J. AMER. SOC. HORT. SCI. 116(2):291-296. 1991.

Distillate Flower Abortion in 'Serr' Walnut Associated with Reduced Carbohydrate and Nitrogen Concentrations in Wood and Xylem Sap

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Additional index words. Juglans regia, nitrogen reserves, starch, fruit set, fruit trees, carbon-nitrogen relationships

Abstract. **Abortion of distillate flowers (PFA) in a protandrous cultivar of walnut (*Juglans regia* L. cv. Serr) was increased by N deficiency. Starch and N concentrations in wood of 2-year-old twigs decreased to minimal levels during abortion of distillate flowers. Nitrogen reserves in woody tissues were reduced by foliar N deficiency, as were concentrations of sugars and N in vacuum-extracted xylem sap. Abortive distillate flowers ceased growth before spur leaves reached 50% of full expansion. PFA may result from transient deficiencies of C and N during the spring flush of growth. Depletion of storage C and N was accentuated before maturation of distillate flowers in this cultivar by the metabolic demands of many catkins, spur growth, and leaf expansion.**

Deciduous trees typically abort high percentages of flowers and immature fruits (Stephenson, 1981). Abortion of immature reproductive organs may result from environmental variables that reduce floral viability and limit pollination. Reduced fruit and seed set may also result from the inability of the maternal parent to provide sufficient metabolic resources for continued development (Leopold and Scott, 1952; Sachs, 1977; Stephenson, 1981).

Distillate flower abortion (PFA) percentages as high as 90% have been measured in 'Serr' walnut trees (Catlin et al., 1987; Ryugo et al., 1985). Ryugo et al. (1985) reported that removal of immature catkins during dormancy increased persistence of distillate flowers during the subsequent spring and postulated that inadequate resources may accentuate PFA. PFA has also been reported in pecan (Sparks and Madden, 1985), another member of the Juglandaceae.

The spring growth flush in deciduous fruit tree species depends largely on the redistribution and use of C and N compounds assimilated from previous year(s) and stored over winter in perennial tissues (Kandiah, 1979; Oland, 1959; Stassen et al., 1981; Titus and Kang, 1982; Weinbaum et al., 1978, 1987). The redistribution of C and N reserves has been studied by determining changes in their concentrations in perennial tissue and xylem sap during the spring growth flush (Ferguson, 1980). Studies using ^{15}N-labeled $(NH_4)_2SO_4$ indicate that a dramatic depletion of storage N from woody tissues occurs before pistillate flower maturation in 'Serr' (Deng et al., 1989a, 1989b).

The objective of this study was to assess the temporal relationship between PFA and the dynamics of storage C and N redistribution in wood and xylem sap in 'Serr' walnut. Nitrogen fertilizer was withheld to manipulate the endogenous pool of storage N, assess the interrelationship between C and N availability, and determine the effect of N deficiency on PFA.

Materials and Methods

Plant materials and treatments. The study used mature 'Serr' walnut trees grafted on Northern California black walnut *[J. hindsii* (Jeps.) Rehder] seedling rootstock. Trees were growing in a Hanford sandy loam soil (coarse-loamy, mixed nonacid, thermic typic xerorphents) in a commercial orchard at Oakdale, Calif. (lat. 37°41'N, long. 12°50'W). The trees selected were similar in size (trunk cross-sectional areas averaged 207 cm^2) and yield before the experiment was initiated (S.A.W., data not presented).

One of two fertilizer treatments were imposed on each of four single-tree replicates. Experimental trees were randomized within the orchard, but were separated from each other by at least three buffer trees to eliminate interference between treatments. Variability of the data about the mean is expressed as standard error. Experimental preconditioning was begun in 1984, although the years of record were 1986 and 1987. Treatments and designations are as follows: Fertilized trees were fertilized annually (from 1984 on) throughout the experiment. These trees are referred to as "+N" trees in 1986 and "+N+N" trees in 1987. Nitrogen-deficient trees (N withheld between July 1984 and Jan. 1987) are designated "– N" (in 1986) and "–N+ N" (in 1987) to indicate that fertilizer N was applied to - N trees in Jan. 1987. Fertilized trees received 2 kg of N annually [applied as $(NH_4)_2SO_4$]; i.e., +N (1986), +N+N (1987), and -N+N (1987).

