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# Nitrogen and Carbohydrate Content of the Strawberry Plant 

 Seasonal Changes and the Effects of FertilizersJ. H. Long and A. E. Murneek

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## TABLE OF CONTENTS

Page
Introduction ..... 3
Review of Literature ..... 4
Materials and Methods ..... 5
Chemical Analyses ..... 6
Presentation of Results ..... 6
General Morphology ..... 6
Changes in Fresh and Dry Weights. ..... 8
Nitrogen Content ..... 14
Carbohydrates ..... 20
General Distribution of Carbohydrates and Nitrogen in the Strawberry Plant-A Summary ..... 32
The Effects of Application of Nitrogen Fertilizers Upon the Nitrogen and Carbohydrate Content, and Flower and Fruit Production ..... 35
Materials and Methods ..... 35
Results of Fertilizer Studies ..... 36
Effects of Fertilizers on Dry Weight and Distribution of Nitrogen and Carbohydrates ..... 36
A Comparison of Plants Fall Fertilized, and Fall Plus Spring Fertilized ..... 41
Relation of Leaf Area and Nitrogen Content to Flower and Fruit Production ..... 45
Summary and Conclusions ..... 48
Literature Cited ..... 51

# Nitrogen and Carbohydrate Content of the Strawberry Plant Seasonal Changes and Effects of Fertilizers 

J. H. Long* and A. E. Murneek

In fertilization and nutrition of plants there are involved two complex systems-the soil and the plant. The soil in relation to application of fertilizers has been investigated extensively. The results obtained from such studies have been, in general, of fundamental value in increasing our knowledge of the soil nutrient supply to most crops grown on the particular type of soil. Unfortunately basic research on the nutrition, physiology, and development of one type of plant cannot so readily be applied to others, even when grown in the same adaphic (soil) environment.

Various groups of crop plants seem to differ greatly in respect to their rate, amount and character of development; and so in their nutrient requirements. Some go through their life cycle with astonishing rapidity while others seem to have the capacity to grow almost indefinitely. Conspicuous examples of the former are most of our cereals, while the latter may be represented by fruit trees, such as the apple and the pear. The strawberry seems to occupy a position halfway between the two extremes.

The divergent results obtained in studies of the nutrition of the strawberry and the lack of a satisfactory fertilization program, suggests the need of more information on the seasonal metabolism of this plant. During the course of a recent investigation of strawberry nutrition at this Station, it was felt once more that more knowledge is required on the physiology of this crop plant before its nutritional requirements could be better evaluated and attempts made to adjust it more successfully.

The present publication deals with a study of the seasonal changes in the nitrogen and carbohydrate content of the cultivated strawberry, var. Aroma. These two groups of substances were selected because of their great abundance and metabolic significance in the plant. Nitrogen apparently is the most important soil nutrient controlling growth, while plant development and fruit yields seem to be determined largely by the carbohydrate supply. This investigation is concerned with the "normal" seasonal trend in concentration of these two groups of substances in the strawberry plant and as they are affected by the application of organic and inorganic nitrogen fertilizers.

[^0]
## REVIEW OF LITERATURE

Information on the metabolism of the strawberry is very meagre indeed. Darrow ${ }^{5 *}$ studied growth of strawberry plants by measuring the increase in leaf area ("leaf product" index). Of the 7 varieties under investigation, Aroma produced the least foliage. It was noted that the earliest produced leaves died first and that vigor of plants was increased by removal of runners. Leaf area in the fall apparently determines the extent of fruit-bud production and hence the crop in the following year. ${ }^{33}$

As a part of his strawberry fertilization studies Loree ${ }^{18}$ determined the effect of soil nutrients on top and root development, and the mineral, nitrogen, and carbohydrate content of the plants. Those receiving nitrogen alone had a top to root ratio of 3 to 2 . When the fertilizer contained also phosphoric acid and potash, the ratio was 2 to 1 . Spring application of nitrogen caused vigorous runner production, while the same nutrient supplied in the summer resulted in a better development of crowns. Roots contained more mineral matter than the tops. A noticeable effect of the fertilizer treatments was an increase in sugar and a decrease in polysaccharides. While differences were noted in the percentages of nitrogen and carbohydrates in the tops and roots, their absolute amounts were nearly the same.

Morris and Crist ${ }^{21}$ observed that with decreasing acidity of the soil there was a decrease in dry weight of both tops and roots, a reduction in concentration of iron and aluminum, and augmentation of calcium in roots.

Whitehouse ${ }^{36}$ associated high nitrogen and low carbohydrate, especially starch, content with the application of large amount (triple dose) of nitrogen. When little of this nutrient was given, there was a smaller amount of nitrogen but much starch present. With an intermediate supply of nitrogen, the nitrogen and carbohydrate contents were also intermediate. The opinion is expressed that "fruitfulness in the strawberry plant is apparently correlated with a balance between nitrogenous and carbohydrate materials in the plant at the time of fruit bud differentiation."

Using microchemical methods $\mathrm{Mann}^{19}$ has shown that the carbohydrate content fluctuates in the strawberry during the growing period, and that an accumulation takes place as the dormant season approaches and a depletion during fruiting. Roots seem to serve as reserve organs for carbohydrates.

