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J. Amer. Soc. Hort. Sci. 103(4):516–519. 1978.

Seasonal Variation in Nitrate Uptake Efficiency and Distribution of Absorbed Nitrogen in Non-bearing Prune Trees[1]

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Additional index words. Prunus domestica, fruit trees, nitrogen fertilization, ^{15}N

Abstract. **Non-bearing prune (*Prunus domestica* L. cv. Agen) trees were fertilized with ^{15}N-KNO_3 for 10 days during 9 phenological periods. Nitrate uptake efficienty (NUE) and the distribution of absorbed ^{15}N in the trees were determined for each of these application periods. Nitrate uptake was dependent on presence of leaves, and NUE was low from the period of natural leaf fall until shoot growth had commenced the following spring. NUE increased dramatically during the rapid phase of shoot elongation, and remained high until leaf fall. Nitrogen absorbed from fertilizer was rapidly mobilized by swelling buds and rapidly elongating shoots. The spring flush of vegetative growth utilized both the currently available fertilizer (^{15}N) nitrogen and tree nitrogen reserves. Rapid shoot elongation was primarily dependent, however, on the redistribution of storage N.**

The time of year at which nitrogenous fertilizers are most efficiently applied to deciduous fruit trees remains a subject of debate, and fertilizers have been applied without apparent knowledge of the trees capacity for NO_3^- recovery. Many field trials have been inconclusive because mineralization of organic N by microorganisms increases with rising summer temp, and, consequently, a fluctuation in available N may be superimposed over treatments (18). Furthermore, irrigation practices, soil type, and nitrogen carrier influence the movement and availability of the nitrogen applied.

In this experiment the influence of soil-related processes was minimized to permit determination of the inherent seasonal capacity of the non-bearing prune tree for NO_3^- uptake. The determination of NO_3^- uptake potential has not been emphasized in previous reports (3, 5, 7, 13). Our rationale was the following: if the NO_3^- uptake capacity of the prune tree is high during root interception of the fertilizer, the likelihood of NO_3^- loss as a result of denitrification, biological immobilization, or leaching will be reduced.

Materials and Methods

Ninety 2-year-old 'Agen' prune trees on Mariana 2624 rootstocks were maintained outdoors in 60-liter pots containing acid-cleaned sand. The coarse inorganic medium facilitated the movement of fertilizer N and its interception by the root mass. Potted trees were placed in trenches to provide root-zone temp comparable to that of the surrounding soil. Irrigation and fertilization were conducted as previously described (20).

Nitrogen utilization efficiency (NUE) was defined as:

$$NUE = \frac{\text{Total fertilizer N abosorbed/tree per 10 days}}{\text{Total fertilizer N applied/tree per 10 days}} \times 100$$

Enrichment of fertilizer with the stable isotope ^{15}N permitted direct measurement of nutrient uptake from the fertilizer applied (2). Labeled KNO_3 (0.5g ^{15}N, i.e., 5.4g ^{15}N-KNO_3; 65.57 atom % excess ^{15}N; Monsanto Research Crop., Mound Laboratory) dissolved in standard nutrient solution (20), minus the standard KNO_3, was supplied to 8 trees in 4 equal doses (0.125g ^{15}N/tree per dose) over a 10-day period. This was repeated (with different trees) 9 times during the year (Table 1). To maximize interaction between roots and ^{15}N fertilizer, the fertilizer effluent was collected and reapplied daily during treatment periods. The medium was subsequently leached to limit the period of ^{15}N availability. Root zone temp were monitored continuously during ^{15}N application periods. Two additional trees were maintained on the standard fertilization regime (no ^{15}N) and harvested with the rest to reflect control $^{14}N/^{15}N$ ratios. Ten days after the final ^{15}N application trees were harvested in their entirety and fractionated into the following components when present: leaves, buds, current shoots, 1-year-growth, 2-year-old scion wood, trunk (rootstock), roots > 1mm cross section diam, and fine roots ≤ 1mm cross section diam. Tissue fractions were quick frozen in liquid N_2, lyophilized, weighed, milled, and stored at –60°C until analyzed.

Total N and ^{15}N were determined in 0.5g subsamples as described previously (21).

[1]Received for publication December 31, 1977.
The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper must therefore be hereby marked *advertisement* solely to indicate this fact.
[2]The authors thank the California Prune Advisory Board for partial financial support of this project.

Table 1. Nitrate uptake efficiency of non-bearing prune trees following 10-day exposure to ^{15}N-KNO_3 at different phenological periods.