Tree phenology and distillate flower abortion. Twenty randomly selected catkins were harvested periodically from each tree, oven-dried, and weighed to determine the time of growth resumption. Distillate flowers emerging from 100 randomly tagged terminal buds were counted at 3- to 4-day intervals between late-Mar. and late-Apr. 1987; the percentages of flowers that were receptive (open stigmas), mature (>4 mm in diameter, with fully developed, reflexed stigmas), or abortive (Catlin et al., 1987) were recorded. Leaf areas of five spurs (each spur with six compound leaves) from each experimental tree were measured periodically with a Delta-T area meter (Decagon Devices, Pullman, Wash.) between 4 Apr. and 30 May 1987.

Xylem sap extraction. Xylem sap was extracted under vacuum from twigs cut periodically between mid-February (i.e., before macroscopic growth resumption) and late May (following completion of leaf expansion). Three 2-year-old twigs, ≈50 cm long, were collected periodically from the top of each tree between 9:30 AM and 11:00 AM. All leaves and small twigs present were removed at the time of sampling to minimize the loss of moisture, and excised twigs were kept in plastic bags on ice during transport from field to laboratory.

Sap was extracted by gas displacement according to Bollard

Received for publication 19 Apr. 1990. This work was funded in part by the California Walnut Marketing Board. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

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(1953), with the following modifications: 1) bark was removed before sap extraction to prevent cellular contamination, 2) flask vacuum pressure was reduced to 75–125 mm Hg during sap extraction, and 3) 1-cm sections were cut successively from the distal ends of twigs about every 15 sec during vacuum extraction. The sap collected was centrifuged at 4C, and clear sap samples were then stored at 20C until analysis. About 10 ml of sap was extracted and composite from the twigs of each tree on each sampling date.

Tissue sampling. Two-year-old twigs were collected from each experimental tree. The wood (xylem) was separated from the bark and cut into 0.5-cm-long pieces. Five spurs per tree were collected periodically during the spring. Spurs were separated into leaf blades, new shoots plus rachises, and reproductive organs. Samples were oven-dried at 55C, weighed, ground in a Wiley mill to pass a 10-mesh sieve, and stored in sealed plastic bags until they were anlayzed.

Analyses. Total N in 5 ml of xylem sap or 500 mg of ground dry tissue was determined by a modified macro-Kjeldahl method (Bremner, 1965). Nitrate N was included in the total N measurement by the pretreatment of samples with salicylic acid. Nitrate N in the xylem sap was determined according to Thayer and Huffaker (1980).

Sugars and sugar alcohols in 1 ml of xylem sap were measured using a Shimadzu GC-9AM gas chromatography (Shimadzu, Kyoto, Japan) after evaporation of the sap to dryness. Residues were redissolved in pyridine, silated with hexyamethyl disilazane and trimethyl chlorosilane according to Sweeley et al. (1963).

Soluble sugars were extracted from xylem tissue with 80% ethanol and measured with a gas chromatography according to Sweeley et al. (1963). Strach remaining in the residue after sugar extraction was hydrolyzed by incubation with amyloglucosidase (1,4- α– D glucan glucohydrolase, EC 3.2.1.3, Sigma, St. Louis) solution at 37C for 30 h and then measured as glucose equivalents using anthrone (Sunderwirth et al., 1964).

Results

Tree N status. Trees not supplied with N since early 1984 defoliated prematurely in Oct. 1984 (data not presented). These trees had less vegetative growth and reduced yields than fertilized trees (Weinbaum, unpublished data) and midsummer leaf N concentrations <2.3% in 1985 and 1986 (Table 1). Leaf N concentrations of –N+N trees were increased to near that of control trees (+N+N) by mid-Summer 1987 following N fertilization in Jan. 1987 (Table 1).

