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The Fate of Carbon and Nitrogen from Urea Applied to Foliage of Senescing Apple Trees[1]

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Abstract. Urea was applied to the foliage of 1-year-old apple *Malus pumila* Rehd., cv. Malling Merton 106 (MM 106) trees during senescence and the fate of the urea C and N determined. The urea C was readily released as CO_2, but abscised leaves still contained 18% of the total. Only 5% of the urea C was found in storage tissues (shoot bark and wood, stem bark and wood, and roots). By the time the leaves abscised, this C was found primarily in protein, sugars, and amino acids of storage tissues. Small amounts of urea were still present. The urea N was translocated from the leaves as amino acids or urea. At leaf abscission, 30% of the initial N was still present in the leaves. During senescence, storage tissues from untreated trees increased 1.5-fold in N while similar tissues from urea-treated trees increased 3-fold. This additional N was found primarily in stem and shoot bark and in the roots. Small amounts of N were stored as amino acids but the bulk of the urea N was stored as protein.

Oland (10) first described positive responses of the apple to post-harvest foliar sprays of urea and recently other papers have appeared dealing with this method of supplying N to the apple (2, 8, 13). We have reported some gross responses of 'Golden Delicious' apple trees to 5% and 10% post-harvest urea sprays (15) and found that senescing apple leaves rapidly absorbed urea with 70% of the applied urea being absorbed within 8 hr. Urea was still detected in leaves 168 hr after application to the foliage. Dilley and Walker (3) found unhydrolyzed urea in non-senescing apple leaves 20 hr after the beginning of the absorption period.

We investigated the utilization of urea following application of urea to senescing apple leaves and these results are reported here. One study concerns the fate of urea and how rapidly it is converted to NH_4 and CO_2. Another is the effect of urea sprays on the nitrogenous reserves of different storage tissues of the trees.

Materials and Methods

Plant materials. Rooted cuttings of 1-year-old MM 106 apple trees were grown in 8-liter plastic containers in silica sand under long days (12- to 14-hr photoperiod) in a warm (25°C day/18°C night) glasshouse. The trees were pruned to a height of 24 cm, trained to a single shoot, and irrigated with tap water for 4 weeks. They were then supplied with modified Hoagland's complete nutrient solution on alternate days for 4 weeks at which time senescence was induced by withholding N for 2 weeks in the glasshouse and then transferring the trees to a cold growth chamber (16°C day/5°C night) under short days (6-hr photoperiod). After 4 weeks in the cold growth chamber the experimental treatments were initiated.

Experimental methods. A Latin square, randomized complete block or split-plot design with 3 replicates was used for the experiments.

Urea metabolism and translocation experiments were conducted in the light with trees grown as described above. In metabolism studies, 8 leaves on each of 2 trees were individually dipped for 1 min into 60 ml of 5% urea solution with or without 250 μc of urea-^{14}C (specific activity 3.63 mc/mM). The amount of $^{14}CO_2$ released from urea-^{14}C was determined by placing 7-cm diam midshoots, containing 4 leaves previously dipped in urea-^{14}C, in a large flask. CO_2-free air was pulled through this flask and the respired CO_2 was trapped in Hyamine Hydroxide. The radioactivity in the absorbed CO_2 was determined in a scintillation spectrometer.

Analytical methods. Total N was determined on dry (70°C for 24 hr) tissues by micro-Kjeldahl digestion followed by nesslerization (7).

Samples of apple tissue were extracted in boiling 100% ethanol for 10 min and then homogenized in a VirTis

[1]Received for publication February 14, 1973. Research supported by funds from the Illinois Agricultural Experiment Station.
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homogenizer. The slurry was centrifuged at 6,000 x *g* for 10 min and the ethanol was decanted. The precipitate was extracted an additional 3 times with warm 70% ethanol and each extraction was followed by the above centrifugation. The ethanol-water extracts were combined and analyzed for α-amino N (23) with glycine as the standard and total soluble N by micro-Kjeldahl (7). The ethanol-water insoluble residue was further extracted sequentially with: 1) 5% trichloroacetic acid (v/v) for 1 hr; 2) 0.02 N formic acid in methanol; 3) ethanol:ether:chloroform (2:2:1, v/v/v) for 1 hr at 37°C; and finally, 4) ether. These 4 extracts were discarded and the resulting residue was air-dried and then suspended in 0.5 N KOH for 16 to 24 hr in a 37°C water bath. The solubilized protein was determined by the biuret method (5) with bovine serum albumin as the standard or assayed for ^{14}C. The KOH-insoluble residue was also assayed for ^{14}C (18).

When urea-^{14}C was used, the ethanol-water soluble fraction was taken to dryness under vacuum at 35°C and then washed twice with ether to remove lipids. The lipid-free residue was dissolved in water and separated into amino acids, organic acids, and sugars on ion-exchange resins (20). Each of these fractions was assayed for total ^{14}C and urea-^{14}C. Urea was determined by urease hydrolysis by the modified micro-Conway method (1). Urease solution (1.5 units of Type III--Sigma Chemical Co.) in 0.01 M phosphate buffer, pH 7.0 and 1 ml of the ethanol-water soluble extract dissolved in 0.01 M phosphate buffer, pH 7.0, was added to the outer well of the dish. After the reaction was complete, acid or base was added to the outer well. The released ammonia was measured by titration with HCl. To determine the amount of ^{14}C in urea, Hyamine Hydroxide was placed in the center well and the radioactivity of $^{14}CO_2$ determined.

