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NITRATE CONCENTRATION AND ION BALANCE IN RELATION TO CITRUS NUTRITION

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H. D. CHAPMAN³ AND GEORGE F. LIEBIG, JR.⁴

INTRODUCTION

THE MOST EXPENSIVE ITEM in the citrus grower's fertilizer bill is nitrogen. With the types of fertilizer now in use and present cultural methods, it has been found necessary to apply between 150 and 250 pounds of nitrogen per acre annually in order to maintain commercial yields and tree vigor; indeed, many growers commonly apply considerably more. Calculations based on chemical analyses of the fruit and of tree parts, however, indicate that no more than 35 to 50 pounds of nitrogen per acre annually are utilized in the production of fruit and in the permanent new growth of the trees. This discrepancy between practical and calculated needs is probably accounted for, in part, by leaching and volatilization losses from the soil. It is possible, of course, that the nitrogen requirement of citrus trees as judged by analyses may be in error (23).⁵ In the belief that a better knowledge of the nitrogen nutrition of the citrus tree and of nitrogen gains, losses, and transformations in soils might make possible more effective nitrogen usage, studies relative to these questions were begun several years ago. This paper is concerned only with citrus nutritional studies.

Experiments have been carried out to determine the minimum main-

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⁵ Italic numbers in parentheses refer to "Literature Cited" at the end of this paper.

tained concentrations of nitrate nitrogen adequate for optimum growth of citrus plants. In connection with this study, information has been obtained about the effects of ion balance on nitrate nutrition. In addition, nitrogen determinations made on citrus plants grown under widely different conditions of nitrogen adequacy have made possible the testing, in a preliminary way, of the diagnostic value of nitrogen percentage as an index of nitrogen deficiency or excess. It is the purpose of this paper to describe in detail the results of these experiments.

So far as the authors are aware, no critical studies of the effects of widely varying nitrate concentrations on citrus growth have been made. The results of investigations with other plants grown in water or sand culture, reported by Goedewaagen (11), Mitchell (22), White (26), Kapp (18), and Batjer and Degman (2), are so variable that no generalizations can be drawn. A number of investigators working with soils—Smith (25), Brown (3), and Gilbert and Pember (10)—have indicated desirable soil-nitrate levels to be maintained for satisfactory growth of various field and garden crops. But such plants differ from citrus so profoundly in growth habits that deductions in terms of the latter are unwarranted.

EXPERIMENTAL PROCEDURE

PRELIMINARY EXPERIMENTS

Two exploratory experiments were first carried out under greenhouse conditions with sweet-orange seedlings in large-volume, continuously aerated solution cultures ranging in concentration from 1 to 420 p.p.m. nitrate nitrogen.⁶ Even at the lowest concentration, there was no evidence of nitrogen starvation, the growth being green, vigorous, and healthy. Results with sand cultures, however, were not in agreement and suggested that the stirring of the solution incident to aeration had the same effect as an increase in concentration.⁷ Since there is no close parallel to such a condition in the soil, it was decided to carry out an experiment in sand cultures, where the conditions approach somewhat more closely those of soils.

⁶ Throughout the paper the concentration of nitrogen in the nutrient solutions is expressed in terms of the element nitrogen but is present as nitrate.

⁷ External and internal conditions for nutrient absorption and utilization being favorable, nutrient adequacy is probably determined by the frequency of collision of the nutrient ion with unit absorbing root surface. Frequency of collision, in turn, is determined not alone by the concentration of the ion in question, but also by its diffusion rate, the concentration of other ions, and mass movements of the whole solution. Obviously, stirring a nutrient solution, the root being motionless, increases the frequency of collision of nutrient ion with absorbing surface and thus produces the same effect as an increase in concentration.

SAND-CULTURE EXPERIMENT

A partial account of this experiment has been given (6). Since this material was published in a journal of limited circulation, and the description of experimental procedure and results were both brief and incomplete, a full account is set forth herein.

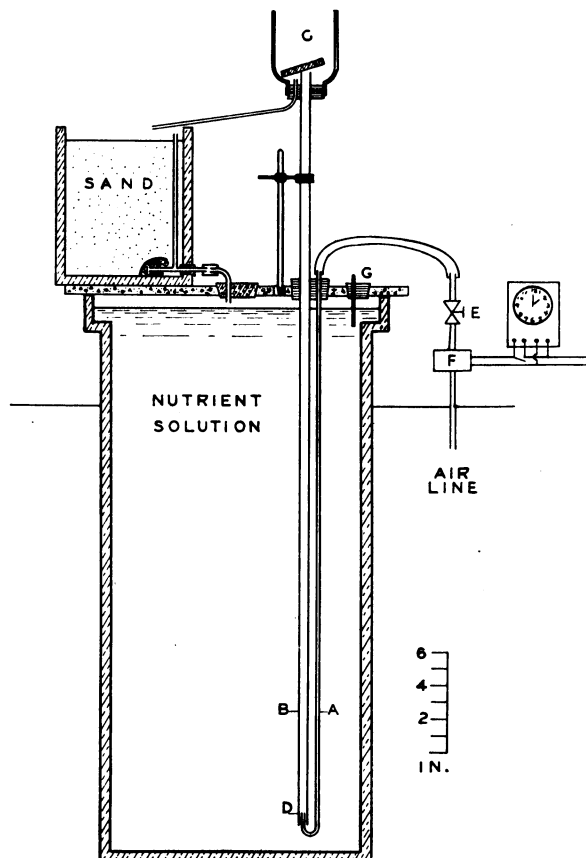


Fig 1.—Automatically operated sand-culture unit: *A*, compressed-air inlet tube; *B*, ejector member; *C*, distributor; *E*, needle valve; *F*, magnetic valve; *G*, volume indicator.

Automatically Operated Sand Cultures.—A line drawing showing the essential details of the sand-culture equipment and a photograph showing a type unit are reproduced in figures 1 and 2. As indicated by the figures, each culture unit consisted of a large reservoir (100-liter-

capacity sewer pipe) containing the nutrient solution, and three glazed earthenware pots (2-gallon size) filled with quartz sand. Three small sweet-orange seedlings, selected for uniformity from a large number originally started in flats of soil, were transplanted into each of the pots, which made a total of 9 plants per culture unit. These seedlings were

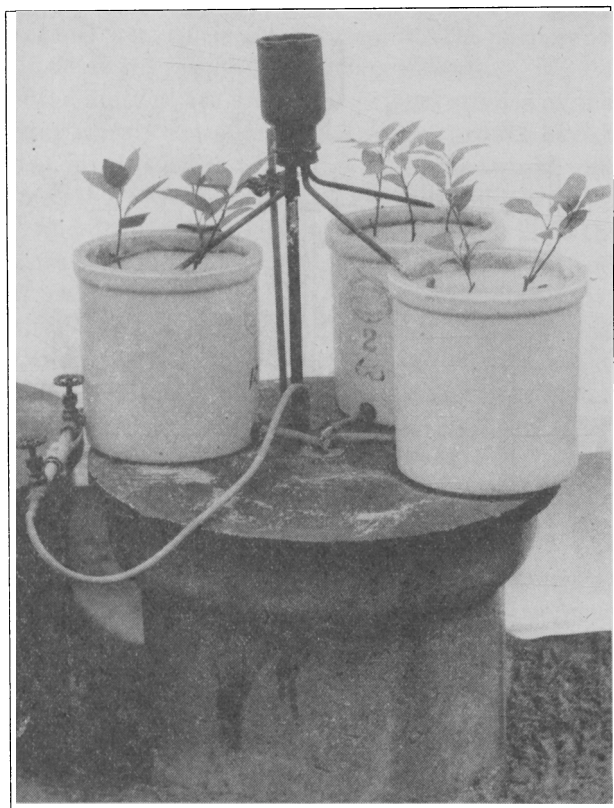


Fig. 2.—Automatically operated sand-culture unit showing size of citrus plants at the beginning of the experiment.

then grown for nearly five and one-half months (from October 29, 1936, to April 9, 1937) in the greenhouse under favorable temperature and light conditions.

In operation, the sand cultures were flushed periodically, at 1-hour intervals during daylight, with the nutrient solution from the reservoir. The pumping mechanism was a glass-tube, ejector-type pump actuated by a clock-controlled magnetic valve in the compressed-air line. The solution held by the sand was thus frequently renewed, the excess flowing by

gravity back into the reservoir where such changes in concentration as occurred from absorption and evaporation were largely equalized by admixture with the very much larger volume of the reserve solution.

Composition of Nutrient Solutions.—Four series of five cultures each were set up, the cultures of each series containing nitrate nitrogen in concentrations of 0.14, 0.7, 1.4, 7.0, and 70.0 p.p.m., respectively. These four series are hereinafter referred to as basic series no. 1, basic series no. 2, high-chloride series, and high-sulfate series.