Phenology and distillate flower abortion. Catkin dry weight began to increase by 1 Mar. and ≈50% of the catkins had matured by 25 Mar. 1987 (Deng et al., 1989a). Maturation of the distillate flowers occurred 20 days later (Deng et al., 1989a). The dates of catkin and distillate flower maturation in 'Serr' were not affected by N status, nor were the kinetics of leaf expansion (Deng, 1987).

PFA occurred in all experimental trees and was 26% higher in –N trees than in +N trees in both 1986 and 1987 (Table 1). Both +N and –N trees (1986) aborted 50% more distillate flowers than did +N+N and –N+N trees in 1987. Since the N status of the fertilized trees (i.e., +N and +N+N) did not vary greatly between 1986 and 1987, PFA appears to have been influenced by variables other than tree N status.

The total N content of leaves, shoots, and reproductive organs of -N+N trees was 10% to 25% lower than comparable organs of +N+N trees during Spring 1987 (Table 2). The N content of spur leaves and distillate flowers on –N+N trees was 12% and ≈15% lower, respectively, than those of comparable samples from +N+N trees at the time of pistillate flower maturation (14 Apr. 1987) (Table 2).

Effect of N status and phenology on N concentration of xylem sap. Total N concentration in xylem sap did not differ among treatments before growth resumption in February (Fig. 1). Total N concentration in xylem sap of +N and +N+N trees was highest at the time of catkin maturation in mid- to late March during 1986 and 1987 (Fig. 1). In –N trees, this increase was considerably less than in +N trees in 1986 and was nonexistent in –N+N trees 1987 (Fig. 1). The concentration of N in xylem sap declined between the time of catkin maturation and the completion of leaf expansion in May (Fig. 1). The concentration of N in xylem sap collected from –N trees was invariably lower than corresponding sap samples extracted from +N trees.

Effect of N status and phenology on nitrate concentration in xylem sap. No nitrate was detected in xylem sap during February, i.e., before growth resumption (Fig. 2). Nitrate in xylem sap was first detected in trace amounts, i.e., ≈0.05% of total sap N at the time of catkin maturation and the onset of leaf expansion in both 1986 and 1987. In +N trees (1986), sap nitrate concentration increased rapidly during the period of leaf expansion, i.e., until early to mid-May and then remained constant at 10% to 12% of total sap N. Sap NO_3^- expressed as a percentage of total sap N only reached 6% in 1987. The percentage of nitrate N in xylem sap of +N trees was invariably greater than that in –N trees (Fig. 2). Nitrogen-deficient (–N) trees that had not been fertilized in 1986 exhibited a quick de-

Table 1. Influence of N treatment on leaf N concentration and pistillate flower abortion (PFA) in 'Serr' walnut.[z]

	Leaf N (% dry wt)		PFA (%)	
Treatment[y]	1986	1987	1986	1987
+N	2.79 ± 0.06	---	45.8 ± 3.7	---
−N	2.04 ± 0.13	---	57.7 ± 3.2	---
+N+N	---	2.61 ± 0.07	---	30.5 ± 2.6
−N−N	---	2.57 ± 0.05	---	38.3 ± 3.1

[z]Data are means ±SE of four individual-tree replicates.
[y]Treatments designated as: 1) +N (1986), +N+N (1987) = N applied annually from 1984 to 1987; 2) −N = no N July 1984–Jan. 1987; 3) −N+N = as in 2 but N applied Jan. 1987.

Table 2. Influence of N treatment on total N content in leaves, shoots, and reproductive organs of 'Serr' walnut trees in 1987.[z]

	N content (mg/spur)			
Treatment[y]	4 Apr.	14 Apr.	8 May	30 May
		Leaves		
+N+N	56.5 ± 2.9	136 ± 11.4	248 ± 20.6	257 ± 13.9
−N+N	45.3 ± 5.9	120 ± 8.8	224 ± 9.0	228 ± 8.6
		Shoots + rachises		
+N+N	23.6 ± 0.7	25.6 ± 1.6	36.9 ± 3.2	43.0 ± 2.6
−N+N	19.3 ± 1.1	24.1 ± 1.8	34.1 ± 2.7	41.3 ± 4.4
	Pistillate flowers		*Fruit*	
+N+N	0.54 ± 0.02	2.0 ± 0.11	85.1 ± 1.3	167 ± 9.8
−N+N	0.46 ± 0.04	1.7 ± 0.12	77.6 ± 3.6	130 ± 9.5
		Spur		
+N+N	80.6 ± 4.9	164 ± 9.3	370 ± 14.5	467 ± 15.2
−N+N	65.1 ± 2.5	146 ± 7.5	336 ± 8.8	400 ± 13.0

[z]Data are means ±SE of four replicates.
[y]See Table 1 for definitions.

