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Fluctuations of Total and Nitrate Nitrogen in Parthenocarpic and Nonparthenocarpic Fig Varieties

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Total and nitrate nitrogen determinations were made on various organs of parthenocarpic Mission and Adriatic fig varieties and nonparthenocarpic Calimyrna and Stanford varieties. Total and nitrate nitrogen fluctuated in definite cycles which were associated with season and plant part. All organs analyzed had the highest percentage of nitrogen relative to dry-weight at the start of growth and the lowest when growth had ceased. Three distinct phases appeared in the nitrogen cycle of the developing fruit; these were shown as a double sigmoid curve of opposite directional trend to the curve showing fruit growth in diameter.

High nitrate nitrogen was present in all plant parts analyzed, particularly in current-season's growth and leaves. While the values for total nitrogen were not greatly different, those for nitrate nitrogen in all plant parts of parthenocarpic varieties were several times higher than in identical parts of nonparthenocarpic varieties. Thus, there was a positive relation between nitrate level and the expression of parthenocarpy.

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Fluctuations of Total and Nitrate Nitrogen in Parthenocarpic and Nonparthenocarpic Fig Varieties[1, 2]

INTRODUCTION

THE FIG is unique among deciduous fruit species in California, because most of its varieties produce two crops of fruit annually under suitable conditions. The first crop is borne on wood of the previous season's growth from buds differentiated in the distal leaf axils during the latter part of the growing season. These buds resume growth the following spring and mature into fruit (often termed the "breba" crop) in June. The second, or main, crop is produced on shoots of the current season; there is usually one fig in the axil of each leaf, with the exception of two or three leaves at the distal end of the shoot whose axil buds produce the breba crop of fruit the following year. The second crop of figs begins to mature at the proximal end of the shoot in late July and continues to mature in August.

On the basis of pollination requirement there are four different types of figs (Condit, 1932)[3] of which only the Smyrna and the common types are considered here. The Smyrna type is almost completely nonparthenocarpic, as its flowers require pollination and fertilization in order for fruits of the breba and second crops to set and mature. Thus, Smyrna figs contain numerous viable seeds. The breba crop of most Smyrna varieties is generally too small to justify commercial cross-pollination, but sometimes a few fruits develop parthenocarpically. The second crop of the Smyrna type is the only one of commercial consequence. The Calimyrna is the leading variety of this type produced in California.

The common type fig, which is the most widely-grown type in California, is completely parthenocarpic when grown under suitable conditions. No cross-pollination and fertilization of the breba or the second crop is required for fruit set and development; thus, the fruits do not contain viable seeds. The three most important varieties of the common type produced in California are Adriatic, Kadota, and Mission. The latter produces a relatively large breba crop, although it is considerably smaller than the second crop.

Extreme diversity in pollination requirements of different types of fig might be associated with a relationship

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[2] This work formed part of a thesis submitted in September, 1958, by the senior author to the Graduate Division of the University of California, Davis, in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Plant Physiology.

[3] See "Literature Cited" for citations referred to in the text by author and date.

between nutrition and fruit setting, although Crosby and Crane (1952) found no differences in the seasonal levels of certain carbohydrate fractions that could be related to differences in expression of parthenocarpy. Because nitrogen status has a marked influence on the fruit-setting response of various species (Childers, 1954), its relationship to the expression of parthenocarpy in the fig was investigated. This paper presents data concerning the cyclic fluctuations of total and nitrate nitrogen in parthenocarpic and nonparthenocarpic varieties.

EXPERIMENTAL PROCEDURE

Two parthenocarpic varieties, Mission and Adriatic, and two nonparthenocarpic varieties, Calimyrna and Stanford, were employed. Calimyrna and Mission trees were sampled throughout 1956 and during the vegetative growth and fruit-setting period in 1957. The Adriatic and Stanford varieties were sampled only during the 1957 vegetative growth and fruit-setting period. Trees in the experiment were of uniform age, growing under comparable conditions of soil, culture and environment in adjacent commercial orchards at Planada, California. The trees had not received nitrogen fertilizer for at least 3 years.