TABLE 1
COMPOSITION OF NUTRIENT SOLUTIONS, IN AMOUNTS PER LITER*

| Series | Ca ⁺⁺ | Mg ⁺⁺ | K ⁺ | Na ⁺ | Cl ⁻ | PO ₄ ⁻⁻⁻ | SO ₄ ⁻⁻ | NO ₃ ⁻ |
|--------------------|-------------------|-------------------|-------------------|-------------------|-------------------|--------------------------------|-------------------------------|------------------------------|
| | milli-equivalents | milli-equivalents | milli-equivalents | milli-equivalents | milli-equivalents | milli-equivalents | milli-equivalents | milli-equivalents |
| Basic..... | 2.12 | 1.06 | 2.12 | 0.28 | 0.28 | 0.30 | 5.00 | 0.01 |
| | 2.14 | 1.07 | 2.14 | 0.28 | 0.28 | 0.30 | 5.00 | 0.05 |
| | 2.16 | 1.07 | 2.16 | 0.28 | 0.28 | 0.30 | 5.00 | 0.10 |
| | 2.32 | 1.16 | 2.32 | 0.28 | 0.28 | 0.30 | 5.00 | 0.50 |
| | 4.12 | 2.06 | 4.12 | 0.28 | 0.28 | 0.30 | 5.00 | 5.00 |
| | 14.12 | 7.06 | 14.12 | 0.28 | 0.28 | 0.30 | 5.00 | 30.00 |
| | 26.12 | 13.06 | 26.12 | 0.28 | 0.28 | 0.30 | 5.00 | 60.00 |
| High-sulfate..... | 10.12 | 5.06 | 10.12 | 0.28 | 0.28 | 0.30 | 25.00 | 0.01 |
| | 10.14 | 5.07 | 10.14 | 0.28 | 0.28 | 0.30 | 25.00 | 0.05 |
| | 10.16 | 5.08 | 10.16 | 0.28 | 0.28 | 0.30 | 25.00 | 0.10 |
| | 10.32 | 5.16 | 10.32 | 0.28 | 0.28 | 0.30 | 25.00 | 0.50 |
| | 12.12 | 6.06 | 12.12 | 0.28 | 0.28 | 0.30 | 25.00 | 5.00 |
| High-chloride..... | 10.12 | 5.06 | 10.12 | 0.28 | 20.28 | 0.30 | 5.00 | 0.01 |
| | 10.14 | 5.07 | 10.14 | 0.28 | 20.28 | 0.30 | 5.00 | 0.05 |
| | 10.16 | 5.08 | 10.16 | 0.28 | 20.28 | 0.30 | 5.00 | 0.10 |
| | 10.32 | 5.16 | 10.32 | 0.28 | 20.28 | 0.30 | 5.00 | 0.50 |
| | 12.12 | 6.06 | 12.12 | 0.28 | 20.28 | 0.30 | 5.00 | 5.00 |

* In addition to the ions indicated, 0.5 p.p.m. each of B and Mn were supplied; and 0.1 per cent magnetite was incorporated in the sand as a source of iron.

Two additional cultures containing nitrate nitrogen in concentrations of 420 and 840 p.p.m., respectively, were included in basic series no. 1; the two basic series were otherwise identical. They occupied widely different locations in the greenhouse, however. The duplication of this series of cultures provides a basis for judgment as to the significance of differences in plant growth and composition resulting from the various treatments. The high-chloride and high-sulfate series were made up by adding 20 milliequivalents of mixed chlorides and mixed sulfates, respectively, per liter of solution to the solutions used in the basic series. These two series were included for the purpose of determining what effect, if any, wide variations in the nutrient medium would have on the nitrate optimum.

The increases in nitrate, chloride, and sulfate concentrations were accomplished by adding appropriate salts of calcium, magnesium, and potassium, the ratios between these bases being kept constant in all solutions. The phosphate was uniform in all cultures, and within any one series sulfate and chloride were constant. Traces of manganese and boron (0.5 p.p.m. each) were added, and iron was provided by mixing 0.1 per cent magnetite into the sand. The composition of the basic, high-sulfate, and high-chloride series of solutions is shown in table 1. The

TABLE 2
THEORETICAL AND ACTUAL AVERAGE CONCENTRATION OF NITRATE NITROGEN
IN NUTRIENT SOLUTIONS FOR ENTIRE EXPERIMENTAL PERIOD*

| Theoretical concentration | Actual average concentration | | | |
|---------------------------|------------------------------|-----------------------|------------------------|---------------------------|
| | Basic series no. 1 | Basic series no. 2 | High-sulfate series | High-chlo- ride series |
| <i>p.p.m.</i> | <i>p.p.m.</i> | <i>p.p.m.</i> | <i>p.p.m.</i> | <i>p.p.m.</i> |
| 0.14 | 0.20 | 0.21 | 0.13 | 0.36† |
| 0.70 | 0.67 | 0.68 | 0.59 | 0.64 |
| 1.40 | 1.35 | 1.25 | 1.24 | 1.53 |
| 7.00 | 7.18 | 6.71 | 6.64 | 6.60 |
| 70.00 | 68.10 | 68.80 | 68.60 | 69.50 |
| 420.00 | 419.00 | | | |
| 840.00 | 837.00 | | | |

* Determinations of nitrate nitrogen were made by the phenoldisulfonic-acid method. Silver sulfate was used to remove chloride in the high-chloride series.

† The accuracy of this figure is in question.

acidity of the culture solutions was kept between pH 5.0 and pH 5.5, though occasionally some of the cultures became somewhat more alkaline. Adjustments were made with dilute H_2SO_4 .

Control of Nutrient Concentration.—By frequent analyses for nitrate, phosphate, and pH, accompanied by adjustments with appropriate nutrients and complete renewal of the solutions at monthly intervals, it was possible to maintain the concentrations of all the major ions within narrow limits.

Daily records of the determined or calculated nitrate concentrations in each culture were kept, and from these it was possible to estimate the average concentration of nitrate in each culture for the entire experimental period. These data are shown in table 2. Some idea of the frequency of nitrate determinations is indicated by the data of table 3. As regards other elements, the change in concentration during an absorption period of one month is indicated by the compositions of theoretical, fresh, and month-old solutions given in table 4. The month-old solutions were samples secured at the termination of the experiment and were

therefore from solutions which had been in use during a period when the plants were absorbing at a maximum rate.

The displacement of the solution held by the sand, at 1-hour intervals during daylight, served to maintain within a narrow range the fluctuations of nitrate concentration in the solution film surrounding the absorbing roots. This is indicated by the results of an experiment involving comparisons between the effects of 1- and 2-hour pumping intervals. With nutrient solutions of identical composition, containing nitrate

TABLE 3
NITRATE DETERMINATIONS IN NUTRIENT SOLUTIONS DURING THE LATTER PART
OF EXPERIMENTAL PERIOD

| Date, 1937* | Basic series† | | | | | High-chloride series† | | | | |
|---------------|---------------|---------------|---------------|---------------|---------------|-----------------------|---------------|---------------|---------------|---------------|
| | 0.14 | 0.70 | 1.40 | 7.00 | 70.00 | 0.14 | 0.70 | 1.40 | 7.00 | 70.00 |
| | <i>p.p.m.</i> | <i>p.p.m.</i> | <i>p.p.m.</i> | <i>p.p.m.</i> | <i>p.p.m.</i> | <i>p.p.m.</i> | <i>p.p.m.</i> | <i>p.p.m.</i> | <i>p.p.m.</i> | <i>p.p.m.</i> |
| March 15..... | 0.14 | 0.70 | — | — | — | 0.14 | 0.70 | — | — | — |
| March 16..... | — | — | 1.40 | 7.00 | — | — | — | 1.40 | 7.00 | — |
| March 17..... | 0.12 | 0.60 | 1.30 | 7.00 | 70.00 | 0.07 | 0.85 | 0.70 | 6.10 | 70.00 |
| March 18..... | 0.12 | 0.60 | 1.30 | 7.00 | — | — | — | — | — | — |
| March 19..... | 0.10 | 0.50 | 1.10 | 6.00 | — | 0.10 | 0.70 | 1.80 | 6.80 | 64.00 |
| March 23..... | 0.08 | 0.60 | 1.20 | 6.40 | — | 0.00 | 0.30 | 0.80 | 5.00 | 78.00 |
| March 24..... | — | — | — | — | 68.00 | — | — | — | — | — |
| March 25..... | 0.12 | 0.60 | 1.20 | 6.40 | — | 0.20 | 0.80 | 1.80 | 6.90 | 70.00 |
| March 30..... | 0.12 | 0.60 | 1.30 | 6.60 | — | 0.25 | 0.90 | 1.00 | 6.00 | 70.00 |
| March 31..... | — | — | — | — | 66.00 | — | — | — | — | — |
| April 1..... | 0.10 | 0.55 | 1.10 | 6.00 | — | 0.00 | 0.50 | 1.40 | 6.60 | 66.00 |
| April 6..... | 0.07 | 0.65 | 1.00 | 5.80 | — | 0.25 | 0.60 | 0.80 | 4.60 | 66.00 |

* To compensate for nitrate absorption, additions of a mixed nitrate solution were made, not only on the dates of analyses, but on the intervening days.

† Cultures of this series are designated by theoretical concentration of nitrate nitrogen in solution.

nitrogen at a suboptimum concentration (0.7 p.p.m.), no significant difference in growth or appearance of the nitrogen-starved plants developed. If in an absorption period of 1 hour there had been a substantial drop in the nitrate concentration of the solution film surrounding the root, there should, then, have been greater nitrate starvation and hence less growth in the culture flushed at 2-hour intervals than in the one flushed at 1-hour intervals. Since the growth in both cases was nearly the same, it is probable that the reduction in nitrate concentration during a 1-hour absorption period was small. In contrast, great differences in growth developed in plants grown simultaneously (under the 1-hour flushing technique) in solutions with concentrations of nitrate nitrogen somewhat less (0.14 p.p.m.) and somewhat greater (1.4 p.p.m.).

During the flushing period and while the excess solution was draining out of the sand, there was obviously motion of the solution in relation

to the roots similar to that prevailing in stirred solutions. As the cultures were flushed for periods of but 5 minutes every hour during daylight, however, the total time during which the solution was in motion amounted to but a small fraction of that in continuously stirred culture solutions. The technique described comes fairly close to the ideal of maintaining a film of motionless nutrient solution of constant composition in contact with the absorbing root.