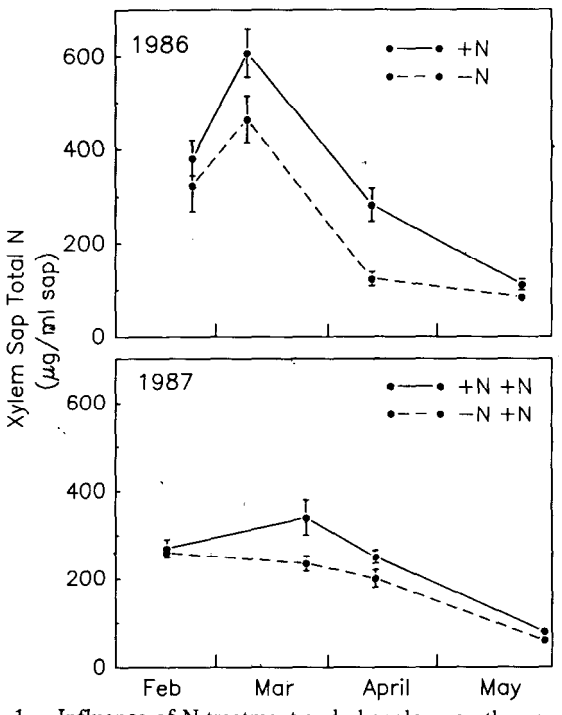

Fig. 1. Influence of N treatment and phenology on the concentration of total N in xylem sap of 'Serr' walnut. Vertical bars represent the SE of four replicates. Treatments designated as: 1) +N (1986), +N+N (1987) = N applied annually from 1984 to 1987; 2) –N = no N July 1984–Jan. 1987; 3) –N+N = as in 2 but N applied Jan. 1987.

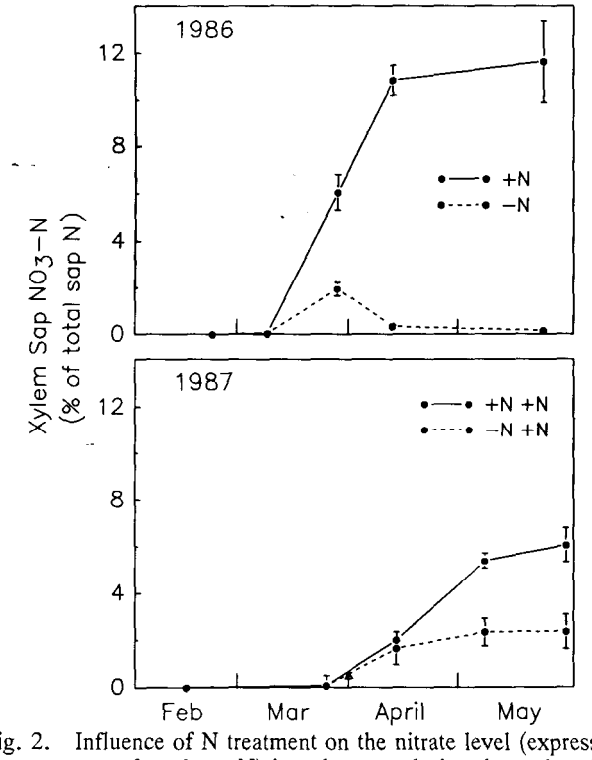

Fig. 2. Influence of N treatment on the nitrate level (expressed as a percentage of total sap N) in xylem sap during the spring. Vertical bars represent the SE of four replicates. See Fig. 1 for treatment definitions.