For each variety, 20 comparable shoots (2 on each of 10 trees) were selected and tagged for length measurements of vegetative growth. The growth in diameter of fruits produced on these shoots was measured periodically with a vernier caliper. With breba fruits, 20 distal-most figs on as many shoots were measured; with second-crop fruits, 20 proximal-most figs on 20 current-season's shoots were measured.

For nitrogen determinations, two shoots were collected periodically from each tree. Sampling was always done in mid-morning to avoid diurnal fluctuations in sample composition. Samples collected were: (1) leaves subtending the basal-most fruits; (2) basal-most second-crop fruits; (3) terminal-most breba-crop fruits; and (4) 1 to 1½ inches of the basal portions of current season's and 1-year-old growth. The 1-year-old shoot samples were separated into bark and wood including pith. Fruit samples were sliced with a single-edged razor blade. All samples were dried in a forced-draft oven at 65 to 70° C. The leaves were ground in a Wiley mill; the other samples were put through a standard Labconco mill and reduced to 20-mesh.

Total nitrogen was determined by the Kjeldahl method (Horowitz, 1955) for nitrate-containing samples, with the following modification: approximately 10 gm of digestion catalyst mixture (1 gm $CuSO_4$, 2 gm $FeSO_4$, 20 gm Na_2SO_4) and 2 or 3 drops of selenium oxychloride were added to the Kjeldahl flask. Selenium greatly accelerates the rate of oxidation and materially shortens digestion time, which never exceeds 50 minutes. Nitrate nitrogen was determined by a modification of Blom and Treschou's (1929) method using 2,4-dimethylphenol. This method involes (1) nitration of 2,4-dimethylphenol by nitrate in the sample and in contact with approximately 70 per cent sulfuric acid, (2) distillation of the colored nitrated compound, and (3) measurement of the color intensity for comparison with that of a known standard. Duplicate and sometimes triplicate nitrate and total nitrogen determinations were made on all samples, and the data presented are averages expressed on a per cent dry-weight basis.

RESULTS

Leaves

Total nitrogen. In general, there was a gradual decrease in the percentage of total nitrogen in Mission and Calimyrna leaves throughout the sampling period of 1956, 1957 (fig. 1). Decreases from 3.56 to 0.76 per cent and from 3.40 to 0.78 per cent occurred in Mission and Calimyrna leaves, respectively. The greatest decrease occurred during early development of the leaves, when apparently there was a heavy demand for nitrogen by all growing organs, and again late in the fall when nitrogen was translocated from leaves to wood. Seasonal changes in total nitrogen of leaves of both varieties were practically identical.

The 1956 curves for total nitrogen in Mission and Calimyrna leaves are similar in conformation to those for 1957, as well as to those for the Adriatic and Stanford varieties in 1957 (fig. 2). During the period of second-crop fruit set (June 20 to July 1), total nitrogen in Mission leaves averaged 10 per cent greater than in Calimyrna leaves, while Adriatic leaves averaged about 12 per cent higher than did Stanford leaves.

Nitrate nitrogen. Figures 1 and 2 show considerable concentrations of nitrate nitrogen in fig leaves and also show rapid increases as the leaves expanded and matured. Basal leaves on Mission and Calimyrna fig shoots were fully expanded on April 27 and May 11, 1956, respectively, when the highest percentages of nitrate occurred in the leaves. Following these peaks there were sharp declines, the decline in Calimyrna being more pronounced than in Mission. The