TABLE 4

CHANGE IN COMPOSITION OF SOLUTION DURING A ONE-MONTH ABSORPTION PERIOD

| Series | NO ₃ ⁻ per liter, theoretical | Cl ⁻ per liter, theoretical | Age of solution | Composition of solution, amounts per liter | | | |
|-----------------|---|--|-------------------------|---|--------------------------|--------------------------|-------------------------------|
| | | | | Ca ⁺⁺ | Mg ⁺⁺ | K ⁺ | SO ₄ ⁻⁻ |
| | | | | <i>milli-equivalents</i> | <i>milli-equivalents</i> | <i>milli-equivalents</i> | <i>milli-equivalents</i> |
| Basic..... | 0.05 | 0.28 | { Fresh, theoretical... | 2.14 | 1.07 | 2.14 | 5.00 |
| | | | { Fresh, actual..... | | | | |
| | | | { One month old..... | 2.17 | 1.21 | 2.12 | 5.30 |
| Basic..... | 5.00 | 0.28 | { Fresh, theoretical... | 4.12 | 2.06 | 4.12 | 5.00 |
| | | | { Fresh, actual..... | 4.29 | 2.31 | 4.40 | 5.20 |
| | | | { One month old..... | 4.13 | 2.45 | 4.36 | 5.75 |
| High-chloride.. | 5.00 | 20.28 | { Fresh, theoretical... | 12.12 | 6.06 | 12.12 | 5.00 |
| | | | { Fresh, actual..... | 11.41 | 6.17 | 11.69 | 4.88 |
| | | | { One month old..... | 11.98 | 6.50 | 11.76 | 5.67 |

METHODS OF HARVESTING AND ANALYSIS

In harvesting, the sand was carefully washed away from the roots; the plants were thoroughly washed in distilled water; and the stems, leaves, and roots, respectively, from the 9 plants of each culture were combined. These were dried at 50° C, ground in a Wiley mill, and stored in sealed bottles. Moisture determinations were made on these samples, and all weights and analyses recorded in the subsequent tables and graphs are of these 9-plant composites and are expressed on a moisture-free basis.

Nitrogen.—Total nitrogen was determined by the salicylic acid modification of the Kjeldahl method.

Phosphorus.—One gram of the ground dried plant material was ashed with Mg(NO₃)₂, the residue was taken up in HNO₃ made to a volume of 100 cc, and the phosphate in an aliquot was determined by the blue colorimetric method (5).

Sulfur.—Samples were ashed with Mg(NO₃)₂, dissolved in HCl made to volume, and sulfur was determined as BaSO₄ on an appropriate-sized aliquot.

Chlorine.—Samples were ashed with Na_2CO_3 , taken up in water and dilute HNO_3 , neutralized, and titrated with standard AgNO_3 , potassium chromate indicator being used.

Calcium, Magnesium, and Potassium.—A 2-gram sample was ashed at low heat and taken up in HNO_3 . Silica was removed by dehydration and filtering. The filtrate was made to a volume of 200 milliliters; of this, 100 milliliters was taken for the calcium and magnesium determinations and

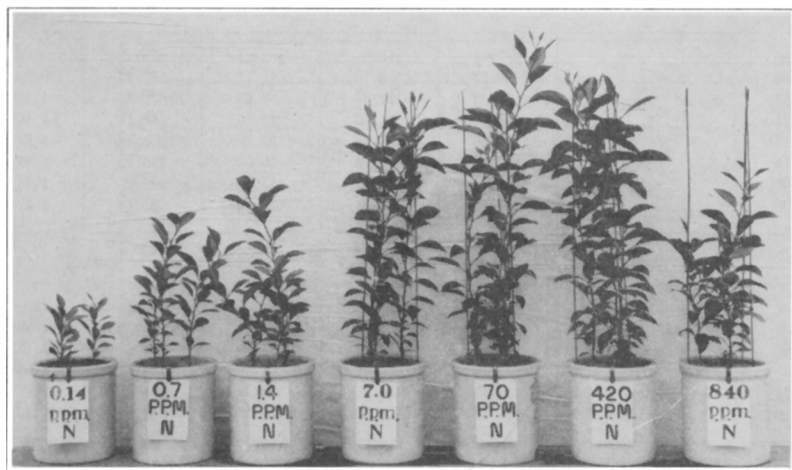


Fig. 3.—Relative growth of sweet-orange seedlings in solutions of various maintained nitrate concentrations (basic series no. 1)

25 milliliters for the potassium determination. Calcium was double-precipitated as the oxalate and titrated with KMnO_4 . After ammonium and oxalate salts had been destroyed, magnesium was determined in the filtrate with 8-OH quinoline. Potassium was determined by the cobaltinitrite method, as outlined by Wilcox (27).

RESULTS

The relative growth of citrus plants as influenced by various maintained nitrate concentrations is shown in figure 3. The dry-weight data for all series are given in table 5. In the three lowest concentrations of nitrogen, namely, 0.14, 0.7, and 1.4 p.p.m., the plants of all series showed typical symptoms of nitrogen starvation, although there were pronounced growth differences between each of these cultures. Plants in all series supplied with solutions containing 7 p.p.m. nitrogen were deep green and vigorous and made almost as good growth as those in solutions containing 70 p.p.m. From this it is inferred that the minimum maintained

TABLE 5
 DRY WEIGHT OF SWEET-ORANGE SEEDLINGS GROWN IN SOLUTIONS OF VARIOUS
 MAINTAINED NITRATE CONCENTRATIONS

| Average nitrate nitrogen in nutrient solution | Dry weight* | | | | Top: root ratio* |
|--|--------------|--------------|--------------|--------------|---------------------|
| | Leaves | Stems | Roots | Total | |
| Basic series no. 1 | | | | | |
| <i>p.p.m.</i> | <i>grams</i> | <i>grams</i> | <i>grams</i> | <i>grams</i> | |
| 0.20..... | 6.12 | 6.10 | 15.71 | 27.93 | 0.78 |
| 0.67..... | 19.62 | 19.06 | 33.65 | 72.33 | 1.15 |
| 1.35..... | 31.51 | 27.10 | 40.50 | 99.11 | 1.45 |
| 7.18..... | 82.99 | 67.19 | 52.25 | 202.43 | 2.87 |
| 68.10..... | 110.50 | 92.79 | 60.00 | 263.29 | 3.39 |
| 419.00..... | 108.67 | 84.29 | 55.70 | 248.66 | 3.46 |
| 837.00..... | 44.80 | 24.81 | 28.15 | 97.76 | 2.47 |
| Basic series no. 2 | | | | | |
| <i>p.p.m.</i> | <i>grams</i> | <i>grams</i> | <i>grams</i> | <i>grams</i> | |
| 0.21..... | 5.77 | 4.70 | 15.23 | 25.70 | 0.69 |
| 0.68..... | 17.46 | 13.73 | 28.00 | 59.19 | 1.11 |
| 1.25..... | 45.46 | 37.41 | 50.80 | 133.67 | 1.63 |
| 6.71..... | 85.05 | 65.76 | 52.22 | 201.03 | 2.89 |
| 68.80..... | 98.87 | 77.20 | 56.50 | 232.57 | 3.12 |
| High-chloride series | | | | | |
| <i>p.p.m.</i> | <i>grams</i> | <i>grams</i> | <i>grams</i> | <i>grams</i> | |
| 0.36..... | 10.02 | 5.69 | 11.54 | 27.25 | 1.36 |
| 0.64..... | 23.17 | 16.01 | 24.55 | 63.73 | 1.59 |
| 1.53..... | 50.49 | 37.28 | 41.80 | 129.57 | 2.10 |
| 6.60..... | 85.99 | 80.55 | 54.60 | 221.14 | 3.05 |
| 69.50..... | 95.27 | 78.22 | 51.25 | 224.74 | 3.38 |
| High-sulfate series | | | | | |
| <i>p.p.m.</i> | <i>grams</i> | <i>grams</i> | <i>grams</i> | <i>grams</i> | |
| 0.13..... | 9.15 | 7.00 | 19.71 | 35.86 | 0.82 |
| 0.59..... | 36.96 | 30.32 | 43.65 | 110.93 | 1.54 |
| 1.24..... | 66.85 | 54.25 | 53.50 | 174.60 | 2.26 |
| 6.64..... | 95.70 | 76.65 | 56.15 | 228.50 | 3.07 |
| 68.60..... | 111.10 | 89.90 | 56.50 | 257.50 | 3.56 |

* The 9 plants of each culture are treated as a unit.

concentration of nitrogen for optimum growth under the conditions of this experiment would have been somewhere near 10 p.p.m. The growth in solutions maintained at 420 p.p.m. was not materially different from that made in the very much lower concentrations. At 840 p.p.m., growth was markedly reduced, and some of the leaves were injured. Leaf anal-

yses and subsequent observations indicated that this injury resulted from an excessive accumulation of potassium rather than of nitrogen, though high nitrate may have favored potassium absorption.

