.5 c		green flower spikes
June 25	22.0 a	20.4 a	10.2 a	19.6 a	27.8 a	small pods
July 22	29.4 a	16.1 b	0.7 c	3.8 a	50.0 a	pod elongation
July 22	19.7 b	13.2 b	1.7 c	3.6 c	61.8 a	green pods
August 4	22.6 b	18.6 b	2.5 c	7.1 c	49.2 a	red pods
August 19	18.5 b	15.6 b	3.5 b	7.1 b	55.3 a	mature pods
September 15	35.0 a	49.2 a	4.2 b	11.6 b		no pods

[1]Relative total activity is defined as the ^{14}C in a plant fraction expressed as a percentage of the total ^{14}C recovered.
[2]Values within a harvest date not followed by a similar letter differ significantly as the 10% level.

Table 3. Relative total activity (%) in plant fractions common to all honey mesquite trees 1 week after exposure to $^{14}CO_2$ on eight treatment dates.[1]

Harvest date	Plant fraction: ^{14}C-labeled tissue				Phenological stage
	Leaves	Twig	Basal buds	Stem	
May 28	87.2 a[2]	10.0 d	1.2 de	1.2 d	light green leaves
June 10	77.2 a	18.6 cd	0.7 e	3.5 cd	green flower spikes
June 25	30.5 e	28.6 bc	14.1 a	27.1 a	small pods
July 7	58.8 b	32.2 b	1.5 c	7.5 bc	pod elongation
July 22	51.5 bc	34.5 b	4.5 bc	9.5 bc	green pods
August 4	44.6 bcd	36.6 ab	4.8 bc	14.0 b	red pods
August 19	41.4 cde	34.9 b	7.8 b	15.9 ab	mature pods
September 15	35.0 de	49.2 a	4.2 bcd	11.6 b	no pods

[1]Relative total activity is defined as the ^{14}C in a plant fraction expressed as a percentage of the total ^{14}C recovered.
[2]Values within a plant fraction not followed by a similar letter differ significantly at the 10% level.

Relative Total Activity

Within Harvest Dates

Relative total activity measured the status of fixed $^{14}CO_2$ 1 week after exposure on eight treatment dates during 1975 (Table 2). During the light green leaf to green flower spike stage, over 90% of the recovered ^{14}C-labeled TNC was extracted from the tagged tissue. Pod development (June 25 to August 19) reduced retention of ^{14}C-labeled TNC by the leaves to an average of 22.5% as a greater proportion of the label was being translocated to other TNC sinks, especially to the pods. The pods were a stronger sink for ^{14}C-labeled TNC than the basal buds or stems except during initial pod development (June 25) when all plant parts examined contained equal concentrations indicating bidirectional translocation. The radioactive label was equally distributed between the basal buds and stems on all sampling dates.

Across Harvest Dates

The RTA values within a plant fraction and across harvest dates are illustrated in Table 3. Only those plant fractions common to all trees on all harvest dates are included. Pods are excluded from Table 3 because they were not present on the mesquite trees on May 28, June 10, and September 15.

Twig RTA increased during the growing season while leaf RTA decreased (Table 3). Initial pod formation on June 25 contributed to decreased leaf RTA while basal bud and stem RTA values increased concomitantly. During pod elongation (June 25 to July 7) basal bud and stem RTA decreased (Table 3) as most of the ^{14}C-labeled TNC was recovered in the leaves and pods (Table 2). Increased twig RTA between August 19 and September 15 (Table 3) may suggest that TNC storage organs closest to the photosynthetic source are replenished first.

RTA/TNC Ratio

A ratio between the relative amount of ^{14}C-labeled TNC in a plant fraction (RTA) and the TNC concentration of the fraction is proposed as providing a useful understanding of source-sink relationships and direction of carbohydrate translocation in plants. An increase in the RTA/TNC ratio would indicate an active sink that was importing TNC for use in growth and maintenance of cells. A decrease in the RTA/TNC ratio would indicate decreased sink strength and minimal growth. The RTA/TNC ratio may either substantiate or reject conclusions based on either TNC or RTA data used alone.

