

# Translocation of Foliar-applied Urea $^{15}\text{N}$ to Reproductive and Vegetative Sinks of Avocado and Its Effect on Initial Fruit Set

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**Abstract.** Translocation of  $^{15}\text{N}$  from foliar-applied urea to vegetative and reproductive sinks of avocado (*Persea americana* Mill, cvs. Fuerte and Hass) was evaluated during inflorescence development and the early stages of fruitset. Urea (2%) increased the number and the total dry weight of the lateral inflorescence per shoot. The concentration of  $^{15}\text{N}$  in avocado inflorescences increased proportionately to the concentration of urea applied to the old leaf surface. The amount of  $^{15}\text{N}$  translocated was not affected by the proximity of the source leaf to the "terminal" inflorescence.  $^{15}\text{N}$  translocated to developing fruit and to new sprouting leaves in similar amount. Urea N was translocated basipetally from current flush leaves to developing fruit. Removing the vegetative sink reduced N influx to the reproductive tissue and increased initial fruit set by a factor of 1.7 to 2.1 in urea-treated and -untreated shoots, respectively. These data indicate that shoot growth does not limit fruit set in avocado via competition for N.

All plants are dependent on soil-derived N for maintenance of vegetative growth and completion of the reproductive cycle. When N uptake from the soil is insufficient to satisfy the requirement for growth, woody species, unlike herbaceous plants, can draw on internal pools of N stored within perennial tissues (14, 17, 22, 24, 26, 28). Deciduous trees store sufficient N in their shoots, trunk, and roots to support the initial reproductive and vegetative growth (14, 22, 24, 25, 28). In evergreens (e.g., citrus, olive), the overwintering leaf is an additional reservoir of carbohydrate (19) and N (15, 17) that can support early spring growth. In fruit trees in general, fruit set and growth can be reduced when vigorous vegetative growth occurs concomitantly and, vice versa, a heavy fruit

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load can severely restrict vegetative growth (2-4, 6, 11, 20, 21). The physiological basis of this reciprocal inhibition is not fully understood, but competition for hormones, carbohydrates, and/or N are thought to be involved (8, 11, 12, 21, 25).

Foliage-applied urea N reportedly increased fruit set in avocado (1) and other species, presumably when the internal pools of N were limiting (8, 13, 18, 22). Foliar uptake, metabolism, and translocation of urea is rapid in avocado (16) and other species (7, 13, 15, 18, 22). Using isotopically labeled N, it has been possible to demonstrate that rapidly developing inflorescences and fruits are a strong N sink (15).

The avocado tree flowers abundantly, but < 0.2% of the blossoms ultimately mature to fruits (8, 21). A heavy initial fruit drop is accompanied by vegetative shoot growth, extending from beyond the inflorescence.

Our objective was to determine whether vegetative growth competes with N acquisition of concurrently developing reproductive organs. Foliage-applied [ $^{15}\text{N}$ ]-urea was used as a tracer to follow N redistribution from treated leaves to developing inflorescences, fruits, and vegetative growth.

## Materials and Methods

All experiments were conducted at the horticultural farm of The Volcani Center, Bet Dagan, and in a commercial plantation at Naan on the coastal plain of Israel. In all experiments  $^{15}\text{N}$ -enriched urea (4.975%  $^{15}\text{N}$  atom excess) was dissolved at the indicated concentration in 0.1% Triton X-100 surfactant and carefully applied using a micropipette and a fine brush to old ( $\approx$ 1 year old) or to young ( $\approx$ 1 month old) leaves. Each leaf was treated with 100 and 200  $\mu\text{l}$  on the upper and lower surfaces, respectively. These volumes were sufficient to wet uniformly the leaf surfaces while avoiding solution run-off. The percent N derived from applied urea has been calculated by multiplying the value of the percent  $^{15}\text{N}$  atom excess in the tissue by factor 20.1 (the ratio between the 100% total N to the 4.975%  $^{15}\text{N}$  atom excess of the enriched urea).

All tissues sampled were dried at 70°C to constant weight and ground. Plant N was determined by wet digestion and nesslerization. The wet digests also were used for  $^{15}\text{N}$  analysis by emission spectrometry. The gas samples were prepared according to the modified Dumas method (9) and analyzed with a Yasco  $^{15}\text{N}$  analyzer (10).