^{15}N-KNO_3 application periods	Tree harvest dates	Nitrate uptake efficiency (%)
Dormant (Jan. 16-26)	Feb. 5, 1976	4.75[z] A
Bud swell (Mar. 5-15)	Mar. 25	4.34 A
Rapid shoot growth (April 2-12)	April 22	30.52 C
Shoot growth cessation (May 14-24)	June 3	39.02 C
(July 9-19)	July 29	32.73 C
(Aug. 6-16)	Aug. 26	35.91 C
(Sept. 10-20)	Sept. 30	32.73 C
Mid-leaf fall (Oct. 22-Nov. 1)	Nov. 11	16.14 B
Dormant (Dec. 3-13)	Dec. 23	3.66 A

[z]Mean separation within columns by Duncan's multiple range test, 1% level.

Results and Discussion

By standardizing the interaction between the root mass and a constant amount of isotopic NO_3^- in a coarse inorganic medium, our results presumably reflect the short-term physiological potential for NO_3^- uptake during different phenological stages of tree development and under the fertilization regime employed (8).

Seasonal efficiency of NO_3^- uptake. Nitrate uptake efficienty (NUE) was minimal during dormancy and remained low during bud swell (Table 1). It is doubtful whether low temp was the primary limitation to NO_3^- absorption since daytime root-zone temp averaged 15°C during the Jan. application period. Fertilizer uptake increased greatly between bud swell and rapid shoot elongation and remained relatively constant until leaf fall. NUE was about 10× higher during the growing season than the dormant period. The NUE in bearing trees may be reduced in early- and mid-summer as a result of assimilate diversion to the developing crop (11). NUE decreased rapidly during natural leaf fall (Table 1).

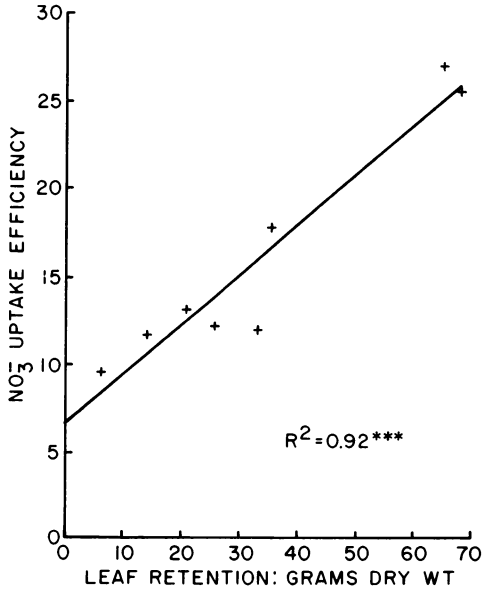

Fig. 1. The relations between nitrate uptake efficiency of non-bearing prune trees and leaf mass of individual trees during the mid-leaf fall ^{15}N application period.

Table 2. Relation between presence of leaves, leaf N (% dry wt) and nitrate uptake efficiency of non-bearing prune trees during mid-leaf fall.

Tree number	Leaf mass		Nitrate uptake efficiency (%)
	Dry wt (g)	% N	
1	35.74	1.54	12.3
2	68.42	1.62	27.0
3.	33.34	1.42	13.2
4	14.31	1.59	9.6
5	6.48	1.30	11.7
6	21.18	1.40	12.0
7	65.61	1.78	25.5
8	25.84	1.50	17.7

The correlation between the presence of leaves and NUE (Fig. 1) was highly significant (0.1%) indicating that metabolic activity correlated with the delay of natural leaf fall prolonged NO_3^- uptake to autumn. These data are consistent with previous indications of a functional relation between natural leaf fall and the decline in N uptake (5, 6). Our data did not permit discrimination between quantitative vs. qualitative influences of the foliage. Trees with the greatest leaf mass (corresponding to greatest NUE) also had the highest N content in the foliage (Table 2).

Nitrate uptake is an energy-requiring process, and depends upon the availability of soluble carbohydrate (9, 12). Reduced carbon assimilation following defoliation or shading (10), or a diversion of assimilate to the developing crop (11) limits root growth (and presumably nutrient uptake) during the growing season; in autumn, however, carbohydrates accumulate in perrenial tissues (4), and hence, a reduced dependence of root growth on photosynthesis may have been anticipated. Carbohydrate utilized for NO_3^- assimilation in autumn, therefore, may be more closely related to levels of recently transported assimilate than total extractable root carbohydrate (16). Hormonal involvement in root proliferation and function cannot be precluded. Richardson (17) has demonstrated a positive relation between root growth and the presence of leaves which was quite independent of photosynthesis. Root temp influences both root growth and salt uptake since these activities are metabolically dependent. In the present experiment, however, the variation in NUE among individual tree replicates during mid-leaf fall was clearly independent of root zone temp. Also, since NO_3^- uptake is reportedly independent of water flow across the root (4, 14, 15), differential NUE appears independent of transpiration, although we can't rule it out.