In translocation experiments, some trees were harvested and designated as day 0. All of the leaves of other trees were dipped in urea, as described above, and harvested 2, 7, 14, and 21 days after the urea treatment. Leaf fall commenced at day 21. At harvest each tree was separated into leaves, shoot bark, shoot wood, stem bark, stem wood and roots. The tissues were cut into small pieces, freeze-dried for 36 hr, ground to pass a 20 mesh sieve and weighed. Total N was determined by micro-Kjeldahl (7). One g samples were successively extracted with boiling 100% ethanol, boiling water, warm 70% ethanol and extracts combined. The amount of α-amino N in these extracts was determined with glycine as a standard. The ethanol-water insoluble residue was extracted sequentially with: 1) 10% trichloroacetic acid (v/v) for 1 hr; 2) 0.02 N formic acid in methanol; 3) ether. The resulting residue was air dried and analyzed for Kjeldahl N to estimate the insoluble N (protein).

Results

Four hours after the senescing leaves were treated with urea-^{14}C, only 3% of the absorbed radioactivity had been released as CO2 (Fig. 1). After this time, however, there was approximately a linear rate of production of $^{14}CO_2$ and by 24 hr, 56% of the radioactivity appeared in CO_2. Concomitantly with the increase in $^{14}CO_2$, there was a decrease in soluble ^{14}C. There was only negligible radioactivity in the ethanol-water insoluble fraction at any time. Over the 4-hr sampling period, a maximum of 3% of the label appeared as $^{14}CO_2$ and urea was continually absorbed (Table 1). Carbon 14 increased in the leaf-blade tissue 12-fold and in the petiole 3-fold. The ratio of the total ^{14}C in blade vs.petiole tissue increased from about 1:1 at 0.25 hr to 5:1 at 4 hr. Initially urea accounted for 84% of the total radioactivity and in 4 hr urea still accounted for 80% of the ^{14}C. Urea contained 86% of the total ^{14}C in the blade and 81% of the total ^{14}C in the petiole after 0.25 hr. Carbon 14 accumulated rapidly in amino acids but slowly in sugars and organic acids. Amino acids accounted for about 15% of the radioactivity absorbed at each sampling time. Little ^{14}C occurred in the residue and lipid fractions.

Table 1. The distribution of ^{14}C in the soluble fraction from senescing apple leaf-blade and petiole tissues from trees kept in the light and given urea-^{14}C. Leaves were dipped in a solution of urea-^{14}C for 1 min and incubated for the times shown.

Fraction	Tissue	0.25 hr	0.5 hr	1 hr	4 hr
		(cpm x 10^{-3}/g fresh wt)			
Urea	Blade	66.8	82.9	305.8	739.8
	Petiole	47.8	48.6	95.2	150.6
Amino acids	Blade	9.6	13.3	56.2	139.5
	Petiole	9.9	10.0	19.0	24.2
Organic acids	Blade	0.1	1.0	1.5	6.4
	Petiole	0.2	0.1	0.4	1.5
Sugars	Blade	0.3	1.8	3.6	47.4
	Petiole	0.8	0.8	1.5	4.2
Others	Blade	0	0	0.4	0.9
	Petiole	0.2	0.4	0.7	1.0
Total	Blade	76.8	99.1	367.5	934.0
	Petiole	58.1	59.8	116.8	181.5
Total	Leaf ^{14}C	134.9	158.9	484.3	1115.5

After 1 day, 56% of the absorbed radioactivity had been released as CO_2 and this increased to 77% by leaf fall (Fig. 2). Thus, only 23% of the total ^{14}C was present in various tissues of the tree and only 5% was present in the storage parts after leaf fall. The bulk of the tissue ^{14}C was in the leaves, where 40% of the total ^{14}C was found after 1 day and the percentage then decreased almost linearly until leaf fall. The abscised leaves still contained 18% of the absorbed ^{14}C. In the shoot bark