**TRANSLOCATION OF FOLIAGE-APPLIED UREA  $^{15}\text{N}$  TO INFLORESCENCES.** Uniform shoots with at least six old leaves each and a single visible terminal inflorescence were selected for treatment with various concentrations of  $^{15}\text{N}$ -enriched urea on 18 Mar. 1985. The inflorescences were < 25% (100-250 mg dry weight) of their final size. Varying amounts that totaled from 16.8 to 67.2mg urea-N were applied to the six distal leaves on each shoot. Terminal and lateral inflorescences that developed subsequent to 18 Mar. were sampled and counted at the beginning of anthesis 27 days later, when about 30% were flowering. Abscission of old leaves was monitored throughout the experiment.

The effect of proximity of the treated leaf on uptake and translocation of urea  $^{15}\text{N}$  to developing terminal inflorescences was monitored in a separate experiment. A 6% solution of [ $^{15}\text{N}$ ] urea was applied in each treatment to one old leaf per shoot (total of 8.4 mg N) on uniform shoots carrying six leaves each. Treatments were applied on 26 Mar.,

when the inflorescence dry weight was 200 to 300 mg, which was about 30% of final size. The lateral reproductive buds were pinched off at the time of application. The experiment was terminated at full bloom, 30 days later.

**TRANSLOCATION OF FOLIAGE-APPLIED UREA <sup>15</sup>N TO DEVELOPING FRUIT AND VEGETATIVE SINKS.**

One hundred uniform shoots of 'Fuerte' avocado, each carrying three leaves, and one to four inflorescences were selected on 15 trees during initial fruit set. Fruitlets were 1 to 3 mm in diameter (12.1 ± 0.2 mg dry weight/fruit) and many of them were still covered by the sepals. Translocation of <sup>15</sup>N from old leaves to fruit and vegetative sinks was measured. Leaves of one half of these shoots were treated with a 6% solution of <sup>15</sup>N-enriched urea (total of 25.2 mg N/shoot) on 29 Apr. 1985. At the time of treatment the vegetative shoots, which were beginning to grow, were removed from one-half of the urea-treated and -untreated shoots. A total of 200 to 400 fruitlets were counted and percent fruit set was calculated periodically following treatment. Fruit and new leaf samples were collected for analysis 6 and 14 days after urea application. Sampling could not be continued longer because of heavy fruit drop. Sample size on both dates consisted of three or four replicates of four to ten fruitlets each.

**BASIPETAL TRANSLOCATION OF UREA <sup>15</sup>N FROM NEW LEAVES TO DEVELOPING FRUIT.** Shoots carrying a single fruit and only new leaves were selected for treatment in 'Hass' avocado. The first three leaves, located immediately distal to the fruit, were treated with a 3% solution of [<sup>15</sup>N]-urea (12.6 mg N/shoot) on 30 May 1985 when average fruit dry weight was 1.2 g. Six replicates of two fruits each were sampled for analysis 17, 28, and 38 days after treatment.

Table 1. Translocation of urea <sup>15</sup>N from leaves to reproductive tissues of 'Fuerte' avocado and its effect on inflorescence development. Six uppermost leaves of six replicate shoots were treated on a single tree with <sup>15</sup>N-labeled urea.

<sup>15</sup> N-urea applied		Inflorescence				
%	mg/shoot	No. per shoot	Dry wt/shoot (mg)	N in dry wt (%)	N derived from urea (%)	Urea N translocated to inflorescence (%)
<i>Terminal inflorescence</i>						
0			1141 ± 159 <sup>z</sup>	1.89 ± 0.14		
2	16.8		1372 ± 161	2.08 ± 0.18	8.6 ± 1.5	16.1 ± 3.6
4	33.6		926 ± 48	2.24 ± 0.16	13.8 ± 0.4	8.0 ± 1.1
6	50.4		1113 ± 53	2.55 ± 0.16	21.4 ± 4.2	11.1 ± 1.1
8	67.2		964 ± 241	2.50 ± 0.17	26.7 ± 3.0	12.8 ± 2.5
<i>Lateral inflorescence</i>						
0		0.5 ± 0.2	280 ± 134	1.84 ± 0.22		
2	16.8	1.0 ± 0.3	671 ± 156	1.93 ± 0.08	7.5 ± 1.2	6.5 ± 1.1
4	33.6	1.2 ± 0.4	512 ± 67	2.21 ± 0.14	16.0 ± 2.5	5.5 ± 1.4
6	50.4	1.7 ± 0.2	440 ± 42	2.45 ± 0.07	20.6 ± 2.8	5.7 ± 1.0
8 <sup>y</sup>	67.2	0.2	232			

<sup>z</sup>Mean ± SE.