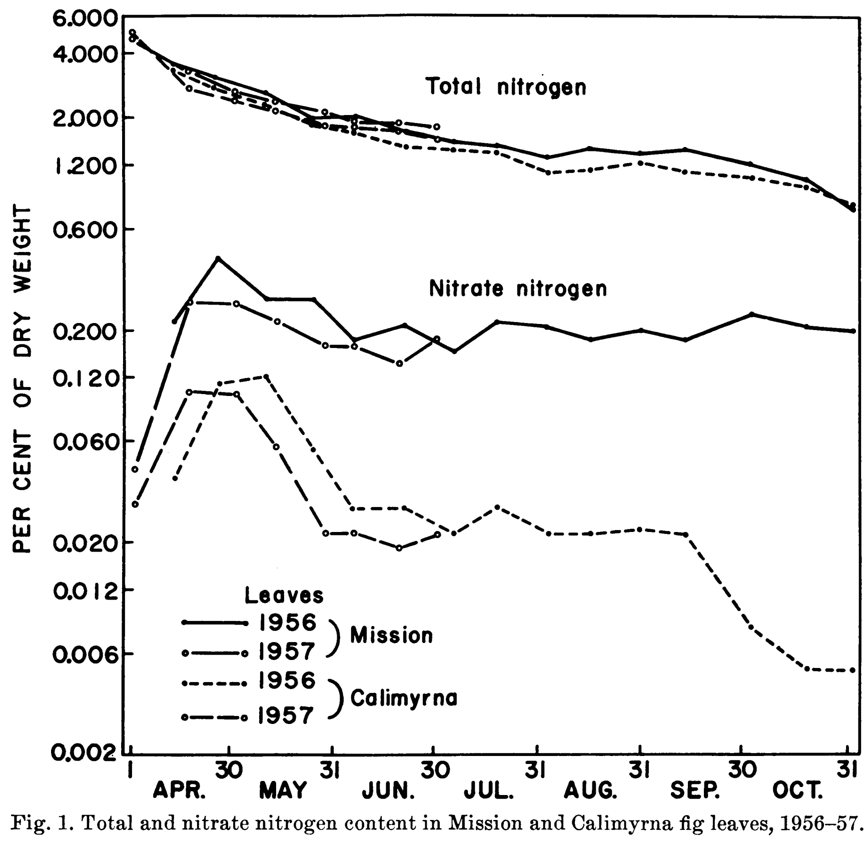

Fig. 1. Total and nitrate nitrogen content in Mission and Calimyrna fig leaves, 1956–57.

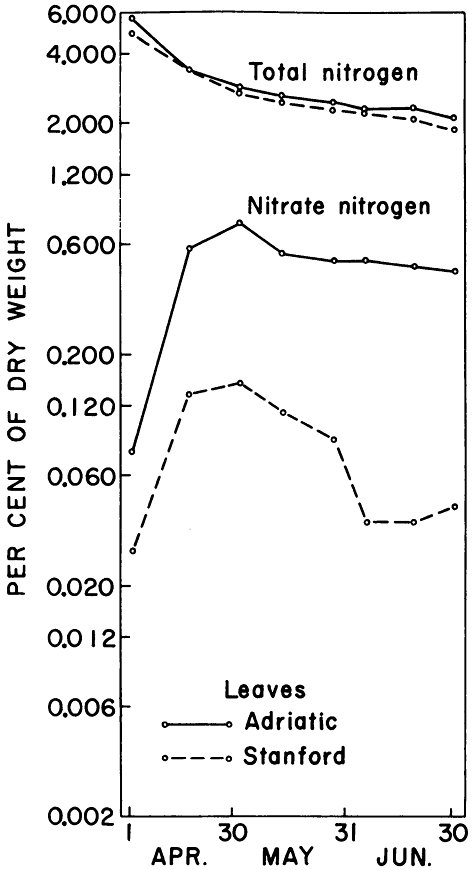

Fig. 2. Total and nitrate nitrogen content in Adriatic and Stanford fig leaves, 1957.

per cent of nitrate nitrogen in Mission leaves during the 1956 sampling period averaged more than five times that found in Calimyrna leaves.