Within tree distribution of recently absorbed ^{15}N. The ^{15}N absorbed during dormant periods remained within the rootstock and was concentrated in the fine roots (data not presented). Although NUE did not increase between dormancy (Jan.) and bud swelling (March) the movement of fertilizer N, (i.e., ^{15}N distribution patterns within the trees) differed markedly (Table 3). Of the ^{15}N abosrbed in the March application period, 23% was mobilized by the expanding buds. Proportionately less ^{15}N remained in the roots as compared with the previous (dormant) application period. The fertilizer N mobilized by expanding buds represented about 2% of the total N content of these buds; the remainder (98%) was apparently redistributed from storage (data not presented). Of the ^{15}N absorbed during the April (rapid shoot growth) application period, 70% was found in the new shoots and leaves. At the same time only 18% of the fertilizer N absorbed remained in the rootstock (Table 3).

Our data do not support the idea (19) that N in the storage

Table 3. Comparative distributions of ^{15}N in non-bearing prune trees absorbed during 10-day ^{15}N-KNO_3 applications during various phenological periods.

^{15}N-application period	^{15}N distribution (%)				
	Current growth[z]	1-year scion wood	2-year scion wood	Rootstock	
				Trunk	Roots
Dormant (Jan. 16-26)	–[y]	–	0.1	8.3	81.6
Bud swell (Mar. 5-15)	23.0	4.1	1.9	9.3	61.7
Rapid shoot growth (April 2-12)	70.6	5.3	1.6	3.7	17.8
Shoot growth cessation (May 14-24)	36.8	6.5	3.5	8.6	44.7
(Sept. 10-20)	19.6	3.7	2.3	7.9	66.6
Mid-leaf fall (Oct. 22-Nov. 1)	13.0	5.8	2.9	11.2	66.4

[z]Includes buds and leaves plus new shoots when present.
[y]Percent of total absorbed ^{15}N.

Table 4. Relative contributions of previously assimilated N vs. recently absorbed N to the N demands of the new growth.

Nitrogen source	N content (mg)		% in current growth
	Current growth[z]	Entire tree	
Fertilizer (^{15}N)	108	153	70
Previously assimilated N	1154	2168	53

[z]Includes new shoots and leaves.

pool (i.e., previously assimilated N) is preferentially utilized to support new growth rather than currently available (fertilizer) N. The recently absorbed nitrogen satisfied only a small part of the N requirement of elongating shoots and their dependence on previously-assimilated (stored) nitrogen was apparent (Table 4). That is, 153 mg of fertilizer N was absorbed per tree during the April ^{15}N-application period and 70% of this, i.e., 108 mg, was mobilized by current growth. The total N content of the new growth (1154 mg) greatly exceeded the total amount of fertilizer N absorbed and, therefore, 90% of the N in the new growth was mobilized from storage and/or absorbed prior to the April ^{15}N-application period.

We contend that NO_3^- utilization may be improved by maintaining low NO_3^- levels in soil solution when leaching and/or denitrification is likely to occur. This period occurs in winter in northern California (1) and coincides with the period of minimum NUE (Table 1). Fertilization when trees are dormant does not appear consistent with efficient N use; however, our data are not sufficient for recommendation of specific fertilizer application regimes. The N carrier, soil type, irrigation practices, and climatic influences will all affect the movement and availability of fertilizer N. Furthermore, tree age and crop load may modify seasonal patterns of NO_3^- uptake.

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J. Amer. Soc. Hort. Sci. 103(4):519–522. 1978.