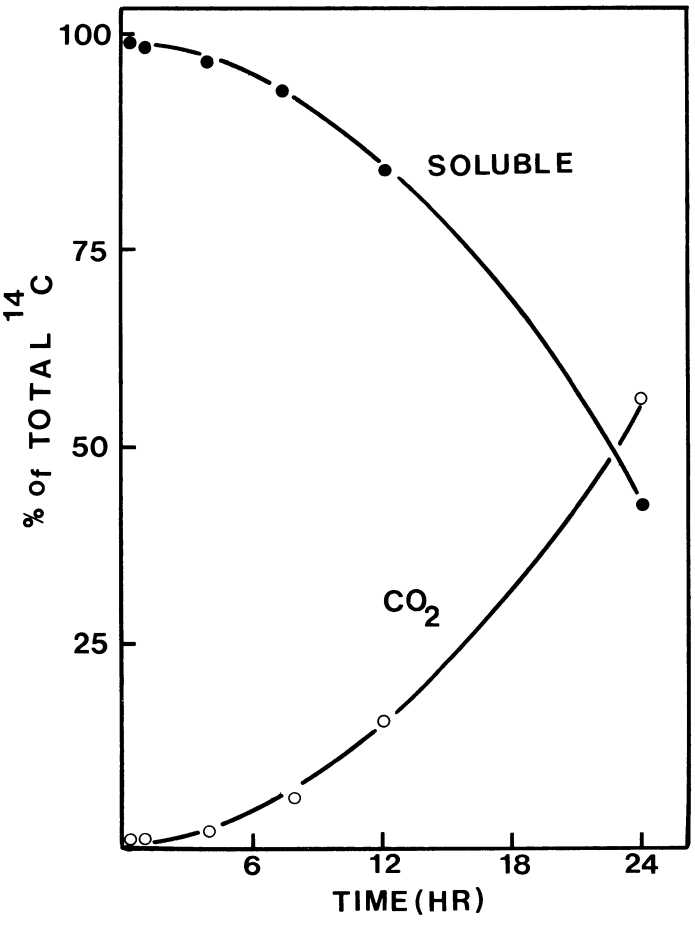

Fig. 1. The distribution of ^{14}C from urea-^{14}C by senescing apple leaves. Leaves were dipped in urea-^{14}C solution for 1 min and incubated for the times shown. Trace amounts of ^{14}C were found in the ethanol-water insoluble residue.

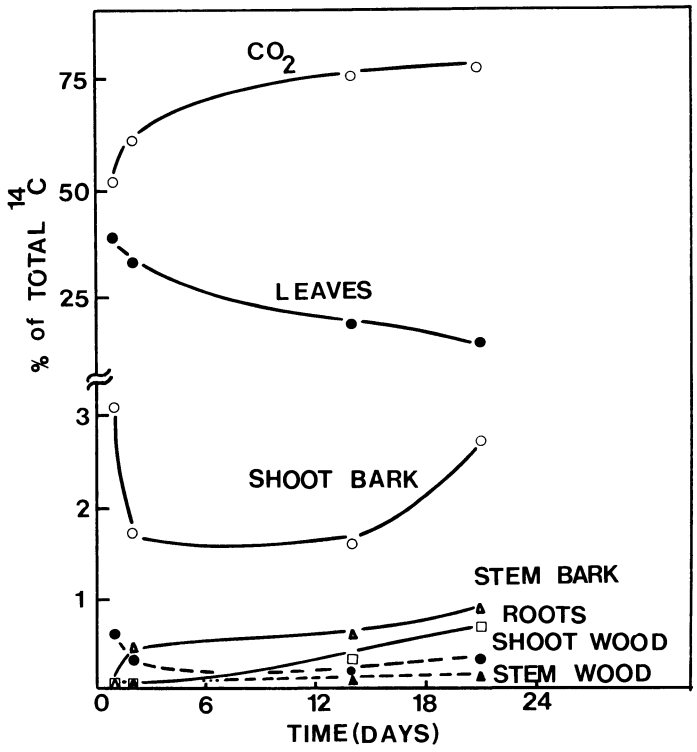

Fig 2. The percentage of radioactivity in various parts of apple trees after the leaves were dipped in urea-^{14}C. Trees were 1 year old and leaves had abscised by 21 days. The amount of $^{14}CO_2$ was determined 1 day after the application of urea-^{14}C and the remaining $^{14}CO_2$ values were then calculated with the following formula: Total ^{14}C absorbed - total non-gaseous ^{14}C = $^{14}CO_2$.

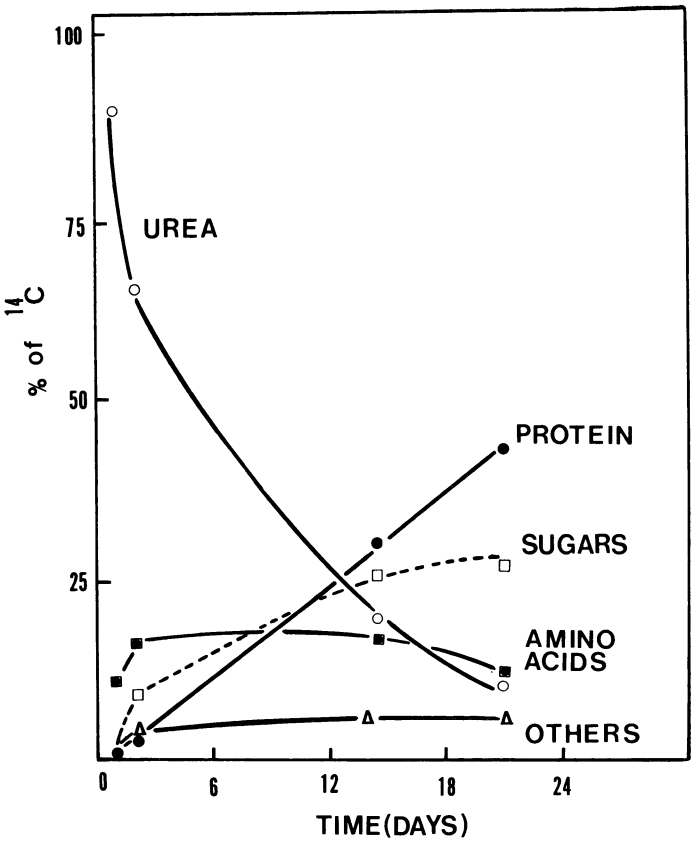

Fig 3. The percentage of radioactivity from urea-^{14}C within various fractions of storage tissues of apple trees. Senescing leaves on 1-year-old apple trees were dipped in urea-^{14}C for 1 min and the storage tissues analyzed for ^{14}C at the times shown. Storage tissues consisted of stem wood, stem bark, shoot wood, shoot bark and roots. The leaves abscised by 21 days.