cline in the percentage of nitrate N in xylem sap, while nitrate N in xylem sap of N-deficient trees with current-season appli-

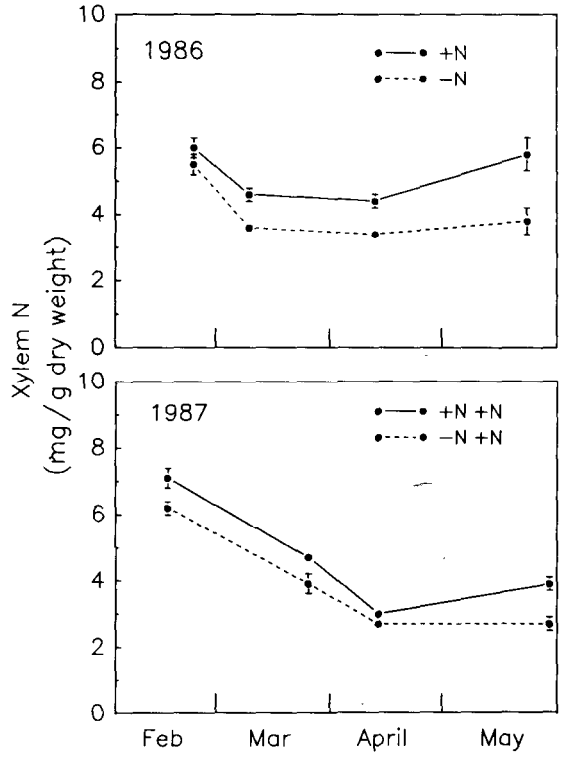

Fig. 3. Influence of N treatment and sampling date on the total N concentration in xylem of 2-year-old shoots. Vertical bars represent the SE of four replicates. See Fig. 1 for treatment definitions.

cation of N fertilizer (–N+N) (1987) remained at a relatively constant level throughout May (Fig. 2).

Effect of N status and phenology on the amount and depletion of storage N. The N concentration in xylem of 2-year-old shoots decreased ≈30% and 60% in 1986 and 1987, respectively, between mid-February and the time of pistillate flower maturation in April (Fig. 3). The concentration of N in xylem of –N trees was invariably lower than that of +N trees. Nitrogen concentration in xylem of +N trees, but not –N trees, increased between mid-April and late May (Fig. 3), presumably as it was replaced by N absorbed from the soil in the current year.

Effect of N status and phenology on total sugar concentration in xylem sap. The concentration of total sugars in xylem sap was lower in early Spring 1986 than during a comparable period in 1987 (Fig. 4). The concentration of total sugars in xylem sap in +N+N trees was 6.0 $mg \cdot ml^{-1}$ before growth resumption (15 Feb. 1987) and increased by ≈50% to 9.0 $mg \cdot ml^{-1}$ in +N trees by the time of catkin maturation (25 Mar.) (Fig. 4). In contrast, the concentration of total sugars in xylem sap of –N+N trees decreased by ≈50% during the same interval. In 1987, the concentration of total sugars in xylem sap decreased by ≈90% between 15 Feb. and the time of distillate flower maturation (14 Apr.), irrespective of tree N status. The concentration of total sugars increased slightly following leaf expansion in May, particularly in the +N+N trees. The concentration of total sugars in sap decreased during leaf expansion (Fig. 4). The minimum sugar concentration corresponded temporally to ≈50% of full leaf expansion (Fig. 4). Spur leaves reached 50% of full expansion at the time of distillate flower maturation (14 Apr.) and were fully expanded by early to mid-May (Fig. 4).