The curves of the two parthenocarpic varieties are similar, and those of the two nonparthenocarpic varieties are similar—but the two sets of curves are quite different from each other. The striking differences between parthenocarpic and nonparthenocarpic types are in the percentages of nitrate nitrogen found and in the rates at which they decreased after maximum values were reached in early spring. As in 1956, leaves of the Mission variety contained an average for the sampling period in 1957 of almost four times as much nitrate nitrogen as Calimyrna leaves, while Adriatic leaves contained slightly over six times as much as did Stanford leaves. After nitrate nitrogen reached its peak (between the middle and end of April) it rapidly decreased in Calimyrna and Stanford, and slowly decreased in Mission and Adriatic. The difference in nitrate nitrogen content between leaves of parthenocarpic and nonparthenocarpic varieties during fruit set is particularly striking. Commercial caprification (cross-pollination) in 1957 began on June 20 and the last caprifigs were placed in the trees on July 1, about a week earlier than in 1956. During this critical period of fruit set, leaves of the parthenocarpic varieties contained from four to twenty-three times as much nitrate nitrogen as did those of nonparthenocarpic varieties.

Current Season's Growth

Length. Separation of terminal-bud scales and initiation of shoot growth occurred during the last week in March. Increase in length was relatively slow during the first 2 to 3 weeks, but rapidly accelerated to a maximum between the middle of April and the first of June; growth then decreased until it stopped at the end of June.

Total nitrogen. The high total nitrogen content in expanding terminal buds (4.38 per cent for Mission and 3.67 per cent for Calimyrna in 1956) decreased rapidly during shoot elongation in April and May (fig. 3). From June until about the first week in October, total nitrogen content decreased gradually to a minimum for the year. As leaf senescence began, there was a gradual but slight accumulation of total nitrogen in current-season's growth, and this continued through the dormant period. The 1957 curves displayed the same general patterns as those for comparable sampling periods in 1956. As with leaves, the curves for total nitrogen in current-season's wood of the two varieties showed practically identical seasonal fluctuations, although values for total nitrogen averaged about 20 per cent

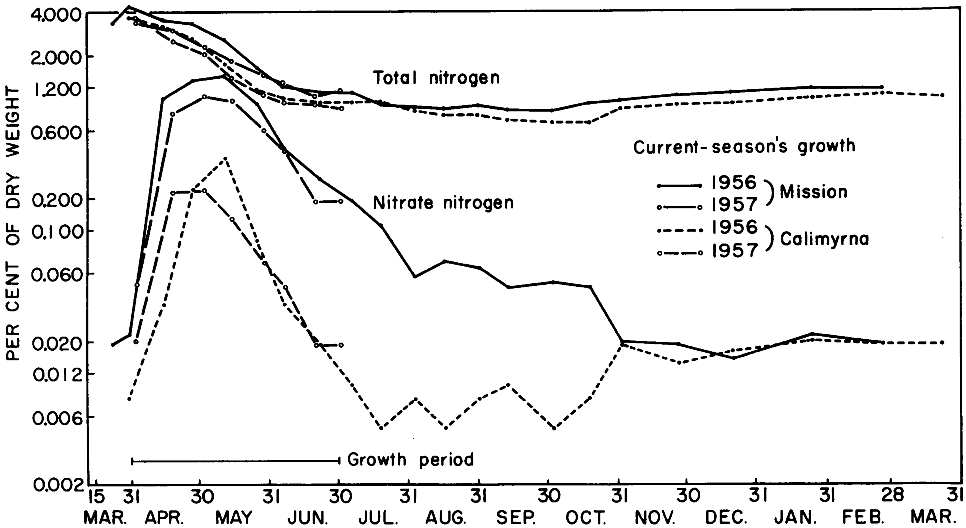

Fig. 3. Total and nitrate nitrogen content in current-season's shoots of the Mission and Calimyrna fig, 1956–57.

greater in Mission than in Calimyrna.

Values for total nitrogen in the four varieties in 1957 (figs. 3 and 4) were initially comparable, but during the vegetative growth period they decreased more in Calimyrna and Stanford than in Mission and Adriatic. Total nitrogen content in current growth of Mission throughout the sampling period averaged about 15 per cent greater than that of Calimyrna, but it was the same as that of Stanford. Total nitrogen in Adriatic throughout the sampling period averaged 21 and 39 per cent greater than in Stanford and Calimyrna, respectively. During fruit set, however, total nitrogen in current growth of the parthenocarpic varieties averaged from 12 to 80 per cent greater than in the nonparthenocarpic varieties.