<sup>y</sup>Only a single lateral inflorescence was developed.

## Results

**TRANSLOCATION OF UREA  $^{15}\text{N}$  TO DEVELOPING INFLORESCENCES.** Application from 2% to 8% urea (16.8 to 67.2 mg N/shoot) to old leaves of a single shoot had no significant effect on dry weight of the "terminal" inflorescences but significantly increased N concentration from 1.89% to a maximum of 2.55% (Table 1). The mean number of "lateral" inflorescences on a shoot, which developed subsequent to urea application, increased progressively from 0.5 to 1.7 as urea concentration was increased to 6%. An 8% urea application inhibited development of lateral inflorescences (Table 1). The total dry weight of the combined lateral inflorescences on a shoot was greatest when 2% urea was used (671 mg) and decreased at higher concentrations, although the number of inflorescences increased progressively. The N concentration of lateral inflorescences was similar to that of terminal inflorescences.

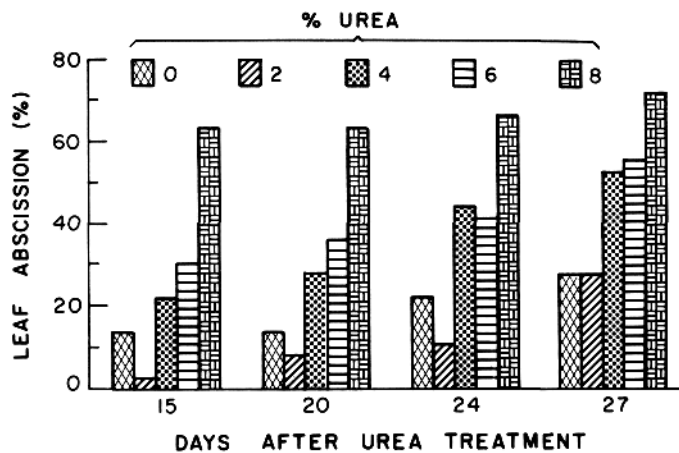


Fig. 1. The effect of urea concentration on leaf abscission in 'Fuerte' avocado following foliar application of  $^{15}\text{N}$  urea. Generalized SE for each urea concentration was 10.3, 7.4, 10.6, 10.0, and 17.1 for 0%, 2%, 4%, 6% and 8% urea, respectively.  $n = 6$ .

Percent N derived from foliage-applied urea in the inflorescences was proportional to the quantity applied. From 8% to 16.1% of the urea N applied to the leaves was translocated to the terminal inflorescence and an additional 5.5% to 6.5% to the lateral inflorescences, regardless of application concentration. About 30% of old 'Fuerte' leaves abscised with either 0% or 2% urea application between 18 Mar. and 14 Apr. (Fig. 1). Four percent and 6% urea generally increased abscission over time, whereas 8% urea resulted in the most leaf abscission within 15 days. Translocation of labeled urea-N from a source leaf to the terminal inflorescence was not affected consistently by leaf proximity to the reproductive sink (Table 2). Overall, an average of 9.6% of the inflorescence N was derived from foliage-applied urea, and 26.9% of the urea applied to the leaf was translocated to the inflorescence.

**TRANSLOCATION OF FOLIAGE-APPLIED UREA  $^{15}\text{N}$  TO DEVELOPING FRUIT AND VEGETATIVE SINKS.** Initial fruit set on intact shoots decreased from 100% on 29 Apr. (the date of treatment) to 4.3% 14 days later (data not shown). During the second half of this period (5 to 13 May), the dry weight of persisting fruits of intact and deshooted branches increased more than three-fold (Table 3). Nitrogen concentration in fruit on intact shoots remained constant between 5 and 13 May, but decreased when new vegetative growth was removed. Percent  $^{15}\text{N}$  atom excess and percent fruit N derived from urea were greater on intact shoots than on deshooted branches. N concentration of the new spring flush growth leaf was similar to those of the fruit. However, percent N derived from urea of fruit increased and that of new leaves decreased between 5 and 13 May. Removal of the new shoot growth on 29 Apr. increased 'Fuerte' avocado fruit set on 13 May by a

factor of 1.7 and 2.1 in urea-treated and untreated shoots, respectively (Fig. 2). The effect of shoot removal on fruit set became evident by 10 days after the treatment.