Effects of N status and phenology on total soluble sugars in xylem of 2-year-old twigs. Analyses were performed only in 1987. A >30% decline in the concentration of total soluble

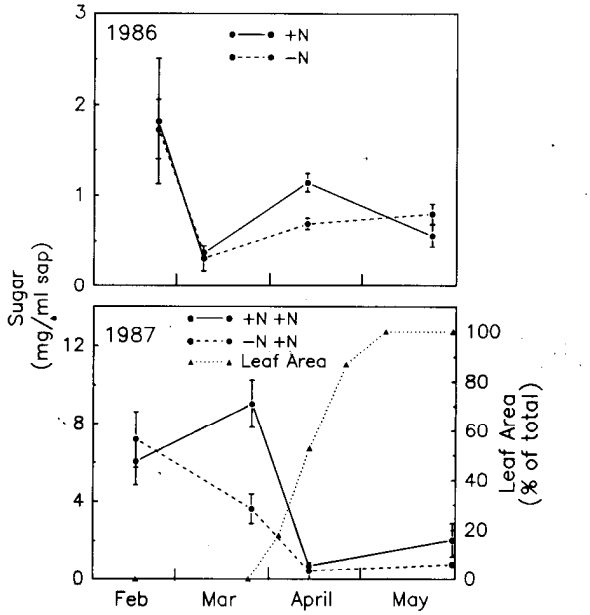

Fig. 4. Influence of N treatment, phenology, and leaf expansion (1987 only) on the concentration of total sugars in xylem sap. Vertical bars represent the SE of four replicates. See Fig. 1 for treatment definitions.

Table 3. Influence of N treatment on total soluble sugars in xylem tissue of 2-year-old shoots of mature 'Serr' walnut trees.[z]

	Total soluble sugar (mg·g^{-1} dry wt)[x,w]			
Treatment[y]	15 Feb.	25 Mar.	14 Apr.	30 May
+N+N	29.2 ± 1.1	18.8 ± 0.8	16.6 ± 0.5	15.7 ± 2.4
–N+N	27.2 ± 2.11	18.4 ± 1.6	25.5 ± 2.9	16.8 ± 1.1

[z]Total sugars represent the sum of all soluble sugars plus sugar alcohols if present.
[y]See Table 1 for definitions.
[x]Sampling dates correspond to dormancy, i.e., before macroscopic growth resumption, 15 Feb.; catkin maturation, 25 Mar.; maturation of pistillate flowers, 14 Apr.; and full leaf expansion, 30 May.
[w]Data are means ± SE of four tree replicates.

sugars in xylem of 2-year-old twigs occurred between growth resumption and the maturation of catkins in late March, irrespective of N status (Table 3). Although the concentration of total sap sugars decreased to a minimum at the time of distillate flower maturation (Fig. 4, 14 Apr.), the total soluble sugars in xylem of both control and –N+N trees remained at relatively high levels (Table 3). The concentration of sugars in xylem of –N+N trees was conspicuously higher than that of +N+N trees at the time of distillate flower maturation (Table 3).

Effect of N status and phenology on the concentration of starch in the xylem of 2-year-old twigs. The concentration of starch in xylem decreased following growth resumption and reached minimum levels (<2% of the level measured on 15 Feb.) at the time of pistillate flower maturation in both 1986 and 1987 (Fig. 5). Starch levels increased slightly in late May, i.e., following full leaf expansion. Starch concentrations were higher before growth resumption in 1987 than in 1986, and the rapidity and extent of hydrolysis was greater in 1987 than in 1986 (Fig. 5). Starch concentrations in xylem were higher in –N trees than in +N trees in 1986 (Fig. 5). Differences between treatments were minimal in 1987 (Fig. 5).