The Occurrence and Some Effects of Raspberry Bushy Dwarf Virus in Red Raspberry[1]

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Additional index words. Rubus idaeus, crumbly fruit

Abstract. **Raspberry bushy dwarf virus (RBDV) was found in 25 of 75 cultivars maintained in the British Columbia red raspberry (*Rubus idaeus* L.) breeding program. Crumbly-appearing fruit and leaf abnormalities were associated with infection in some of the cultivars. No RBDV was found in commercial fields of the Willamette cultivar. Comparisons of RBDV-infected and virus-free plants of BC 64-6-68, a selection from the breeding program, showed that the virus reduced yield and fruit size, and increased drupelet abortion resulting in crumbly fruit. RBDV infection did not affect vegetative growth. Field spread of the virus in BC 64-6-68 was through pollen.**

Raspberry bushy dwarf virus (RBDV) has been reported in red raspberry, black raspberry (*R. occidentalis* L.) and loganberry (*R. ursinus* Cham. & Schlect. var. *loganobaccus* Bailey) (13). The results of RBDV infection in different red raspberry cultivars have varied from latent (3) to the production of crumbly fruit (15) and reduced cane growth (5). The virus is seed-borne, through pollen and ovules, and is spread in the field by pollen (13).

The purpose of this investigation was to determine: (a) the occurrence of RBDV infection in a collection of cultivars maintained in the British Columbia red raspberry breeding program, (b) the occurrence of RBDV in some British Columbia red raspberry fields, (c) the effects of RBDV on the growth and fruiting of a selection from the breeding program and (d) the spread of RBDV in this selection over a 3 year period.

Materials and Methods

To determine the occurrence of RBDV in 75 cultivars, which had been maintained in field plots for at least 4 and up to 10 years, leaf tissue of each was tested for RBDV by mechanical inoculation to *Chenopodium quinoa* Willd. A piece of immature tissue about 5 mm^2 was ground in 0.5 ml of 0.02 ml phosphate buffer. pH 7.2, containing 1% nicotine and 1% polyvinyl pyrrolidone, then rubbed onto 2 or more leaves of the indicator plant. Indexing was done in the spring or early summer. Cultivars that gave a negative reading were reindexed. Infected *C. quinoa* plants developed systemic mottle and ringspot symptoms on the youngest leaves 6-8 days after inoculation. In addition all cultivars were examined for leaf abnormalities over a period of several years.

To determine the presence and distribution of RBDV in commercial plantings, leaf samples were taken from 36 plants in each of 13 fields of 'Willamette', the most widely grown cultivar in British Columbia. Testing was done for the presence of RBDV by mechanical inoculation to *C. quinoa.*

The effects of RBDV on growth and fruiting were determined on BC 64-6-68, a selection from a 1964 cross of 'Carnival' × 'Willamette'. The selection, which is immune to the aphid vector, *Amphorophora agathonica* (Hottes), of red raspberry mosaic virus and is thus free of this virus, was made in 1967. It first attracted attention because of its large, firm attractive fruit which had a full complement of drupelets. The selection was propagated in 1973 for establishment in a replicated yield trial. At that time, the stock plant, from which root cuttings were obtained for propagation, was indexed for RBDV and for tomato ringspot virus (Tom RSV) (16). It was found to be free of both viruses. In 1975 it was observed that some of the plants in the trial produced fruit with a crumbly appearance due to reduced numbers of drupelets. The 30 plants (10 in each of 3 replications of a randomized block design) in the trial were subsequently indexed to *C. quinoa* for the presence of RBDV and to cucumber for the presence of Tom RSV. Some plants indexed positively for RBDV and there was an association between infection and crumbly fruit. Each plant was subsequently indexed for RBDV in 1976 and 1977. The incidences of crumbly fruit and of leaf abnormalities were also recorded in these years.

In 1976 and 1977 fruit yields and sizes were recorded from a virus-free (VF) and RBDV-infected plant, in each replication of BC 64-6-68. In 1977 cane heights and diameters were also obtained from these plants.

The possible causes of the reduced drupelet set in the RBDV-infected plants of BC 64-6-68 were investigated in 1976 and 1977. In each year drupelet set was determined by bagging 5 flower clusters on a VF and RBDV-infected plant in each replication and subsequently moving pollen from flower to flower within each bag every other day (6). Percent drupelet set from each cluster was obtained for each of 6 fruits in 1976 and 7 fruits in 1977 by recording the number of well-formed drupelets and the number of aborted drupelets.

To determine whether RBDV-infected pollen would reduce drupelet set of fruit on VF plants, 5 flower clusters, each with 7 flowers, on a VF plant in each replication were pollinated in 1977 with pollen from flowers on RBDV-infected plants. The reciprocal of this pollination treatment was also done.

To determine any association between reduced drupelet set

[1]Received for publication February 28, 1978.
The cost of publishing thie paper was defrayed in part by the payment of page charges. Under postal regulations, this paper must therefore be hereby marked *advertisement* solely to indicate this fact.

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