tissues, 3.1% of the absorbed radioactivity was found after 1 day, this decreased to 1.6% by 14 days and then increased to 2.7% by leaf fall. The changes in ^{14}C in the shoot wood tissues paralleled the changes found in the shoot bark although the shoot wood contained considerably less ^{14}C. After 1 day, only 0.1% of the radioactivity was present in each of the stem bark, stem wood, and root fractions and this increased to 0.9%, 0.2%, and 0.8%, respectively, by leaf fall.

The stem, shoot bark, wood, and roots store various materials which are utilized in growth the next spring. After 1 day, the total ^{14}C from urea in these tissues (Fig. 2) was only 4% of the absorbed radioactivity and 21 days later the total ^{14}C in these tissues was still only 5% of the absorbed radioactivity. Many changes occurred within the individual fractions in these storage tissues (Fig. 3). After 1 day, 90% of the ^{14}C in these tissues was in urea and this declined to 10% by 21 days. Over this same time period, the ^{14}C in protein increased from 1% to 44% and the ^{14}C in sugars increased from 1% to 27% of the ^{14}C found in the storage tissues. The amino acid ^{14}C remained fairly constant with about 12% of the ^{14}C at all times.

In the leaves (Fig. 4), the amount of urea-^{14}C continuously decreased until 55% of the initial ^{14}C was lost by leaf fall. The amount of ^{14}C in the amino acid fraction remained fairly constant over the entire 21-day sampling period and did not follow the decline in urea-^{14}C. After the leaves had abscised, 61% of the ^{14}C remaining was found in urea and 30% was found in amino acids. Little ^{14}C was found in other fractions from the leaves at any time. In the roots (Fig. 4), the amount of urea-^{14}C decreased 87% by leaf abscission while the ^{14}C in sugars, amino acids, and protein increased 150-fold. Carbon 14 in the other fractions (organic acid, lipid and KOH-insoluble residue) increased 50-fold. After the leaves had abscised, 38% of the ^{14}C remaining in the roots was found in sugars, 29% in amino acids, 20% in protein and only 3% in urea.

In the shoot bark tissues (Fig. 4), 86% of the initial urea-^{14}C was lost by leaf fall. The ^{14}C in protein increased 103-fold and that in sugars increased 15-fold during the same period. By the time the leaves had abscised, the shoot bark contained 47% of the ^{14}C in protein, 24% in sugars and 15% in urea. In the shoot wood tissues, urea and amino acids initially contained 95% of the ^{14}C and this decreased to 20% by leaf abscission. The ^{14}C in sugars had increased 43-fold by leaf abscission. At this time, 65% of the remaining ^{14}C in was sugars, 15% in protein, 13% in amino acids and only 7% was in urea.

In the stem bark tissues (Fig. 4), the ^{14}C in urea increased 2-fold from 1 to 2 days and then 80% of the ^{14}C was lost by 21 days. During this same period, the ^{14}C in protein increased 300-fold. The remaining ^{14}C was about equally divided among the amino acid, organic acid, sugar, lipid, and KOH-insoluble residue fractions. By the time the leaves had abscised, 68% of the ^{14}C in this tissue was in protein and 5% remained in urea. In the stem wood tissues, the ^{14}C urea decreased from 99.5% of the total ^{14}C at 1 day to only a trace at 21 days. Over this interval, the ^{14}C in sugars and protein increased about 50-fold and the ^{14}C in other fractions (amino acid, organic acid, lipid and KOH-insoluble residue) increased 10-fold. By leaf abscission, 45% of the ^{14}C in the stem wood was in sugars and 34% in protein.

During senescence, N is transported from the leaves and in the present studies, 70% of the initial N in the leaves was transported out before leaf abscission. During this period, the storage tissues (shoots, stems, and roots) increased in total N from 82 to 130 mg per untreated tree (Fig. 5). Nitrogen accumulation was greatly enhanced after a foliar urea application and in urea-treated trees 3 times as much N was recovered from storage tissues 21 days after application as was present at treatment. The change in total N in the different tissues is presented in Fig. 6. Leaf N declined in the untreated