Nitrate nitrogen. During the first half of the period of shoot growth—the first of April to the middle of May—nitrate nitrogen increased approximately 48 and 65 times for Calimyrna and Mission, respectively (fig. 3). At maximum nitrate contents (May 11, 1956) there was almost 4 times as much in current-season's growth of Mission as in that of Calimyrna. At that time nitrate nitrogen was 21 and 56 per cent of total

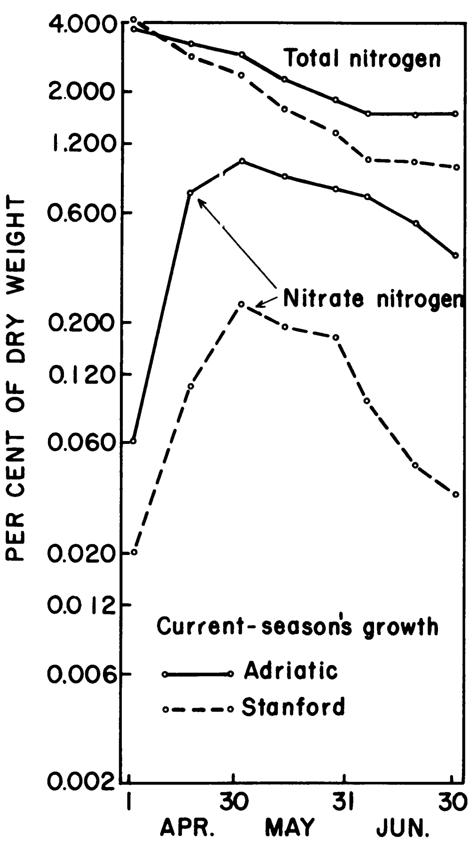

Fig. 4. Total and nitrate nitrogen content in current-season's shoots of the Adriatic and Stanford fig, 1957.

nitrogen in current-season's growth of Calimyrna and Mission, respectively. After May 11 the rate of nitrate decrease in Calimyrna was much more rapid than in Mission; the minimum level in Calimyrna was reached July 19, and on December 21 in Mission.

Commercial caprification of the Calimyrna variety began on June 29, 1956, and the last caprifigs were placed in the trees on July 6. Mission figs were practically at the same stage of fruit development but, of course, developed parthenocarpically. Although total nitrogen content in current-season's shoots of the Mission variety during fruit setting averaged only 7 per cent greater than that in Calimyrna shoots, the nitrate nitrogen content in the former averaged almost 22 times greater than that found in the latter.

The general trends of the curves for nitrate nitrogen in current growth of the four varieties were practically identical with those previously discussed for leaves, except that the maximal values attained were from 84 to 278 per cent greater than in leaves, depending upon variety. Nitrate nitrogen in current growth was consistently higher than in leaves of a particular variety, but total nitrogen was consistently lower.

The same differences found in the nitrate nitrogen content of leaves of parthenocarpic and nonparthenocarpic varieties were also found in current-season's growth. Current growth of the Mission variety in 1957 contained an average for the sampling period of 4 to 9 times as much nitrate nitrogen as that of the Stanford and Calimyrna varieties, respectively, while Adriatic growth was from 5 to 10½ times richer in this component than was that of Stanford and Calimyrna, respectively (figs. 3 and 4).

After nitrate nitrogen in current growth reached its peak in late April, 1957, its rate of decrease was more rapid in Calimyrna and Stanford than in Mission and Adriatic. Consequently, during fruit set the current growth of parthenocarpic varieties contained 4½ to 25 times more of this component than did that of nonparthenocarpic varieties.