Table 2. Translocation of urea  $^{15}\text{N}$  from leaves to terminal inflorescences of 'Fuerte' avocado as affected by proximity to terminal inflorescence. A single leaf on six replicate shoots was treated on a single tree.

Proximity of treated leaf (nodes from inflorescence)	Inflorescence			Urea N translocated to inflorescence (%)
	Dry wt (mg)	N in dry wt (%)	N derived from urea (%)	
1 <sup>z</sup>	1374 ± 220 <sup>y</sup>	1.64 ± 0.12	7.9 ± 0.1	20.2 ± 1.2
2	1153 ± 134	1.78 ± 0.09	12.1 ± 0.5	36.5 ± 2.1
3	1250 ± 123	1.57 ± 0.17	9.0 ± 0.5	20.0 ± 1.8
4	1144 ± 152	1.55 ± 0.04	10.3 ± 1.3	27.3 ± 3.3
5	1395 ± 210	1.68 ± 0.08	10.3 ± 0.9	29.2 ± 1.3
6	1406 ± 119	1.94 ± 0.20	8.0 ± 1.0	28.9 ± 3.7
Mean	1287	1.69	9.6	26.9

<sup>z</sup>“1” refers to leaf adjacent to inflorescence; “6” refer to the leaf six nodes from the inflorescence.

<sup>y</sup>Mean ± SE.

Table 3. Translocation of urea  $^{15}\text{N}$  from old 'Fuerte' avocado leaves to developing fruit and new vegetative leaves. Each treatment was replicated three or four times on a total of 25 shoots carrying each with three leaves and one to four inflorescences.

Sampling date	Fruit			New leaves	
	Dry wt (mg)	N in dry wt (%)	N derived from urea (%)	N in dry wt (%)	N derived from urea (%)
	<i>Intact branch</i>				
5 May	10.6 ± 1.7 <sup>z</sup>	3.14 ± 0.08	10.8 ± 0.4	3.20 ± 0.26	12.3 ± 0.5
13 May	37.4 ± 14.7	3.10 ± 0.05	13.5 ± 0.4	3.03 ± 0.16	10.9 ± 0.8
	<i>Deshooted branch</i>				
5 May	8.8 ± 1.6	3.18 ± 0.08	7.21 ± 0.8		
13 May	41.0 ± 3.8	2.85 ± 0.10	10.10 ± 1.0		

<sup>z</sup>Mean ± SE.

**BASIPETAL TRANSLOCATION OF UREA  $^{15}\text{N}$  FROM NEW LEAVES TO GROWING FRUITS.** Fruit dry weight increased considerably and N concentration decreased only slightly, indicating an active influx of N to the fruit (Table 4). Percent fruit N derived from urea was consistently higher than background in all measurements. Fruit N of 'Hass' derived from the foliage-applied urea decreased gradually as the urea N translocation from new, fully expanded leaves to the fruit increased.

## Discussion

Urea phytotoxicity in avocado can be expressed as marginal scorch (unpublished data) and/or as leaf abscission. Leaf abscission may continue for several weeks after

treatment of 1-year-old leaves (Fig. 1.). Urea hastened abscission of physiologically older leaves, which would have abscised naturally at some later stage.

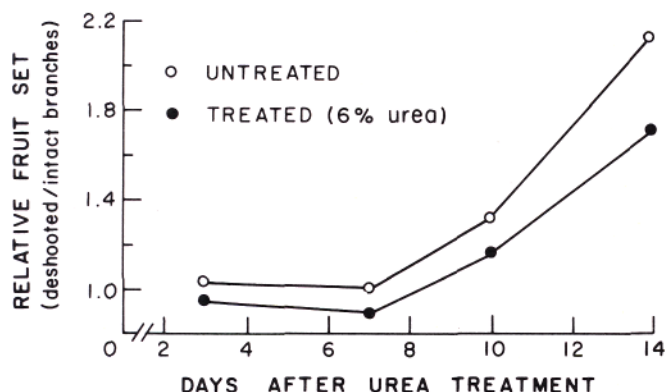


Fig. 2. The effect of shoot removal on the ratio of percent fruit set between deshooted branches to intact branches of urea-treated and untreated 'Fuerte' avocado. Generalized SEs of the ratios were 0.078, 0.150, 0.290, and 0.522 for 3, 7, 10, and 14 days after urea treatment, respectively.  $n = 5$ .

either as a direct result of increased N or indirectly as a consequence of leaves defoliating.