THE EFFECTS OF HIGH CHLORIDE AND HIGH SULFATE

The dry-weight data for the two basic, the high-chloride, and the high-sulfate series of cultures are shown graphically in figure 4. When the variations in total yield of the two basic series are considered, it will be

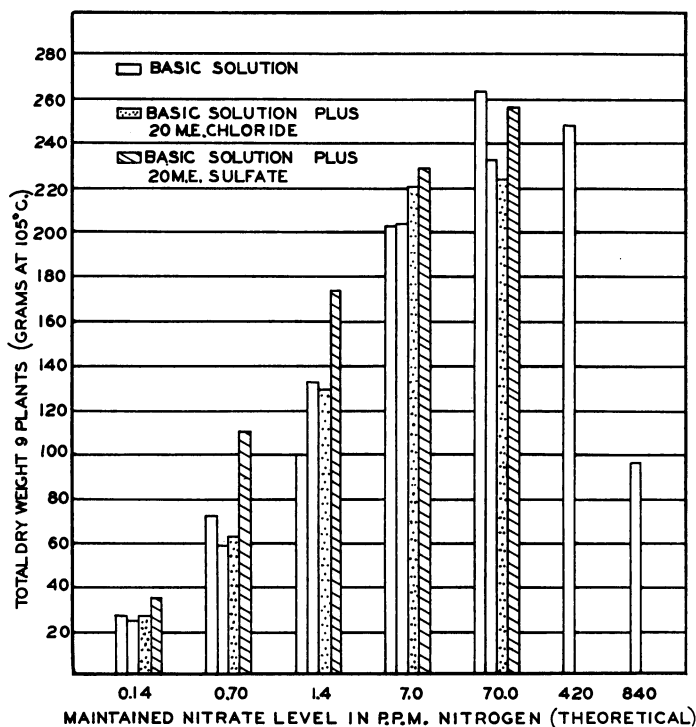


Fig. 4.—Total dry weight of the 9 sweet-orange seedlings of each culture in relation to the nitrate concentration of the nutrient solution.

seen that the addition of 20 milliequivalents of chloride per liter of solution has been without significant effect. This is of interest in that, in view of certain results reported by other investigators, such a concentration was expected to decrease nitrate absorption and thus depress yield, especially in cultures containing insufficient nitrate. Hoagland and Davis (17), for example, in work with *Nitella* cells, showed that as little as 0.5 milliequivalents of chloride per liter depressed the absorption of nitrate

ions. Haas and Reed (13), in short-term absorption experiments with citrus seedlings, found that nitrate absorption was depressed by the addition of 8 milliequivalents of chloride per liter. Eaton (8), in work with a number of different crops, found that growth was markedly depressed by 50 milliequivalents of chloride per liter, though the plants showed no tangible symptoms of injury. From his observations in general, Eaton reached the conclusion that much lower concentrations of chloride might reduce growth. Consideration of the results of the high-sulfate series may provide a partial explanation of the failure of chloride to depress growth under the conditions of this experiment.

Except in solutions of the highest nitrogen concentration, the growth of the plants of the high-sulfate series was definitely *increased* over that of the plants of the two basic series. This growth increase was especially marked in cultures of low nitrate content. The effect was so clearly manifest as regards both total growth and color of each of the 9 plants in each of these treatments, as compared with the plants of the basic series, that there can be no doubt as to its significance. The probable explanation is indicated by leaf analyses. These data are shown in table 6. As previously stated, the increases of nitrate, chloride, and sulfate in the nutrient solutions were accomplished by adding salts of calcium, magnesium, and potassium, the ratios of these cations being kept constant. The leaf analyses show that despite the increased calcium content of the high-sulfate and high-chloride nutrient solutions, the calcium in the leaves of the plants of these cultures was lower than in those of the basic series, whereas potassium was higher. The data of this table also show that both nitrogen and phosphorus were higher in the leaves of plants grown in the high-sulfate series, though the concentrations of these ions in the nutrient solution were the same as those in the basic series. These results suggest that the shift in calcium and potassium absorption caused by a simultaneous increase of both ions in the high-sulfate and high-chloride cultures had a favorable effect on nitrate absorption.

The findings of other investigators are in harmony with the preceding interpretation. For example: Collison and Harlan (7), in apple fertilizer experiments, found that in comparison with equivalent amounts of many other nitrogen fertilizers, potassium nitrate gave superior results. In absorption experiments, Hoagland (15) found that nitrate was absorbed more rapidly from potassium salts than from calcium salts. In experiments with corn, Loo (19) observed that the absorption of nitrate was favored by the presence of potassium salts and somewhat depressed by calcium salts; he also noted that the sulfate ions tended to increase nitrate absorption. Pryanishnikov (24), in experiments with sugar beets,

found that high calcium was detrimental to sugar beets given nitrate as the sole source of nitrogen. Millar (21) found an inverse correlation between the nitrogen and calcium content of plants and a positive correlation between nitrogen and potassium. Anderssen (1), in analyses of juice of citrus fruit from differentially fertilized plots, found inverse relations between nitrogen and calcium and positive relations between nitrogen and potassium. All of these results indicate that in some manner

TABLE 6
COMPOSITION OF LEAVES FROM THE BASIC, HIGH-SULFATE, AND
HIGH-CHLORIDE SERIES

| Theoretical nitrate nitrogen in nutrient solution | Series | Actual average nitrate nitrogen in nutrient solution | Composition of leaves, in per cent of dry matter* | | | | | | |
|---|-------------------|--|--|----------------|----------------|----------------|----------------|----------------|----------------|
| | | | Ca | Mg | K | N | P | S | Cl |
| <i>p. p. m.</i> | | <i>p. p. m.</i> | <i>percent</i> | <i>percent</i> | <i>percent</i> | <i>percent</i> | <i>percent</i> | <i>percent</i> | <i>percent</i> |
| 0.70 | { Basic..... | 0.67 | 2.99 | 0.23 | 3.06 | 2.05 | 0.27 | 0.35 | — |
| | { High-sulfate... | 0.59 | 2.66 | 0.20 | 3.93 | 2.48 | 0.35 | 0.69 | — |
| | { High-chloride.. | 0.64 | 2.98 | 0.28 | 4.02 | 2.36 | 0.30 | — | 2.78 |
| 1.40 | { Basic..... | 1.35 | 3.03 | 0.24 | 2.65 | 2.61 | 0.27 | 0.34 | — |
| | { High-sulfate... | 1.24 | 2.47 | 0.22 | 3.22 | 2.79 | 0.32 | 0.51 | — |
| | { High-chloride.. | 1.53 | 2.68 | 0.25 | 3.10 | 2.48 | 0.27 | — | 1.79 |
| 7.00 | { Basic..... | 7.18 | 2.67 | 0.27 | 2.56 | 3.21 | 0.27 | 0.23 | — |
| | { High-sulfate... | 6.64 | 2.19 | 0.19 | 3.46 | 3.48 | 0.29 | 0.29 | — |
| | { High-chloride.. | 6.60 | 2.23 | 0.23 | 2.90 | 3.18 | 0.28 | — | 0.87 |
| 70.00 | { Basic..... | 68.10 | 2.48 | 0.24 | 2.76 | 3.62 | 0.26 | 0.26 | — |
| | { High-sulfate... | 68.60 | 2.08 | 0.19 | 3.57 | 3.68 | 0.27 | 0.26 | — |
| | { High-chloride.. | 69.50 | 2.09 | 0.22 | 3.21 | 3.70 | 0.27 | — | 0.53 |

* The 9 plants of each culture are treated as a unit.

potassium is favorable, and calcium unfavorable, to nitrate absorption. This suggests that, within limits, the calcium-potassium balance of a nutrient solution may influence nitrate accumulation or use, the balance depending upon both the proportion and the concentration of these ions.

As regards the failure of chloride to depress yields, it is reasonable to suppose that the potentially depressing effect of this ion on nitrate absorption was offset by the favoring effect of the calcium-potassium balance, higher concentrations of both ions being more favorable to potassium and hence to nitrate absorption. Attention is directed to the fact, however, that if comparisons are made between the plant growth in the high-sulfate series and that in the high-chloride series, it would appear that chloride had depressed growth; while from comparisons between the plant growth in the high-chloride series and that in the basic

series, it would appear that chloride had not depressed growth. This is a good illustration of the need for caution in drawing general conclusions from single comparisons and of the complexity of the problem of interionic relations as they affect plant behavior.

CALCIUM-POTASSIUM RELATIONS

The shift in calcium and potassium absorption with increasing concentration of these two ions, discussed in the preceding section in connection with nitrate absorption, is also of interest from another point of view.

TABLE 7

CALCIUM, MAGNESIUM, AND POTASSIUM CONTENT OF LEAVES* IN RELATION TO THE AMOUNTS OF THESE IONS IN THE NUTRIENT SOLUTION

| NO ₃ ⁻ per liter of nutrient solution, theoretical | Series | Per liter of nutrient solution | | | Per 100 grams of dry leaves | | | |
|--|-----------------------|-----------------------------------|--------------------------|--------------------------|--------------------------------|--------------------------|--------------------------|---------------------------|
| | | Ca | Mg | K | Ca | Mg | K | Total Ca, Mg, and K |
| <i>milli-equivalents</i> | | <i>milli-equivalents</i> | <i>milli-equivalents</i> | <i>milli-equivalents</i> | <i>milli-equivalents</i> | <i>milli-equivalents</i> | <i>milli-equivalents</i> | <i>milli-equivalents</i> |
| 0.1 | { Basic | 2.2 | 1.1 | 2.2 | 151 | 20 | 68 | 239 |
| | { High-sulfate | 10.2 | 5.1 | 10.2 | 123 | 18 | 82 | 223 |
| | { High-chloride | 10.2 | 5.1 | 10.2 | 134 | 21 | 79 | 234 |
| 0.5 | { Basic | 2.3 | 1.1 | 2.3 | 133 | 22 | 65 | 220 |
| | { High-sulfate | 10.3 | 5.1 | 10.3 | 109 | 16 | 89 | 214 |
| | { High-chloride | 10.3 | 5.1 | 10.3 | 111 | 19 | 74 | 204 |
| 5.0 | { Basic | 4.1 | 2.0 | 4.1 | 124 | 20 | 71 | 215 |
| | { High-sulfate | 12.1 | 6.0 | 12.1 | 104 | 16 | 91 | 211 |
| | { High-chloride | 12.1 | 6.0 | 12.1 | 104 | 18 | 82 | 204 |
| 30.0 | Basic | 14.1 | 7.0 | 14.1 | 108 | 17 | 86 | 211 |
| 60.0 | Basic | 26.1 | 13.0 | 26.1 | 89 | 16 | 124 | 229 |

* The 9 plants of each culture are treated as a unit.