One-Year-Old Bark and Wood

Total nitrogen. Total nitrogen in 1-year-old bark and wood of Mission and Calimyrna remained at comparatively constant levels throughout the year (fig. 5), but greater fluctuations occurred in wood than in bark. For example, total

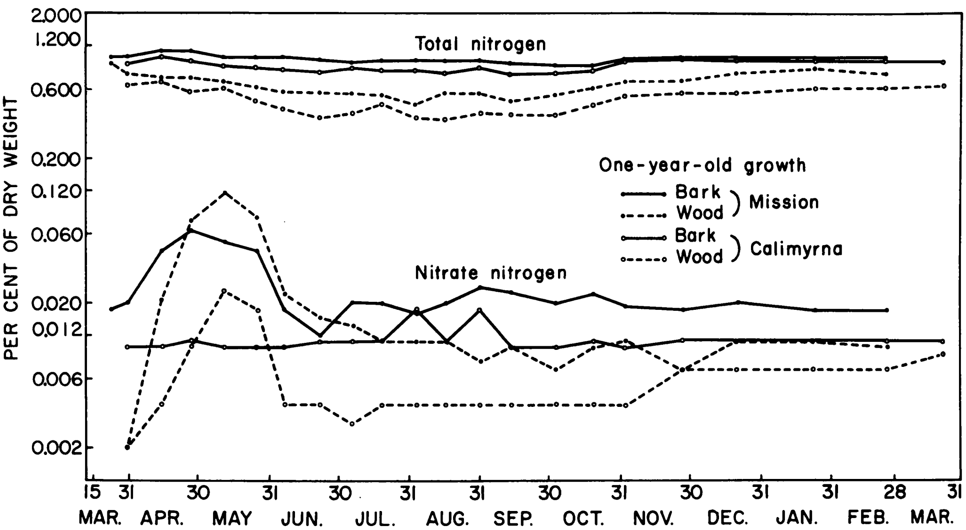

Fig. 5. Total and nitrate nitrogen content in bark and wood of 1-year-old Mission and Calimyrna fig shoots, 1956.

nitrogen in Mission bark varied between 0.88 and 1.18 per cent while that in wood reached a minimum of 0.47 and a maximum of 0.91 per cent. The bark of both varieties was consistently higher in total nitrogen than was the wood.

The average total nitrogen content in Mission bark and wood for the entire sampling period was 15 and 27 per cent greater, respectively, than in Calimyrna bark and wood.

Nitrate nitrogen. Nitrate nitrogen in 1-year-old bark and wood showed marked seasonal fluctuation during the year (fig. 5). As vegetative growth began in spring the nitrate nitrogen content in the wood of both varieties, and in the bark of the Mission variety increased very rapidly and reached maximal values about the middle of May when growth was about half completed. It then decreased rapidly in these tissues until about the last of June when vegetative growth had ceased; throughout the rest of the year only minor variations occurred in nitrate nitrogen content of these tissues. Nitrate nitrogen in the bark of Calimyrna did not fluctuate, but remained fairly constant throughout the year.

With the exception of the period during which vegetative growth took place, the nitrate nitrogen content of the bark was consistently higher than that of the wood. The nitrate nitrogen content of Mission bark averaged almost 2½ times greater for the entire sampling period than that of Calimyrna bark, while the percentage of this component in wood of the former averaged almost four times that of the latter.

The first part of May was the critical period for fruit set of the breba crop of both varieties. At that time (May 11), total nitrogen in Mission bark was 18 per cent greater than in Calimyrna bark, while nitrate nitrogen was more than five times greater. Similarly, total nitrogen in Mission wood was 11 per cent greater than in Calimyrna wood, and the nitrate nitrogen fraction was 4½ times greater.

Fruits

Growth. Growth of the fig fruit is characterized by two periods of rapid diameter increase separated by a period of slow increase (Crane, 1948). Fruits of both parthenocarpic and nonparthenocarpic varieties normally complete the first period of rapid diameter increase, the end of which rather closely corresponds to the time when the flowers within the syconia are receptive to pollination (late June, fig. 6). Fruits of parthenocarpic varieties continue to grow and eventually reach maturity, even though pollination and fertilization of their flowers do not occur. Fruits of nonparthenocarpic varieties cease growth at this time and drop from the trees unless fertilization of the ovules occurs.