The leaf RTA/TNC ratio decreased between June 10 and June 25 (Table 4) while the ratio for basal buds and stems increased. Substantial translocation of TNC occurred to the basal buds between flowering (June 10) and pod formation (June 25) even though basal bud TNC did not significantly increase (Fig. 1). During pod elongation (June 25 to July 7) RTA/TNC ratios decreased in the basal buds and stems while they increased in twigs, leaves and pods. Decreased RTA/TNC ratios in the twigs and leaves between pod elongation (July 7) and the elongated green pod stage (July 22) indicated TNC was translocated to the pods. Since pod TNC (Fig. 1) and the RTA/TNC ratio (Table 4) remained unchanged, conversion of TNC to structural carbohydrates in the pods probably occurred. The RTA/TNC ratio in the pods decreased with pod maturity after July 22 (Table 4). During the final 2 weeks of pod maturation (August 4 to August 19), basal bud, stem, and pod TNC increased (Fig. 1). However, RTA did not change in these three plant parts so the RTA/TNC ratios remained unchanged or declined. The increased TNC levels in the basal buds, stems, and pods during pod maturation may not be due to increased TNC importation but to decreased cell expansion and growth. Another plausible explanation for increased basal bud TNC during pod maturation may be increased root growth resulting in increased translocation of TNC through the basal buds. Soil moisture (20% w/w) and temperature (25.8° C) were sufficient on August 4 to enhance root growth (Fick 1978). After pod drop, the leaf RTA/TNC ratio dropped, indicating outward translocation of TNC (Table 4). The twigs were the TNC sink between August 19 to

Table 4. Relative total activity/total nonstructural carbohydrate (RTA/TNC) ratios in the plant fractions of honey mesquite 1 week after exposure to $^{14}CO_2$ on eight treatment dates.[1]

Harvest date	Plant fraction: ^{14}C-labeled tissue					Phenological stage
	Leaves	Twig	Basal buds	Stem	Pods	
May 28	13.63 ab[2]	1.55 d	0.09 b	0.22 d		light green leaves
June 10	14.96 a	4.26 c	0.08 b	0.86 cd		green flower spikes
June 25	4.60 d	3.36 cd	1.39 a	3.80 a	6.50 b	small pods
July 7	16.44 a	7.10 a	0.18 b	1.63 bcd	13.46 a	pod elongation
July 22	10.02 bc	4.78 bc	0.48 b	1.14 bcd	12.65 a	green pods
August 4	8.98 c	6.41 ab	0.54 b	2.87 ab	6.61 b	red pods
August 19	8.84 c	4.73 bc	0.50 b	2.45 abc	2.23 c	mature pods
September 15	4.66 d	4.88 bc	0.27 b	1.07 bcd		no pods

[1]Relative total activity is defined as the ^{14}C in a plant fraction expressed as a percentage of the total ^{14}C recovered.
[2]Values within a plant fraction not followed by a similar letter differ significantly at the 10% level.

September 15 as indicated by increased TNC (Table 1) and RTA (Table 3) levels.

Management Implications

Maximum root kills of honey mesquite using foliar-applied herbicides are normally obtained and are expected during accumulation of nonstructural carbohydrates in the basal buds. Downward translocation of ^{14}C-labeled TNC to the basal buds occurred between the phenological stages of green flower spikes (June 10) and initial pod formation (June 25). Fewer honey mesquite trees will be killed if sprayed during pod elongation (June 25 to July 7) because the pods are a strong aerial sink which greatly reduce translocation to the basal buds. Trees with a heavy fruiting load do not translocate much TNC below ground until pod maturation (August 4 to August 19) when basal bud TNC increases. However, few trees may be killed if sprayed during this time because leaf maturity and cuticle development prevent good uptake of the herbicide. Stems are a strong carbohydrate sink in honey mesquite and greatly influence response to herbicidal control practices by reducing the amount of herbicide that reaches the basal buds.

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