Burström (4) has shown that the antagonistic effects of calcium and potassium are most pronounced when the amounts of the two ions are present in about equivalent quantities. A relatively small change in the concentration of either ion, under these conditions, produces greater antagonism than is evident when the amounts of the two ions are greatly out of balance.

The present case is interesting because in all solutions the calcium and potassium were present in chemically equivalent amounts, and the only difference was in the total concentration. As already mentioned, an increase in the concentration of both ions resulted in decreased calcium

PLATES



Plate 1.—Injury to citrus leaves from excessive potassium.

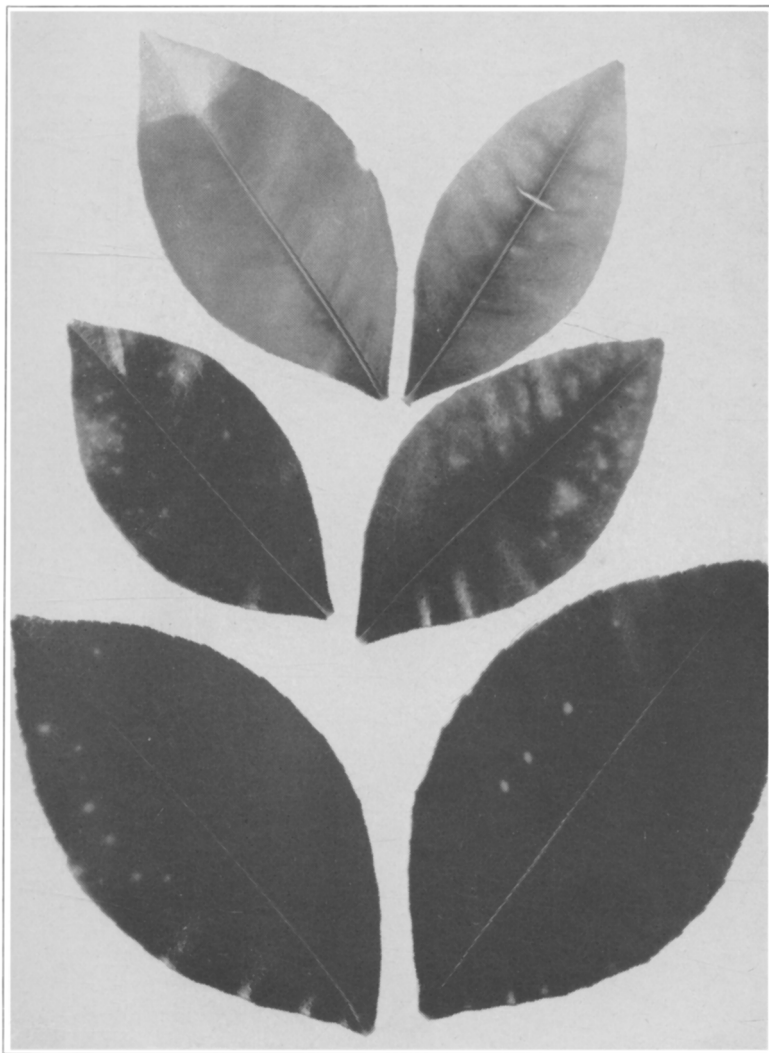


Plate 2.—Various stages of chloride injury.

and increased potassium absorption. In table 7 are shown the calcium, magnesium, and potassium contents of the leaves in relation to the amounts of these ions in the nutrient solution. It will be noted that the shift in absorption of these ions took place irrespective of the salt used to bring about the increases in calcium and potassium. The antagonism, therefore, is direct and not merely a reflection of the effect of some other change in the nutrient solution. There are indications, however, that variations in anions may exert an influence. (Compare the data of the high-sulfate and the high-chloride series in table 7.)

In equilibrium studies with clays, Vanselow⁸ has secured results of a similar nature, having found that with cation pairs involving monovalent and divalent ions, the displacing effect of the monovalent ion increases with increasing concentration. That is, as concentration increases, the monovalent ion seemingly increases in its replacing power; and, vice versa, the divalent ion seemingly decreases in this property. According to Vanselow, this phenomenon does not imply any necessary change in the properties of the ions, of the solution, or of the solid phase, but is, rather, no more than the consequence of mass action when two ions of different valency are involved in the equilibrium. The point of interest here is that in systems involving living matter, the effects are in the same direction as in inorganic systems. While the properties of many colloidal systems have been proved to vary widely when under the influence of different ions, and it is customary to think of antagonism as seated in these changes of properties, the foregoing observations serve to emphasize the importance of mass-action effects in the phenomena of antagonism.

NITROGEN-PHOSPHORUS RELATIONS

Hoagland (16), Anderssen (1), and others have observed that inverse relations exist between nitrogen and phosphorus. Anderssen, in studying the composition of juice of citrus fruit from differentially fertilized plots in South Africa, found reciprocal relations between the nitrogen and phosphorus content of the juice.

The analyses of citrus seedlings grown under the conditions of this experiment provide interesting data on this question. As previously stated, the phosphate in all nutrient solutions was kept uniform and at a low level, namely, about 10 p.p.m. PO_4^{---} . The phosphorus and nitrogen contents of the citrus plants in relation to the varying nitrate concentrations of the nutrient solutions are shown in table 8. The data of this table show that the nitrogen-starved plants were higher in total

⁸ Vanselow, A. P. Equilibrium studies with clays. Unpublished data on file at Citrus Experiment Station, Riverside, California.

TABLE 8
EFFECT OF NITRATE AND OTHER NUTRIENT VARIABLES ON THE TOTAL PHOSPHORUS
AND NITROGEN CONTENT OF SWEET-ORANGE SEEDLINGS

| Average nitrate nitrogen in nutrient solution | Dry matter, total yield* | Phosphorus in dry matter* | | | | Nitrogen in dry matter, weighted average* |
|---|-----------------------------------|---------------------------|-----------------|-----------------|---------------------|---|
| | | Leaves | Stems | Roots | Weighted average | |
| Basic series no. 1 | | | | | | |
| <i>p.p.m.</i> | <i>grams</i> | <i>per cent</i> | <i>per cent</i> | <i>per cent</i> | <i>per cent</i> | <i>per cent</i> |
| 0.20..... | 27.9 | 0.41 | 0.14 | 0.35 | 0.32 | 1.07 |
| 0.67..... | 72.3 | 0.27 | 0.11 | 0.28 | 0.23 | 1.17 |
| 1.35..... | 99.1 | 0.27 | 0.16 | 0.25 | 0.23 | 1.52 |
| 7.18..... | 202.4 | 0.27 | 0.17 | 0.13 | 0.20 | 2.11 |
| 68.10..... | 263.3 | 0.26 | 0.15 | 0.13 | 0.19 | 2.43 |
| 419.00..... | 248.6 | 0.27 | 0.16 | 0.15 | 0.21 | 2.56 |
| 837.00..... | 97.7 | 0.23 | 0.15 | 0.14 | 0.18 | 2.78 |
| Basic series no. 2 | | | | | | |
| <i>p.p.m.</i> | <i>grams</i> | <i>per cent</i> | <i>per cent</i> | <i>per cent</i> | <i>per cent</i> | <i>per cent</i> |
| 0.21..... | 25.7 | — | — | 0.41 | — | 1.23 |
| 0.68..... | 59.2 | 0.43 | 0.20 | 0.35 | 0.34 | 1.47 |
| 1.25..... | 133.7 | 0.31 | 0.18 | 0.27 | 0.26 | 1.55 |
| 6.71..... | 201.0 | 0.28 | 0.19 | 0.13 | 0.21 | 2.14 |
| 68.80..... | 232.6 | 0.27 | 0.17 | 0.15 | 0.21 | 2.54 |
| High-chloride series | | | | | | |
| <i>p.p.m.</i> | <i>grams</i> | <i>per cent</i> | <i>per cent</i> | <i>per cent</i> | <i>per cent</i> | <i>per cent</i> |
| 0.36..... | 27.2 | 0.36 | 0.23 | 0.42 | 0.36 | 1.52 |
| 0.64..... | 63.7 | 0.30 | 0.24 | 0.37 | 0.31 | 1.55 |
| 1.53..... | 129.6 | 0.27 | 0.22 | 0.25 | 0.25 | 1.63 |
| 6.60..... | 221.1 | 0.28 | 0.18 | 0.14 | 0.21 | 2.07 |
| 69.50..... | 224.7 | 0.27 | 0.16 | 0.13 | 0.20 | 2.45 |
| High-sulfate series | | | | | | |
| <i>p.p.m.</i> | <i>grams</i> | <i>per cent</i> | <i>per cent</i> | <i>per cent</i> | <i>per cent</i> | <i>per cent</i> |
| 0.13..... | 35.9 | 0.64 | 0.21 | — | — | 1.27 |
| 0.59..... | 110.9 | 0.35 | 0.20 | 0.39 | 0.32 | 1.54 |
| 1.24..... | 174.6 | 0.32 | 0.21 | 0.31 | 0.28 | 1.80 |
| 6.64..... | 228.5 | 0.29 | 0.22 | 0.18 | 0.24 | 2.37 |
| 68.60..... | 257.5 | 0.27 | 0.16 | 0.15 | 0.21 | 2.49 |

* The yields and analyses shown in this table are of the 9 plants of each culture treated as a unit.

phosphorus than those not lacking nitrogen. This is in harmony with a great deal of other evidence. Plants grown in solutions of high nitrate content, however, were not significantly lower in phosphorus than those just above the deficiency level in nitrogen. (Compare the phosphorus content of the plants grown in solutions having an average nitrogen concen-

tration of 7.18, 68.10, and 419 p.p.m. in basic series no. 1; 6.71 and 68.80 p.p.m. in basic series no. 2; and 6.60 and 69.50 p.p.m. in the high-chloride series). The increased phosphorus content of the plants grown in the low-nitrate series can be explained on the grounds of accumulation owing to varying degrees of nitrogen starvation.