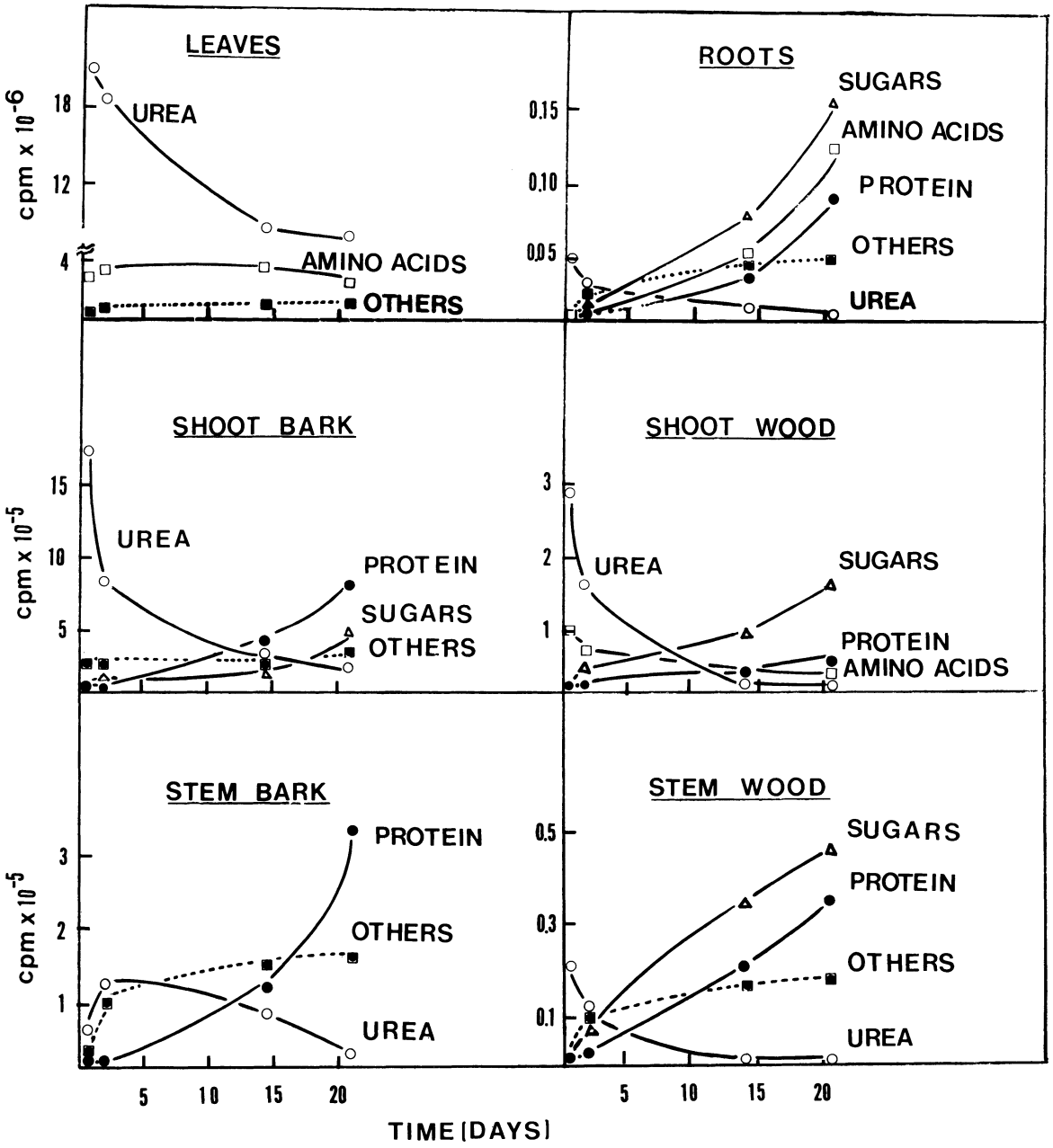

Fig 4. The changes in radioactivity from urea-^{14}C within various fractions from apple leaves, roots, bark, and wood tissues. Senescing leaves on 1-year-old apple trees were dipped in urea-^{14}C for 1 min and tissue ^{14}C determined at various times. The leaves abscised by 21 days.

leaves, but in the urea-dipped leaves, leaf N increased dramatically at the 2-day sample and then steadily declined throughout the 21-day sampling period. Bark tissue of both the shoot and stem accumulated more N than wood tissue and more N accumulated in shoot than in stem tissue. Roots of untreated trees increased in N during leaf senescence and the urea treatment more than doubled the concn of N in the roots.

The α-amino N content of urea-treated leaves increased for 7 days and then declined until leaf abscission, while untreated leaves showed little variation (Fig. 7). By leaf abscission, the treated leaves contained 3 times more α-amino N than similar tissues from untreated trees. By leaf abscission, bark tissue from treated trees contained 4 times more α-amino N, although α-amino N accumulated even in bark from untreated senescing trees. Urea applied to the leaves resulted in steady increases in α-amino N in the roots throughout the 21-day sampling period.

The protein content of the tissues varied considerably with time (Fig. 8). Leaf protein increased 2 days after urea application and then declined steadily, similar to leaves which did not receive a urea treatment. The urea application did not always result in an increase in protein content of the tissues. Shoot wood protein was higher in the 2-, 7-, and 14-day samples of urea-treated trees but by day 21 the protein content of shoot wood was similar to the protein content of shoot wood from untreated trees. Shoot bark protein was not enhanced by the urea treatment until 21 days after treatment. The protein content of stem tissue was initially higher in bark of treated trees but by 14 and 21 days the differences were negligible. Stem wood protein was not affected by the urea treatment. The protein content of the roots increased during senescence, and 14 and 21 days after urea treatment the roots of treated trees and higher protein contents than roots from untreated trees.