An increase in the number and size of lateral inflorescences on the tree without causing defoliation (Table 1, 2% urea) could prolong the flowering period and increase fruit set, as reported for mango following foliage application of 2% to 4% urea (23). An extended period of flowering as a result of urea spray may increase fruit set under fluctuating environmental conditions, independent of its contribution to the N reserves of the tree.

Foliage application of 2% to 8% urea had no effect on the size of the terminal inflorescence. The decrease in total dry weight of the combined lateral inflorescence by urea treatments (Table 1) may be attributed to the reduced leaf area on the shoot as a result of accelerated leaf drop. Thus, lack of carbohydrates rather than N may have limited dry weight accumulation of lateral

inflorescences. The significant increase in N concentration without any increase in weight of the inflorescence after foliage application of urea (Table 1) also indicated that N was not limiting the growth of the inflorescence.

The avocado resumes its spring flush of vegetative growth from the tip of the terminal-like inflorescence during or shortly after flowering. Both reproductive and vegetative growth, developing concurrently, acquired a similar percent  $^{15}\text{N}$  atom excess and therefore were considered to be equally strong sinks for foliar-applied urea N (Table 3).

Up to 85% of the applied urea can be taken up by the avocado leaf within 2 to 5 days (16). In this study, translocation of  $^{15}\text{N}$  to the inflorescence was proportional to the quantity applied (Table 1), substantiating rapid urea uptake and its N translocation out of the leaf before the leaves abscised. Foliage application of a solution of 4% to 10% urea, just before its natural leaf drop, is an efficient N nutritional practice in apple (18, 22), although it causes heavy leaf damage. Urea application increased the number of lateral inflorescences,

Table 4. Basipetal translocation of foliar-applied urea  $^{15}\text{N}$  from the new leaves of the spring flush growth of 'Hass' avocado to growing fruits. Six replicates of two fruits each were sampled at the indicated times.

Days after treatment	Fruit			
	Dry wt (g)	N in dry wt (%)	N derived from urea (%)	Urea N translocated to fruit (%)
17	4.31 ± 0.09 <sup>z</sup>	1.56 ± 0.05	2.44 ± 0.23	15.0 ± 2.5
28	7.06 ± 0.30	1.42 ± 0.11	1.80 ± 0.13	14.5 ± 1.5
38	10.21 ± 0.44	1.44 ± 0.06	1.76 ± 0.32	22.0 ± 4.7

<sup>z</sup>Mean ± SE.

This activity occurred in spite of the fact that the dry weight of the fruit was only a few milligrams, whereas that of the vegetative extension growth increased rapidly and reached several grams at the last sampling date.

Removal of the newly vegetative growth reduced N translocation to the young fruit, indicating that N influx to the reproductive sink at an early stage is enhanced by the presence of vegetative tissues. At the very early stage, the sprouting leaves are an N sink rather than source. This vegetative sink probably sustains the N translocation to reproductive sink as well. However, at a later stage, competition for N among vegetative and reproductive sinks might be demonstrated by increasing yield following foliar application of urea both in avocado (1) and in deciduous crops (8, 13, 18, 22).

In this study, deshooting doubled the initial fruit set (Fig. 2). Temporary inhibition of vegetative growth in avocado using growth retardants (I. Adato, personal communication) or manual pinching of new sprouting shoots (5) also increased fruit set and yield.

The benefit in initial fruit set by deshooting in avocado could not be attributed, therefore, to improve N nutrition of the developing fruit. Thus, other explanations [e.g., improved carbohydrate supply (20) and a more favorable hormonal balance (3)] must be sought to explain the stimulus to initial fruit set by deshooting.

Redistribution of N and other minerals (i.e., Mg, Mn) from old leaves to the vegetative growing tip is a well-known process. The extent of redistribution to the fruit is less well-known. <sup>15</sup>N enrichment of expanding leaves of 'Fuerte' avocado decreased and the enrichment of the fruit increased temporally (Table 3). This change in <sup>15</sup>N enrichment could have resulted from a redistribution of N from new leaves to fruits even before full leaf expansion. Basipetal translocation of urea <sup>15</sup>N in 'Hass' (Table 4) supports this explanation. Similar redistribution of N from almond foliage and pericarp to embryo has been reported (27).

Foliage-applied urea in avocado can be used effectively prior to leaf drop to supplement the N resources. Since the proximity of treated leaves to the inflorescence was unimportant, all the leaves on the avocado tree can be considered equally effective in absorbing urea or supplying N for vegetative and reproductive growth.

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