There is, similarly, no evidence that high chloride or sulfate has depressed phosphate absorption. In fact, accumulation of this ion has, in some cases, been increased. This suggests that, as with nitrogen absorption, any antagonizing effect of nitrate, chloride, or sulfate on phosphate

TABLE 9
EFFECT OF INCREASED NITRATE CONCENTRATIONS ON CHLORIDE
AND SULFATE ABSORPTION

| Theoretical nitrate nitrogen in nutrient solution | High-chloride series* | | High-sulfate series* | |
|---|-----------------------|-----------------------|-----------------------|---------------------|
| | Leaves, dry weight | Chlorine in leaves | Leaves, dry weight | Sulfur in leaves |
| <i>p. p. m.</i> | <i>grams</i> | <i>per cent</i> | <i>grams</i> | <i>per cent</i> |
| 0.14..... | 10.02 | 3.90 | 9.15 | 1.02 |
| 0.70..... | 23.17 | 2.78 | 36.96 | 0.69 |
| 1.40..... | 50.49 | 1.79 | 66.85 | 0.51 |
| 7.00..... | 85.99 | 0.87 | 95.70 | 0.29 |
| 70.00..... | 95.27 | 0.53 | 111.10 | 0.26 |

* Yields and analyses shown are of the 9 plants of each culture treated as a unit.

has been offset by the changes in the calcium-potassium equilibria. Since cation relations have in some manner favorably influenced nitrate absorption, it may also have favored phosphate absorption. Therefore, though under the conditions of this experiment increased nitrate, chloride, or sulfate did not depress phosphorus accumulation, this would not justify the conclusion that under some other condition the result would be the same.

THE EFFECT OF INCREASED NITRATE ON CHLORIDE AND SULFATE ABSORPTION

In table 9 are shown the chlorine and sulfur contents of the leaves from the plants grown in solutions of variable nitrate concentration. Considerable accumulation of both chlorine and sulfur occurred in the leaves of plants retarded in growth for lack of nitrogen. The decreased content of these elements with the increase in nitrogen is perhaps owing to the diluting effect of increased plant growth. Since the total growth of the plants in the cultures maintained at 7 and 70 p.p.m. nitrogen did not differ greatly, the chlorine and sulfur content of these plants is more suggestive as regards antagonism effects. The yields and percentage composition of

TABLE 10
EFFECT OF VARIOUS NITRATE CONCENTRATIONS ON THE CHLORINE AND SULFUR CONTENT OF THE PLANT AND ITS PARTS

| Series | Average nitrate nitrogen in nutrient solution | Chlorine and sulfur in dry matter* | | | | | | | | | | | |
|--------------------|---|------------------------------------|----------|----------|---------|----------|----------|---------|----------|----------|-------------|----------|----------|
| | | Leaves | | | Stems | | | Roots | | | Whole plant | | |
| | | Dry wt. | Cl | S | Dry wt. | Cl | S | Dry wt. | Cl | S | Dry wt. | Cl | S |
| | | grams | per cent | per cent | grams | per cent | per cent | grams | per cent | per cent | grams | per cent | per cent |
| High-chloride..... | { 6.6 69.5 | 86.0 | 0.87 | — | 80.5 | 0.45 | — | 54.6 | 1.41 | — | 221.1 | 0.85 | — |
| | | 95.3 | 0.53 | — | 78.2 | 0.44 | — | 51.2 | 1.16 | — | 224.7 | 0.64 | — |
| High-sulfate..... | { 6.6 68.6 | 95.7 | — | 0.29 | 76.6 | — | 0.11 | 56.1 | — | 0.56 | 228.5 | — | 0.30 |
| | | 111.1 | — | 0.26 | 89.9 | — | 0.09 | 56.5 | — | 0.48 | 257.5 | — | 0.25 |

* Yields and analyses shown are of the 9 plants of these cultures treated as a unit.

TABLE 11
NITROGEN CONTENT OF SWEET-ORANGE SEEDLINGS IN RELATION TO THE
NITROGEN CONCENTRATIONS OF THE NUTRIENT SOLUTIONS*

| Average nitrate nitrogen in nutrient solution | Total nitrogen content | | | |
|--|------------------------|-----------------|-----------------|-------------------------------------|
| | Leaves | Stems | Roots | Weighted average, whole plant |
| Basic series no. 1 | | | | |
| <i>p.p.m.</i> | <i>per cent</i> | <i>per cent</i> | <i>per cent</i> | <i>per cent</i> |
| 0.20..... | 2.01 | 0.55 | 0.90 | 1.07 |
| 0.67..... | 2.05 | 0.62 | 0.97 | 1.17 |
| 1.35..... | 2.61 | 0.77 | 1.18 | 1.52 |
| 7.18..... | 3.21 | 0.96 | 1.83 | 2.11 |
| 68.10..... | 3.62 | 1.08 | 2.32 | 2.43 |
| 419.00..... | 3.67 | 1.17 | 2.50 | 2.56 |
| 837.00..... | 3.33 | 1.49 | 3.06 | 2.78 |
| Basic series no. 2 | | | | |
| <i>p.p.m.</i> | <i>per cent</i> | <i>per cent</i> | <i>per cent</i> | <i>per cent</i> |
| 0.21..... | 2.23 | 0.60 | 1.05 | 1.23 |
| 0.68..... | 2.51 | 0.78 | 1.17 | 1.47 |
| 1.25..... | 2.51 | 0.76 | 1.27 | 1.55 |
| 6.71..... | 3.21 | 1.01 | 1.76 | 2.14 |
| 68.80..... | 3.69 | 1.17 | 2.40 | 2.54 |
| High-chloride series | | | | |
| <i>p.p.m.</i> | <i>per cent</i> | <i>per cent</i> | <i>per cent</i> | <i>per cent</i> |
| 0.36..... | 2.28 | 0.94 | 1.16 | 1.52 |
| 0.64..... | 2.36 | 0.77 | 1.30 | 1.55 |
| 1.53..... | 2.48 | 0.80 | 1.35 | 1.63 |
| 6.60..... | 3.18 | 1.01 | 1.90 | 2.07 |
| 69.50..... | 3.70 | 1.09 | 2.19 | 2.45 |
| High-sulfate series | | | | |
| <i>p.p.m.</i> | <i>per cent</i> | <i>per cent</i> | <i>per cent</i> | <i>per cent</i> |
| 0.13..... | 2.07 | 0.65 | 1.12 | 1.27 |
| 0.59..... | 2.48 | 0.74 | 1.31 | 1.54 |
| 1.24..... | 2.79 | 0.84 | 1.54 | 1.80 |
| 6.64..... | 3.48 | 1.14 | 2.17 | 2.37 |
| 68.60..... | 3.68 | 1.14 | 2.30 | 2.49 |

* The analyses shown in this table are of the 9 plants of each culture treated as a unit.

the various parts of the plant, as well as the total yield and average composition of the whole plant with respect to these elements, are shown in table 10. While the two groups of plants of the high-chloride cultures do not differ significantly in yield, there is some decrease in chlorine content with higher nitrogen concentration, which suggests that in-

creased nitrate may have had a somewhat depressing effect on chloride absorption. With the high-sulfate series, the slightly increased yield of the plants in the higher nitrate cultures makes it impossible to decide whether nitrate exerted a depressing effect on the absorption of sulfate.