Total nitrogen. The total nitrogen curves for breba and second-crop Mission fruits were similar, each displaying two periods of comparatively rapid decrease separated by a shorter period of gradual decrease (fig. 6). These periods corresponded rather closely to those of fruit growth—that is, rapid growth in diameter was accompanied by a sharp decrease in total nitrogen, while a gradual increase in diameter was accompanied by a less pronounced decrease in total nitrogen. The total nitrogen curve for Calimyrna fruits was generally the same as those just discussed, except that a slight increase occurred during the period of slow increase in diameter; developing seeds in fruits of this variety were probably responsible for this increase. The total nitrogen content in second-crop Mission fruits was about 8 per cent higher than that in Calimyrna fruits on July 6 (during fruit set).

Nitrate nitrogen. Total nitrogen decreased as growth of breba Mission fruits progressed, but nitrate nitrogen markedly increased during the first period of rapid growth in diameter, decreased gradually during the depressed period of growth, and then decreased rapidly (fig. 6). The curve depicting

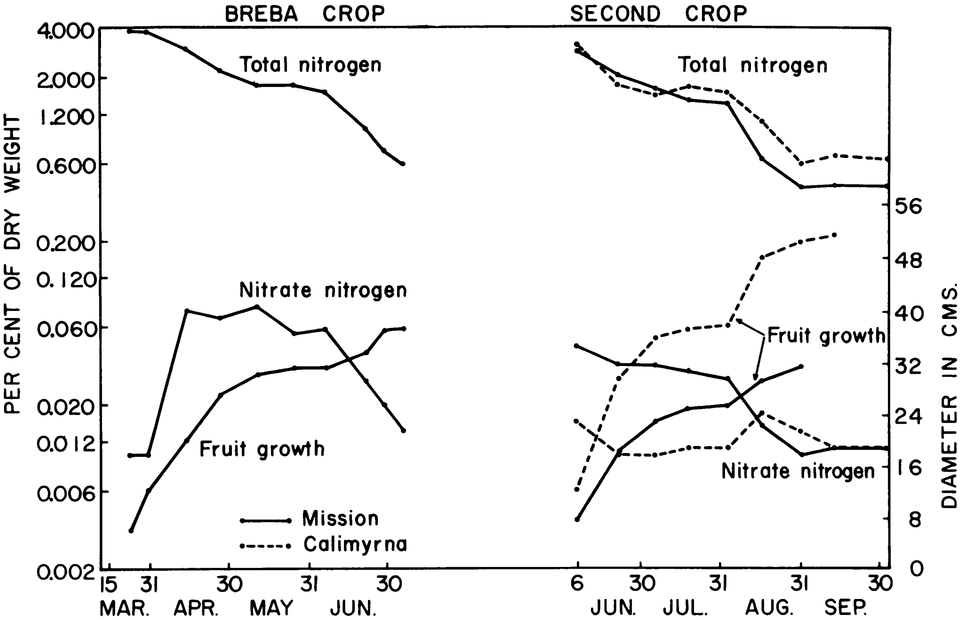

Fig. 6. Total and nitrate nitrogen, and growth in diameter, of Mission and Calimyrna fig fruits, 1956.

nitrate nitrogen in these fruits was similar in shape, and magnitude of change, to the nitrate curve for bark of 1-year-old shoots—the growth on which the fruits were produced (fig. 5). However, the nitrate nitrogen curve for second-crop Mission fruits was practically identical with that for total nitrogen, except that the values were lower. The nitrate nitrogen curve for Calimyrna fruits was different from that of Mission fruits, probably because of seed development. Nitrate decreased during the first period of rapid fruit growth and remained constant during the slow growth period. An increase in nitrate occurred as fruits entered the second rapid growth period; this was followed by a decrease as the fruits matured. Although the total nitrogen in second-crop Mission fruits was only 8 per cent greater than that in Calimyrna fruits during the fruit-setting period, the percentage of nitrate nitrogen in the former was over three times greater than that in the latter.