Discussion

Senescing apple leaves readily metabolized urea-^{14}C (Fig. 1). Urease activity in senescing apple trees has been shown to be

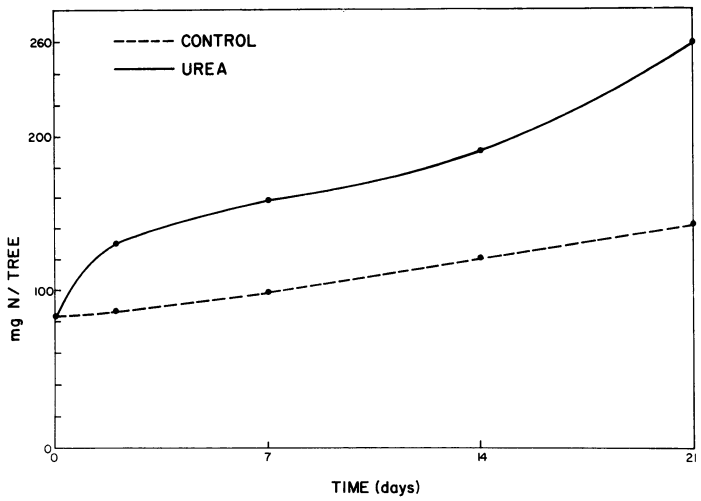

Fig 5. Changes in N content of storage tissues (shoot bark, shoot wood, stem bark, stem wood, and roots) of MM 106 apple trees. Days refers to the time after urea application to senescing foliage.

present in leaves, roots, and bark and urease activity was increased by foliar applications of urea (14). Although much of the N from urea was translocated from the leaves, only 5% of the urea C was translocated. The remaining C was released as CO_2.

Carbon 14 from urea-^{14}C accumulated in amino acids, sugars, and organic acids. Accumulation of ^{14}C was probably due to dark CO_2 fixation (19, 21) and photosynthesis. The bulk of the tissue ^{14}C was found in leaves, even after they had abscised (Fig. 2). It is clear that at least 4% of the absorbed urea-^{14}C was translocated intact to the storage tissues and that the bulk of the ^{14}C was translocated in this manner (Fig. 3, 4). Urea is also translocated from apple roots (22) and some of this urea is metabolized in the storage tissues (15), with the released $^{14}CO_2$ being re-incorporated through dark fixation (19). In the present studies, the ^{14}C in amino acids initially increased in storage tissues and then remained at a fairly constant level. The ^{14}C in protein accumulated linearly during this time. This suggests that the ^{14}C from urea was incorporated into amino acids, and these amino acids were then incorporated into protein in the bark (Fig. 3, 4). Locust (16, 17) trees are capable of protein synthesis in the autumn. After apple leaves were dipped in urea-^{14}C, the bark and wood tissues contained considerably more ^{14}C than the roots (Fig. 4). However, if the apple leaves were supplied with $^{14}CO_2$, ^{14}C accumulated mainly in the roots (6). This difference can be attributed to the C form being translocated: urea-^{14}C in present studies and sugar-^{14}C in previous studies. The present studies show that urea-^{14}C was translocated to the root system.

The increase in N of storage tissues during leaf senescence (Fig. 5) is consistent with the observations of Murneek (9). The increase in N levels in storage tissues following post-harvest urea sprays agrees with the work of Oland (11). More total N was found in bark tissues than wood tissues (Fig. 6) after urea treatments. This observation is consistent with reports that leaf N is exported through the phloem (22). The greater amount of shoot N during senescence compared with stem N is also consistent with Tromp's experiments (22). In the present experiments, however, with foliar applied urea, root N (Fig. 6)