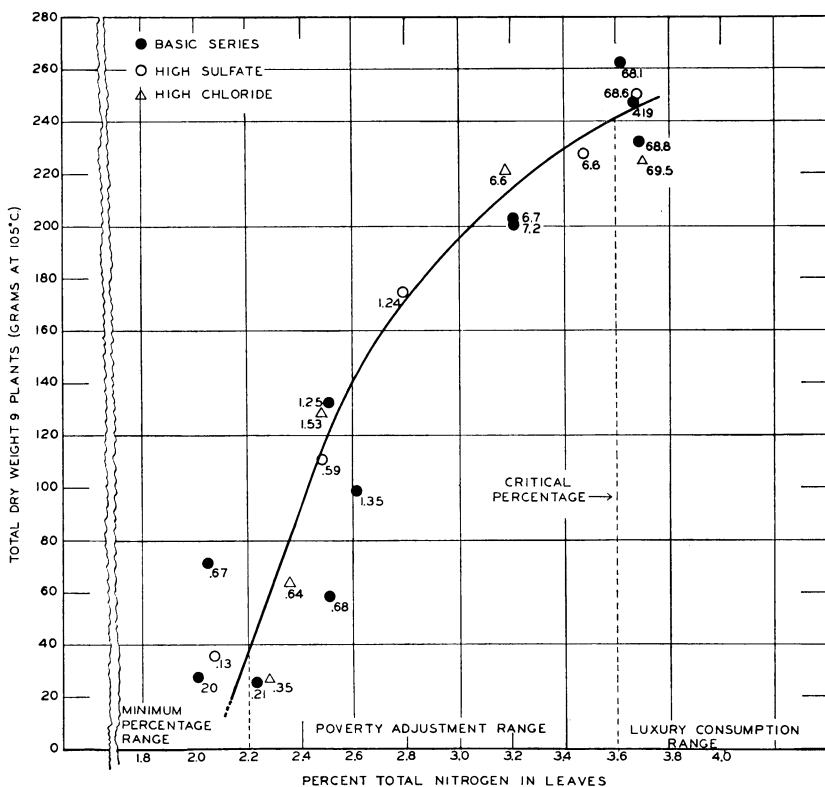


Fig. 5.—Leaf nitrogen: percentage of total nitrogen in leaves as related to total dry weight of citrus seedlings (9 plants) under varying conditions of nitrogen supply. Numbers beside the dots indicate the average nitrogen concentration, in parts per million, in the corresponding nutrient solution.

Foote and McElhiney (9), on the basis of analyses of lemon leaves, are of the opinion that nitrate does hinder sulfate absorption. This is perhaps implied in results reported by Haas and Thomas (14), who found that sulfate injury in citrus could be minimized by increasing the nitrogen supply. As with other anion-pair relations, it is possible that the shift in calcium-potassium absorption with the increase in nitrate concentration has influenced the nitrate-chloride and nitrate-sulfate relations.

LEAF COLOR AND NITROGEN CONTENT AS AN INDEX OF NITROGEN DEFICIENCY OR EXCESS

The results of this experiment are suggestive as regards the value of foliar diagnosis. Although chlorophyll determinations were not made, the plant foliage of the cultures in which nitrogen was deficient showed a distinct difference in greenness, which varied with the degree of nitro-

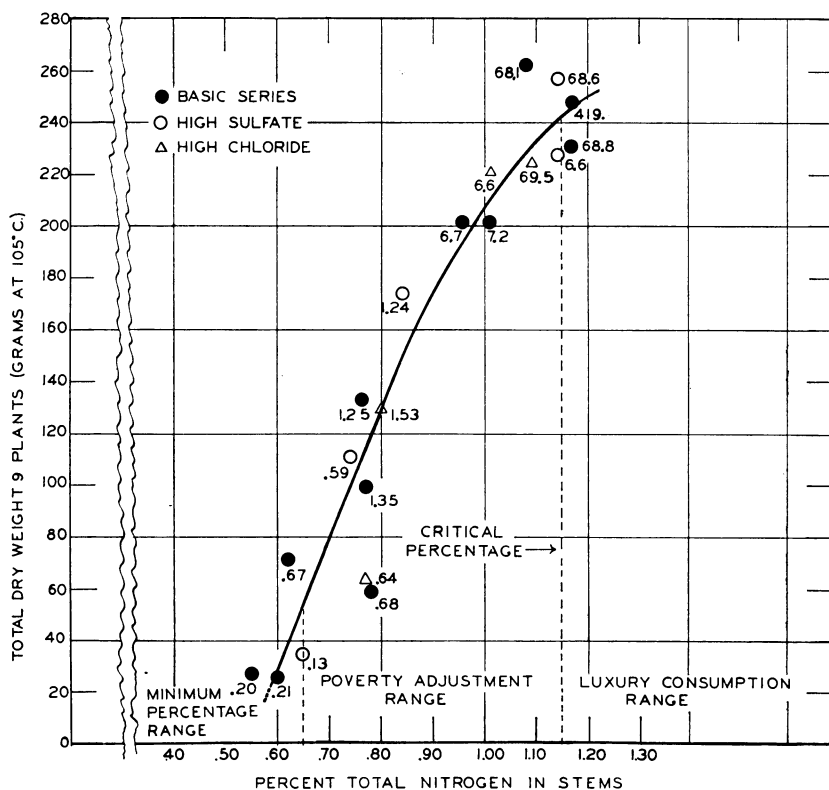


Fig. 6.—Stem nitrogen: percentage of total nitrogen in stems as related to total dry weight of citrus seedlings (9 plants) under varying conditions of nitrogen supply. Numbers beside the dots indicate the average nitrogen concentration, in parts per million, in the corresponding nutrient solution.

gen starvation. When the amounts of nitrate were in excess of that required by the plants, there was no difference in greenness, nor was there any other visible character to denote the presence of excessive nitrogen.

Total nitrogen determinations were made on the leaves, stems, and roots separately; and these data, together with the weighted average for the whole plant, are presented in table 11. As might be expected, these

data show an increase in nitrogen percentage with an increase in nitrogen content of the nutrient solution. But the total nitrogen content of the plants grown in solutions containing excessive nitrate was only slightly greater than that of the plants grown in solutions of much lower concentration.

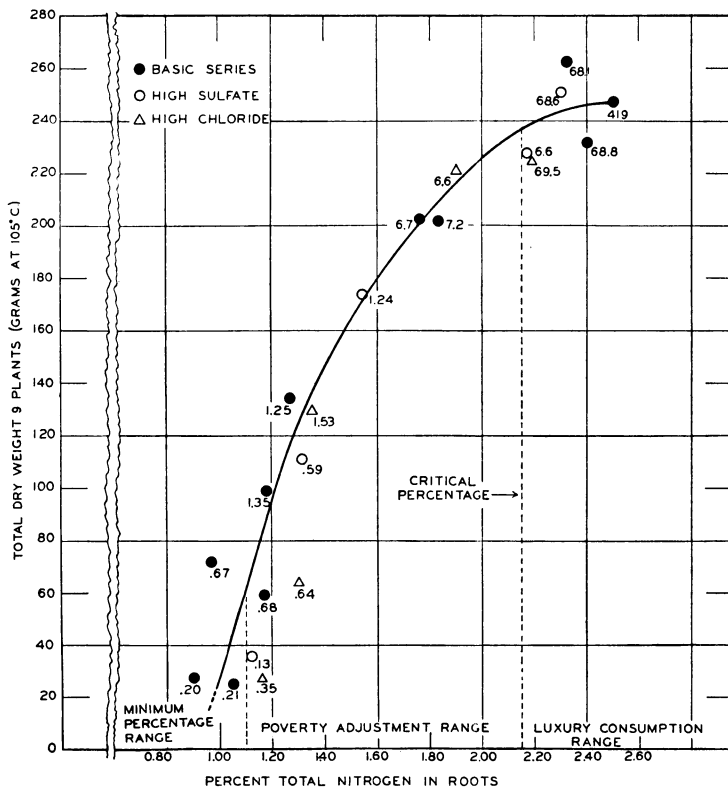


Fig. 7.—Root nitrogen: percentage of total nitrogen in roots as related to total dry weight of citrus seedlings (9 plants) under varying conditions of nitrogen supply. Numbers beside the dots indicate the average nitrogen concentration, in parts per million, in the corresponding nutrient solution.

The results of this experiment make it possible to test the value of nitrogen percentage as an index of nitrogen adequacy or excess. To cite but one of many investigators who have studied this subject: Macy (20) has suggested that for each nutrient element in each kind of plant there is a certain ideal or critical percentage; amounts in excess of this indicate luxury consumption and amounts below, poverty adjustment (figs. 5–8). As the percentage within the poverty-adjustment range decreases, a

point, or a narrow range, of minimum percentage is reached. If this theory is sound, then the nitrogen content of plants in various stages of nitrogen starvation should correlate closely with yield, regardless of conditions under which the plants were grown.

In order to test this hypothesis, the total yield of the plants grown in all of the different series has been plotted against the average nitrogen

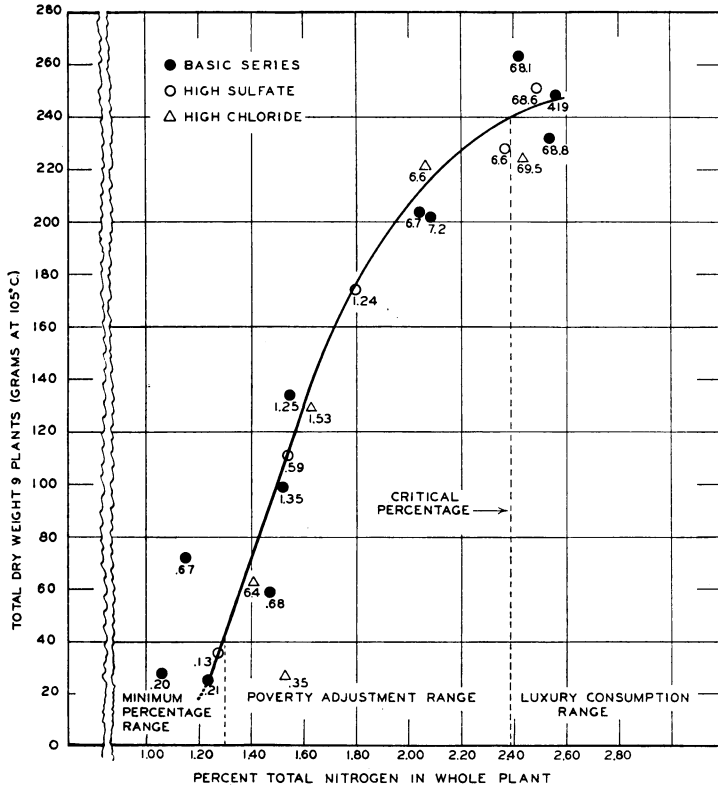


Fig. 8.—Percentage of total nitrogen in whole plant as related to total dry weight of citrus seedlings (9 plants) under varying conditions of nitrogen supply. Numbers beside the dots indicate the average nitrogen concentration, in parts per million, in the corresponding nutrient solution.