DISCUSSION AND CONCLUSIONS

The data presented show that seasonal changes in the percentage of total nitrogen in leaves, current-season's shoots, and fruits of the breba and second crops were large, while those which occurred in the bark and wood of 1-year-old shoots were small. With the exception of the latter, all parts of the plant upon which nitrogen determinations were made contained more total nitrogen just before the initiation of active growth in spring than at any other time of the year. A decrease in per cent nitrogen in all parts occurred during the period of active growth.

Two periods of relatively rapid decrease in per cent total nitrogen occurred in the leaves. The first was during rapid leaf growth when there was also a rapid increase in dry weight and a simultaneous, heavy demand for this element by all growing parts. The second occurred prior to leaf abscission, and reflects the autumnal migration of nitrogen from the leaves to the branches and the concurrent increase in per cent nitrogen in current-season and 1-year-old growth.

Although data for total nitrogen do not suggest any relationship between it and the expression of parthenocarpy, there was a consistent difference in nitrate levels between parthenocarpic and nonparthenocarpic varieties: in all parts analyzed, nitrate concentration was consistently greater in parthenocarpic than in nonparthenocarpic varieties. The difference occurred sufficiently early in the season to be of significance in fruit setting. It occurred throughout the 2-year period for Mission and Calimyrna, and was characteristic of the 1-year data for Adriatic and Stanford.

In leaves, nitrate nitrogen content of the parthenocarpic Mission and Adriatic varieties was much greater than in the nonparthenocarpic Calimyrna and Stanford varieties; maximal levels of 0.44 and 0.74 per cent occurred in the former, while the greatest concentrations in the latter were only 0.13 and 0.15 per cent. Proebsting and Tate (1952), in reporting the relatively high nitrate content of fig leaves, said "There is some indication that levels for the same year and period may be higher in the Calimyrna than the Adriatic." Their data, however, were derived from Adriatic and Calimyrna trees growing under different environmental and cultural conditions in the Merced and Fresno areas of California, respectively.

The data show that current-season's growth is the place where nitrate accumulates in relatively large quantities. About May 1 the maximal nitrate levels in current-season's growth were from 8 to 10 times higher than in 1-year-old growth. This suggests that if 2-, 3- or 4-year-old branches had been sampled the maximal nitrate percentages in them might have been progressively lower. The fig may be like several other plants which have a descending concentration in nitrate from tip to base.

The curve for nitrate content of breba Mission figs had a dome-shaped pattern similar to that exhibited by leaves, current-season's and 1-year-old growth. A concentration of 0.08 per cent was reached at the beginning of the second period of fruit growth, at which time a peak level in nitrate nitrogen occurred in the 1-year-old growth upon which the breba figs were produced.

During the first and second growth periods of second-crop fruits, the average nitrate percentage of Mission fruits was approximately three times higher than that of Calimyrna. There were only traces of nitrate in the third growth period of Mission fruits and in all three growth periods of Calimyrna fruits. Very little nitrate nitrogen accumulated as such in developing second-crop fruits, and this suggests that nitrogen in some form other than nitrate is translocated from leaves into fruit, or that enzymatic transformation of nitrate in fruit takes place as rapidly as it comes from adjacent organs.

The results of this study show a positive relation between nitrate level and the expression of parthenocarpy in the fig. All organs of two parthenocarpic varieties analyzed contained much greater quantities of nitrate than did corresponding organs of nonparthenocarpic varieties, particularly during fruit setting. The precise physiological significance of this fact is difficult to assess at the present time. Varga and Zsoldos (1963), however, found that the activity of indoleacetic acid oxidase in rice plants was progressively inhibited as the concentration of nitrate increased. If a similar situation exists in the fig, parthenocarpic varieties relatively high in nitrate would be expected to contain relatively large amounts of auxin. The fact that exogenous auxin application causes fruit setting in the nonparthenocarpic fig is well-established, as discussed by Crane (1964).

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