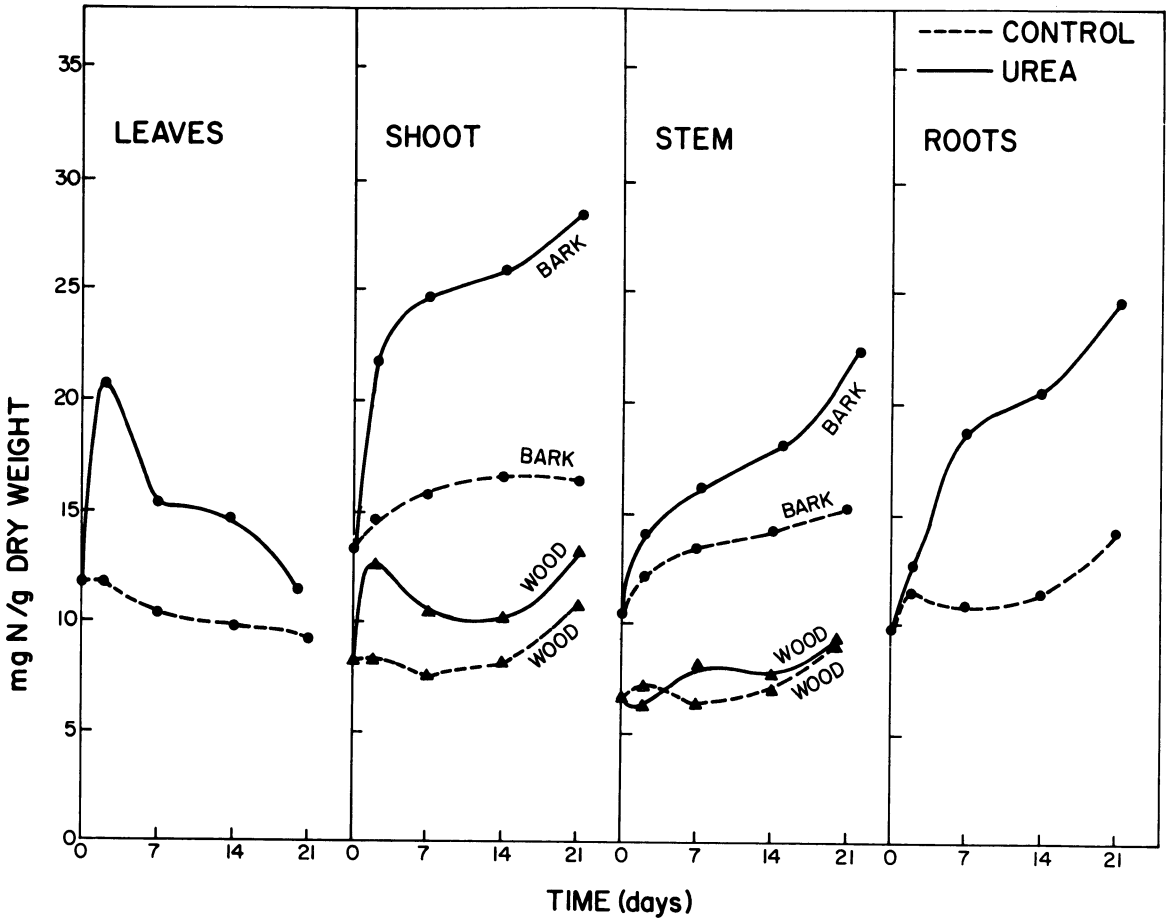

Fig 6. Changes in total N content of leaves, shoot bark, shoot wood, stem bark, stem wood, and roots of MM 106 apple trees. Days refers to the time after urea application to senescing foliage.

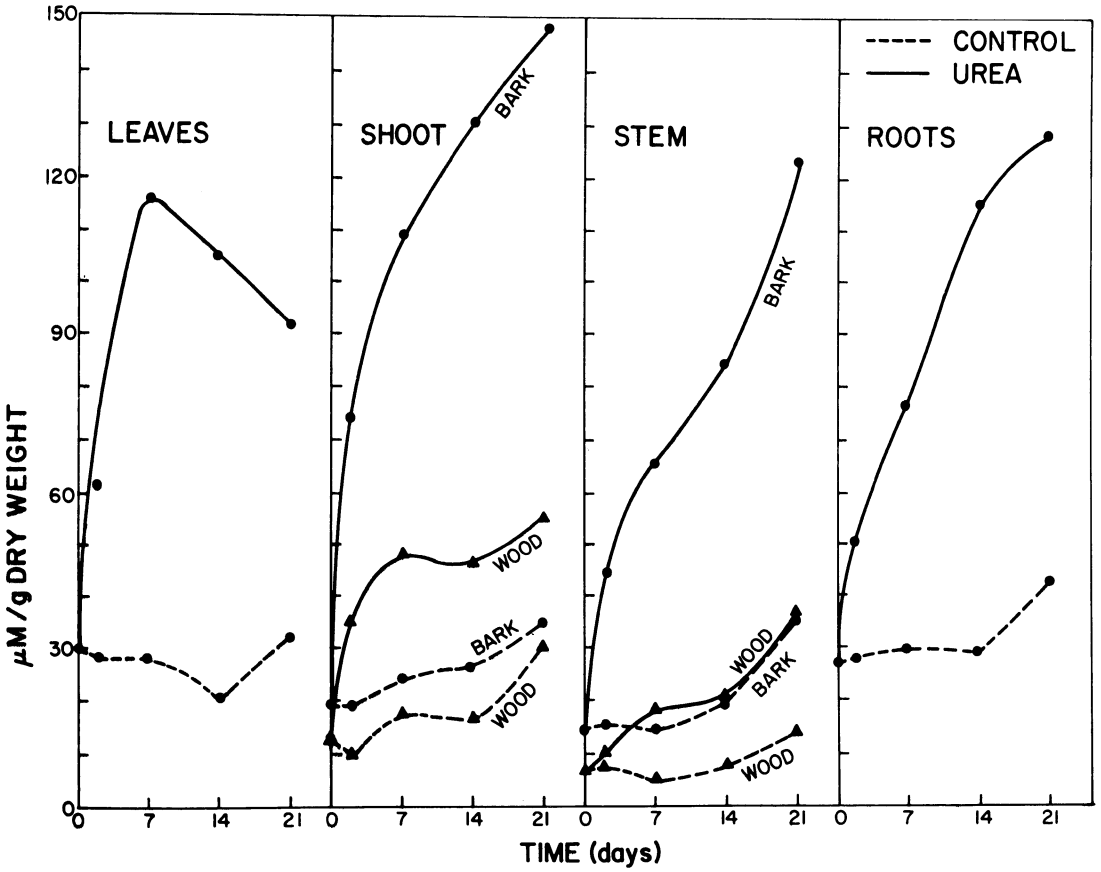

Fig 7. Changes in α-amino N content of leaves, shoot bark, shoot wood, stem bark, stem wood, and roots of MM 106 apple trees. Days refers to the time after urea application to senescing foliage.