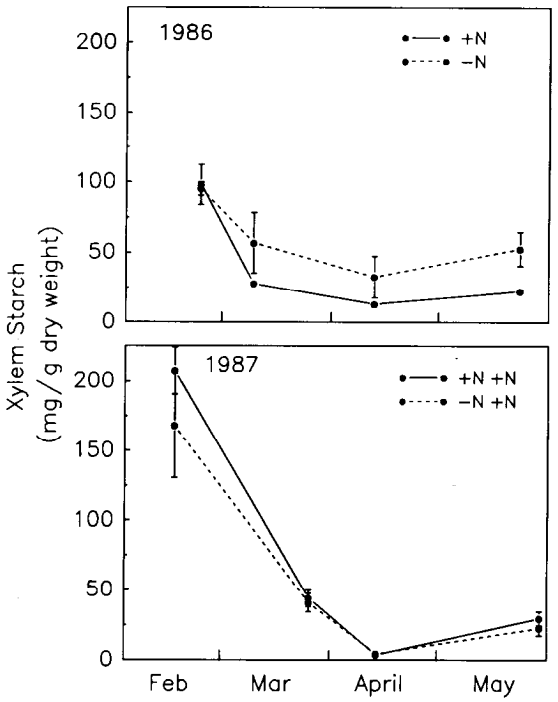

Fig. 5. Influence of N treatment and phenology on the starch concentration in xylem of 2-year-old shoots. Vertical bars represent the SE of four replicates. See Fig. 1 for treatment definitions.

Discussion

The coincidence in peak levels of total sugars and total N in xylem sap of +N and +N+N trees at the time of catkin maturation in late March may reflect the rapid release of both storage C and N into xylem vessels (Figs. 1 and 4). These peaks were less conspicuous in –N trees, presumably due to smaller reserves of C and N. Sugars in xylem sap decreased to minimal levels in both +N and –N trees during distillate flower maturation (Fig. 4), while the concentration of N in xylem sap remained high (Fig. 1). A 90% decrease in the concentration of total sap sugars between mid-February and the maturation of distillate flowers (Fig. 4) presumably indicates a severe depletion of C reserves from the within-tree storage pool in comparison with the relatively slow decrease (≈40% in sap of control trees) in total sap N concentration (Fig. 1) over the same time interval. The decrease in the concentration of C and N in xylem sap following catkin maturation was possibly associated with, at least, three factors: a) exhaustion of previously assimilated substrate stored over winter in perennial tissues, b) dilution of these constituents in the sap with the increasing transpiration rate as the season progressed, and c) use of C and N by other metabolic sinks.

Bollard (1953) pointed out that nutrient concentrations in xylem sap do not, in themselves, reflect the total movement of nutrients through the plant. The decrease in nutrient concentrations in xylem sap that accompanies the spring flush of growth may be due to increasing hydration of the shoot as leaf area and transpiration become established (Ferguson et al., 1983). If the low concentrations of N and sugars in sap in mid-April result primarily from dilution, even lower concentrations would be expected in May when leaves are fully expanded and temperatures are higher. This was not the case.

The abortion of underdeveloped distillate flowers is not attributable to lack of pollination because growth cessation of

these organs, i.e., the commitment to abort, precedes enlargement and maturation of the bifurcate stigma (Catlin et al., 1987; Ryugo et al., 1985). A similar phenomenon has been reported in pecan (Sparks and Madden, 1985).

Our data are consistent with the possibility that a seasonally transient deficit of C and, to a lesser extent, N accentuates PFA. Since distillate flowers are initiated during the summer preceding bloom (Polito, 1985), distillate flowers (which matured in Apr. 1986) had developed entirely during a period of N deficiency in –N trees. Distillate flowers that matured in Apr. 1987 had been initiated during N deficiency (Summer 1986). Although N was applied to –N trees in late Jan. 1987 (-N+N), we contend that these flowers were not influenced appreciably by the N applied in 1987. Maturation of distillate flowers depends primarily on N reserves, because the commitment to abort precedes any significant influx of soil N during the current growing season (Deng et al., 1989a, 1989 b). Given the level of PFA in +N trees and the marginal increase measured in -N trees, it appears unlikely that PFA in 'Serr' walnut can be reduced by fertilizer N applications.

The dependence on reserves to support the early stages of the spring growth flush in woody perennials has long been appreciated. However, the transition from the primary dependence of current-year growth on previously assimilated C and N reserves to a dependence on current-season uptake and assimilation has received considerably less attention (Deng et al., 1989a, 1989b), perhaps because of difficulties in the determination of this transition. Our interest in this phenomenon is in the possible role of transient C and N deficiencies in the abortion of immature reproductive organs of walnut, as well as similar abortion (e.g., "June drop") in most fruit crops and other woody perennial species (Stephenson, 1981). The leaf canopy is only 10% expanded at full bloom in apple (Forshey et al., 1987). Apple fruit are not as easily shaded at bloom as they are 15 to 30 days after full bloom (Byers et al., 1990). The timing of immature fruit abortion may relate to the availability of reserves relative to the metabolic demands of developing fruit.