content of the whole plant and its various parts. These data are shown graphically in figures 5, 6, 7, and 8. Beside each point in these figures is shown, in parts per million, the average nitrogen concentration of the nutrient solution in which the plants were grown. A fairly good correlation is evident between the percentage of nitrogen in any part of the plant and the total yield of plants in various stages of nitrogen defi-

ciency. It will be noted, however, that there are some fluctuations in the yield of plants, or plant parts, of nearly identical nitrogen content. In other words, the nitrogen within a plant may vary in its effectiveness, according to the favorableness or unfavorableness of other factors. Hence, while nitrogen percentage can be relied upon to indicate, in a general way, the degree of nitrogen starvation, it is by no means exact. That total nitrogen content of plant tissue is not a reliable index of the degree of nitrate excess in the nutrient medium, is shown by the fact that

TABLE 12
TOTAL AND NITRATE NITROGEN IN SWEET-ORANGE SEEDLINGS GROWN IN
SOLUTIONS OF VARIOUS MAINTAINED NITRATE CONCENTRATIONS

| Theoretical nitrate nitrogen in nutrient solution | Nitrogen in various plant parts (dry-weight basis) | | | | | |
|---|---|---------------------|-------------------|---------------------|-------------------|---------------------|
| | Leaves | | Stems | | Roots | |
| | Total nitrogen | Nitrate nitrogen | Total nitrogen | Nitrate nitrogen | Total nitrogen | Nitrate nitrogen |
| <i>p. p. m.</i> | <i>p. p. m.</i> | <i>p. p. m.</i> | <i>p. p. m.</i> | <i>p. p. m.</i> | <i>p. p. m.</i> | <i>p. p. m.</i> |
| Nitrogen deficient*... | 10,950 | 70 | 4,250 | 62 | 5,550 | 277 |
| 0.35 | 29,630 | 266 | 9,830 | 393 | 13,260 | 759 |
| 1.40 | 30,500 | 287 | 10,100 | 139 | 17,900 | 534 |
| 70.00 | 34,600 | 864 | 12,300 | 333 | 25,000 | 2,362 |
| 420.00 | 29,400 | 1,290 | 12,500 | 1,010 | 24,600 | 3,920 |

* Seedlings of this group were grown in soil but were the same age as those grown in solutions.

the total nitrogen content of the plants grown in the solution maintained at 420 p.p.m. nitrate nitrogen was not materially greater than that of plants grown in far more dilute solutions.

The nitrate nitrogen content of plants grown in a medium in which nitrate is the sole source of nitrogen is a far better criterion of excess than is total nitrogen. This is shown by the data of table 12, which give the concentration of total and of nitrate nitrogen in the leaves, stems, and roots of citrus seedlings grown for eight months in water cultures of various maintained nitrate concentrations. The analyses were made on a composite of all the leaves, stems, and roots respectively, of the 6 plants grown in solutions as reported.

SYMPTOMS OF POTASSIUM AND CHLORIDE EXCESS

The utilization of a plant symptom, such as leaf appearance, to determine favorable or unfavorable conditions within the soil has been of great service in the diagnosis of nutritional disorders. In connection with this experiment, leaf symptoms of potassium excess at variance with

those previously described (12), and of incipient chloride injury differing from the tipburn and yellowing which characterize the more advanced stages of injury from this element, were obtained.

Leaves burned by excessive potassium absorption are shown in plate 1. These leaves were produced on the sweet-orange seedlings grown in solutions maintained at 840 p.p.m. nitrate nitrogen. They were also produced, though in lesser number, on the older leaves of seedlings grown in solutions of much lower nitrate content but containing 10 to 12 milliequivalents of potassium per liter. That the burning was owing to excessive potassium accumulation rather than to nitrogen accumulation, was indicated in part by leaf analyses, and in part by the development of the same symptoms in cultures of low nitrate but high potassium content. The nitrogen content of the leaves from plants grown in the culture containing 840 p.p.m. was very little higher than that of plants grown in solutions much lower in nitrate concentration; the potassium content, however, was very much higher. The potassium content of mature leaves from healthy field trees ranges ordinarily from 0.5 to 2.0 per cent, whereas the injured leaves from the 840 p.p.m.-nitrogen cultures contained 4.86 per cent potassium. On plants showing potassium burn, the old leaves were the first to be affected, the initial symptoms usually being a series of irregularly shaped, deep green blotches, water-soaked in appearance, of varying size, and occurring any place on the leaf. Around the margins of such blotches, fading of the chlorophyll took place. Subsequently, the tissue of these blotches became necrotic; and the leaf took on a more yellowish-green color, particularly in the areas surrounding the necrotic spots. Such leaves were prematurely abscised.

The incipient as well as the more advanced stages of chloride injury on citrus leaves are shown in plate 2. The more severe stages, characterized by tipburn, yellowing, and a tendency toward mottling, are those usually associated with chloride injury. Leaves less severely affected retained their green color, but scattered over the leaf were small light-green dots about the size of pinheads. Not all the leaves of such plants were affected. These symptoms appeared on plants amply supplied with nitrogen; and of interest is the fact that, whereas the older leaves were the first to be affected by potassium excess, the younger leaves were the first to show injury from chloride.

DISCUSSION AND CONCLUSIONS

The results of this experiment show that low concentrations of nitrate nitrogen (6-7 p.p.m.) if maintained, are adequate for a rapid rate of vegetative development in citrus plants. This was found true of solutions

varying rather widely as regards chloride, sulfate, and cation concentrations. The results of this experiment indicate, however, that a balance between calcium and potassium favorable for potassium absorption exerts a favorable influence on nitrate absorption.

Concentrations of nitrogen over and above the requirement for maximum vegetative growth were without effect upon vegetative development of the tops, though the top:root ratio increased with increasing nitrate—a result in harmony with that reported by many others. The growth of the plants in solutions containing 840 p.p.m. nitrate nitrogen was distinctly impaired, and the leaves displayed a characteristic burn, which leaf analyses indicated to be potassium rather than nitrogen injury.

Contrary to expectations at the outset of this experiment, it was found that increased chloride and sulfate concentrations did not depress nitrate absorption or utilization. This appears partially explicable on the ground that the increased absorption of potassium in proportion to that of calcium which accompanied the increases in the aforementioned anions served in some manner to offset the potentially depressing effect of sulfate and chloride.

With increasing and equivalent concentrations of both calcium and potassium in the nutrient solution, the absorption of calcium decreased, whereas that of potassium increased. This same shift occurs in inorganic base-exchange reactions as an effect of mass action, which suggests that the widely observed antagonism of calcium and potassium as related to plant growth is, in part, but a reflection of mass action.

With reference to other ion-pair relations, increased nitrate concentrations, under the conditions of this experiment, did not depress phosphate absorption. At various stages of nitrogen starvation, the total nitrogen and phosphorus contents of all parts of the plant stood in opposite relations, a decrease in nitrogen content being accompanied by an increase in phosphorus. However, this was probably no more than the accumulation of surplus phosphorus in plant tissue occasioned by a retarded growth rate. Plants not retarded in growth by lack of nitrogen but grown in solutions varying widely in nitrate concentration, gave no significant evidence of decreased phosphorus absorption. Similar relations were noted in cases of nitrogen-chloride and nitrogen-sulfate variables. But just as the increasingly favorable calcium-potassium relation offset the potentially depressing effects of chloride and sulfate on nitrate absorption, so it may also have offset the possibly depressing effects of increased nitrate on phosphate, chloride, or sulfate absorption. The importance of calcium-potassium relations as affecting other ion-pair relations is strongly indicated by the results of this experiment.

Both color of leaves and total nitrogen percentage of vegetative tissue are fairly reliable indexes of the degree of nitrogen starvation of plants; neither is reliable, however, as an index of excess of nitrogen. When the nutrient source of nitrogen is nitrate, a better criterion of excess is nitrate accumulation.

The results of this experiment as bearing on practical problems of fertilization merit brief discussion. The fact that citrus plants can secure adequate nitrogen for growth from solutions of low nitrogen concentration and the fact that nitrogen is easily lost from the soil, suggest that it might be better practice to supply this element in frequent small doses rather than in less frequent larger amounts. It should not, however, be inferred that a soil solution containing 6-7 p.p.m. nitrate nitrogen is ample for citrus growth. Such concentrations to be adequate must be maintained. This means that as quickly as nitrate ions are absorbed, new ions must appear to take the place of those absorbed. It is obviously impractical and probably impossible to attain this ideal in orchards. In dilute solutions the nitrate ion is absorbed more rapidly than the water, and unless the nitrate is renewed, there is increasing dilution, particularly in the moisture films adjacent to the plant roots. Diffusion of nitrate ions into these zones from points removed is relatively slow. Therefore, unless there is close synchronization between absorptive and renewal rates, the low concentrations found to be adequate under the conditions of this experiment would not suffice under soil conditions. The nearest practical approach is that of applying nitrogen in frequent small doses. Though this involves additional labor, the reduction in leaching and volatilization losses may considerably more than cover this item.

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