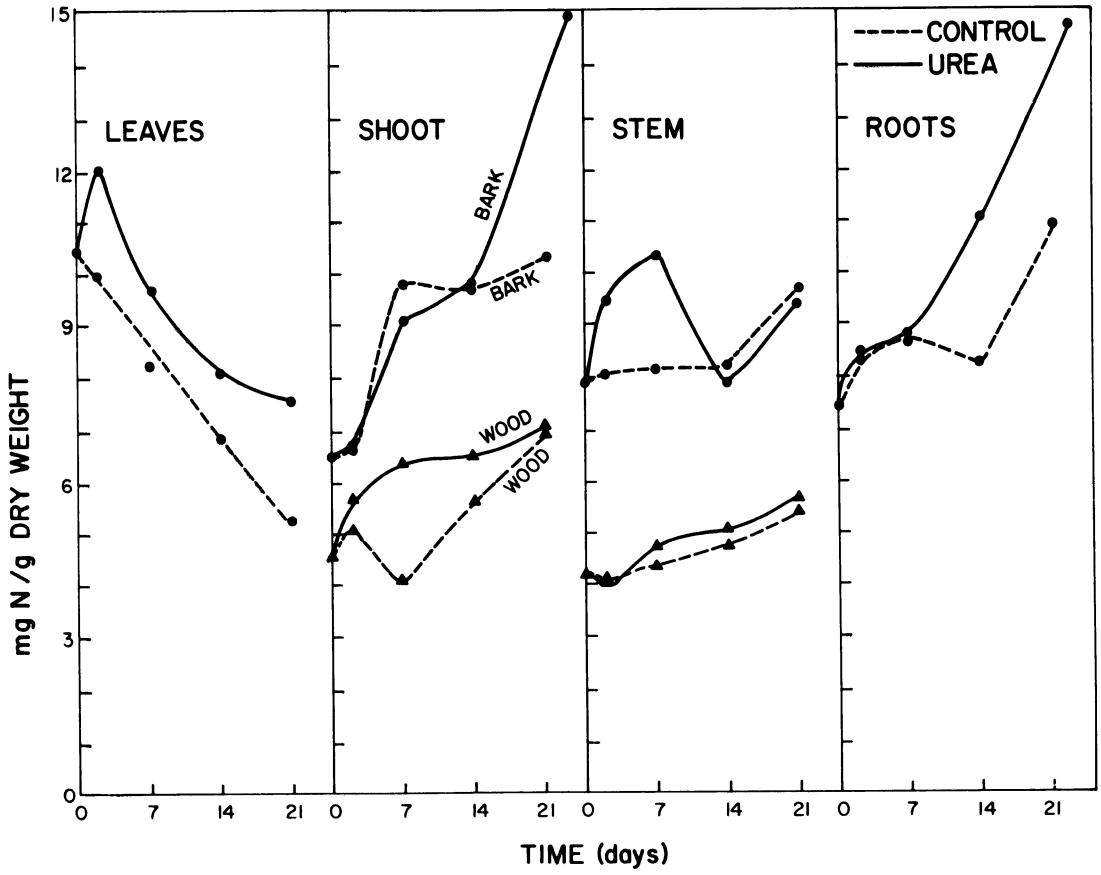

Fig 8. Change in protein content of leaves, shoot bark, shoot wood, stem bark, stem wood, and roots of MM 106 apple trees. Days refers to the time after urea application to senescing foliage.

increased more rapidly than in roots of trees receiving a fall soil application of N (22). Some of the total N in the tissues can be accounted for as urea (15).

Urea treatments increased the α-amino N levels of shoot tissue more than stem tissue. This agrees with Forshey's work (4). Much of the urea N was translocated as urea and urea is readily metabolized in the storage tissues (14, 15). It is probable that the urea N was incorporated into amino acids in these storage tissues, as occurs in apple roots (21). However, some of the urea N was incorporated into amino acids and protein in the leaves and later translocated to the storage tissues as amino acids (Fig. 7). This resulted in a decline in leaf protein (Fig. 8) and is consistent with other senescence studies of apples (14, 15, 18). During senescence, protein levels increased in apple storage tissues and Tromp (22) has reported an increase in shoot bark protein after an autumn application of N. Protein levels increased in the roots and it is unlikely that this increase was the result of increased root growth, as plants were senescing under cool conditions. Rather this newly synthesized root protein probably represents a form of storage protein which can be utilized during spring growth.

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