Sugars redistributed to catkins in xylem sap must have originated from storage since there was insufficient leaf expansion to support photosynthesis before catkin maturation. Thus, there was substantial consumption of C reserves by the developing catkins before maturation of distillate flowers. PFA also occurred before there was sufficient leaf expansion for significant export of photosynthate in the current year. The presumed hydrolysis and virtual disappearance of starch from the wood by the time of distillate flower maturation (Fig. 5) indicates possible exhaustion of C reserves needed for growth and respiration. PFA was inversely correlated with the availability of stored carbohydrates in pecan (Sparks and Madden, 1985), and high levels of C reserves promoted flowering and fruiting in mature pecan trees (Worley, 1979). Changes in xylem starch levels were correlated temporally with the variation in the concentration of total sugars in xylem sap. From 15 Feb. to 25 Mar., the pronounced decline in the concentrations of xylem starch (Fig. 5) and soluble sugars (Table 3), coupled with the increase in levels of total sap sugars of +N trees (Fig. 4, 1987 data), indicates that starch may have been hydrolyzed, released into xylem vessels, and translocated to developing tissues.

Patterns of xylem N and starch use were similar but differed in degree, i.e., a 58% decrease in total xylem N and a 98% decrease in xylem starch between 15 Feb. (before the spring growth flush) and the time of distillate flower maturation in April (Figs. 3 and 5).

The lowest concentrations of total sugars in xylem sap and of starch in xylem tissue occurred around the time of distillate flower maturation (14 Apr.). Research in other species indicates that immature leaves are heterotrophic and that net export of photoassimilates begins when leaves reach 30% to 60% of final size (Turgeon, 1989). A.N. Lakso (personal communication) and DeJong and Goudriaan (1989) calculated that carbohydrates become limiting in apple and peach, respectively, during the postbloom period. Minimum concentrations of carbohydrates in xylem sap and xylem tissue were measured on 14 Apr., the time when leaf area of 'Serr' walnut spurs had reached 52% of full expansion (Fig. 2). Net export of current assimilates may have begun in mid-April, and the limited availability of assimilates during the transition of C availability from storage to current-year photoassimilation may have contributed to the abortion of pistillate flowers. The abortion of immature apple fruit and seed that occurs naturally during the postbloom period may also be linked to C transition period since abortion is accentuated when photosynthesis is reduced by shading (Byers et al., 1985, 1990).

The availability of N and C resources in fruit trees appears to be integrally related. Leaf photosynthetic capacity depends on leaf N content (DeJong, 1982; Evans, 1989). Premature defoliation accompanied N deficiency (data not presented) and can result in a reduced level of carbohydrate reserves (Worley, 1979). Tree N status has been positively associated with the production of structural carbohydrates, as well as nonstructural storage products (starch) (Stassen et al., 1981).

Presumably, resource-limited pistillate flower development may be less likely to occur in protogynous cultivars or in protandrous cultivars that produce a low density of catkins. 'Serr' can produce ≈33,000 catkins/tree (Ryugo et al., 1985).

Only organic N compounds have been detected in tracheal sap of most deciduous fruit tree species (Bollard, 1957), since nitrate reduction occurs primarily in the roots. Nitrate has been found, however, in the sap of several deciduous vines, i.e., kiwifruit (Ferguson et al., 1983) and grape (Bollard, 1957). Our data confirm those of Bollard (1957), who also detected NO_3^- in the xylem sap of *Juglans regia.* We did not detect NO_3^- in the sap during dormancy (February), but its presence was first detected about the time of catkin maturation in late March (Fig. 2). Since the appearance of NO_3^- in xylem sap coincided temporally with the influx of labeled N (supplied to the soil in January, 60 days earlier; Deng et al., 1989a, 1989b), we conclude that the presence of NO_3^- in xylem sap of walnut reflects the influx of soil N derived from current-year uptake.

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