Gardner ${ }^{8}$ found that undefoliated plants, watered with a manure solution, were higher in total carbohydrates than those defoliated or not

[^1]treated with the liquid manure. Based on the experimental evidence obtained, the suggestion is made that variations in carbohydrate content seem to be correlated with sex expression in the strawberry, a low carbohydrate concentration being associated with the female condition, a high concentration with maleness, and an intermediate state with hermaphroditism.

Mention should be made of a preliminary paper by Long ${ }^{17}$ on seasonal changes in nitrogen and carbohydrate content of the strawberry, which is the subject of the present paper.

The physiology and chemistry of the strawberry fruit has been investigated by several workers, ${ }^{13,31,3,14,10,4}$ the object of such studies being almost entirely a determination of the effects of environmental factors and fertilizers on the firmness and quality of the product.

Scarcity of information on the metabolism of the strawberry would seem to make it very desirable to study the seasonal changes of at least the nitrogen and carbohydrate content of this plant. Information thus secured should be of value in the establishment of a more definite and effective fertilization program in strawberry culture.

## MATERIALS AND METHODS

## Materials

The variety Aroma, which was chosen for this investigation, is the most important commercial variety in Missouri because of its excellent shipping qualities and adaptation to the Ozark region, where the industry has reached commercial importance. Plants were set in early April in a fertile propagation bed and irrigated as needed. The primary daughter plants, produced asexually, were used for this investigation. Each year a new series of plants from the original stock was set in March or early April to produce new runner plants. Consequently, the material used throughout the investigation was derived from the original stock secured from the nursery, thus eliminating any possibility of variety mixture.

For all pot cultures, small thumb pots filled with sand or soil (depending upon the particular investigation for which they were needed) were imbedded in the soil beneath the daughter plants, the runners pinned down to facilitate the quick formation of roots, after which they were severed and the plants removed to a shady location. This method eliminated to a large extent the transfer of reserve storage substances from the mother plant.

Before attempting to determine the basic metabolism and the effects of fertilizers upon chemical composition, plants were usually allowed to grow in a rich loam wherein nearly ideal conditions regard-
ing organic matter, nutrients, and water were supplied. The primary daughter plants that were used grew in 5 inch pots filled with rich loam so that the root systems would be easily available at all seasons. Furthermore, these plants grew outdoors, were watered whenever needed, removed from pots and bedded in poor soil just before severe freezing weather, and mulched. Ideal and normal conditions were provided insofar as possible.

Although runner plants formed profusely in the autumn, and again in the spring, they were always removed as soon as noticed. They were not included in the analyses unless desired and so specified.

## Chemical Analyses

The plants used for chemical analyses were grown under outdoor conditions in pots containing either soil or treated clay. No attempt was made to prevent entrance of rain water, and they were mulched during the dormant season. When required, plants were lifted out of pots, roots and all, at 9 a . m. on each day of sampling, washed free of soil and adhering material with a slow stream of water, and separated as rapidly as possible into roots, stems, leaves, buds, flowers or fruits.

The fresh weights having been recorded, the material was dried in a ventilated oven ${ }^{22}$ at $75^{\circ} \mathrm{C}$. Leaf area was determined by a method described by Darrow. ${ }^{6}$ The dried material was ground to a fine powder and kept in stoppered bottles until analyses were made. The official Kjeldahl-Gunning-Arnold method was employed for the determination of total nitrogen. The various carbohydrates-sugars, starch, and hemicelluloses-were determined on 2 gram samples, using the methods and procedure described by Murneek. ${ }^{27}$ In all cases the analyses were made in duplicate, and in the few cases where results disagreed, the sample was reanalyzed till the percentages checked.

## PRESENTATION OF RESULTS

## General Morphology

The mature strawberry plant, var. Aroma, (Fig. 1), a low-growing semi-evergreen perennial, consists of a short crown stem or rhizome located at the surface of the soil, adventitious roots, leaves, and flowers and fruits. ${ }^{35}$

The stem increases in length by apical growth, and in diameter by cambial activity, and may branch into two or more divisions called secondary stems. The stem is short, usually no more and often less than two inches in length. The root system of a young daughter plant grows very rapidly under suitable conditions. Many long white adventitious roots appear from the stem and pierce the old petioles as they


Fig. 1.-A fruiting strawberry plant, var. Aroma, showing size of top and roots.
elongate. These grow to a maximum of $20-30$ centimeters and branch profusely except near the stem. For chemical analyses, only plants grown in pots were used (Fig. 2).

With age, the majority of the long adventitious roots become yellowish brown, only the very young feeding roots remaining white. Some growth of roots occurred even during the dormant season, continuing until the soil was frozen. Only a limited amount of root growth took place in the spring.

After the root system is established the leaves grow very rapidly, reaching a maximum area in late October. Shortly after the removal of plants from the nursery bed, the oldest leaves of the young plant died, thereafter little leaf death occurred until late in October. Beginning with freezing weather in November, most of the leaves undergo senescence, only the small ones living through the winter. Strawberry leaves remain attached to the stem until the laminae decay, with the result


Fig. 2.-Strawberry plants grown in pots were used for
chemical analyses.
that the stem is completely covered with old leaf bases. Leaf area reaches a minimum in February, and a maximum early in the spring, which is not exceeded until after fruiting is over. Then it increases once more. Unless specified to the contrary, all leaves were included in a sample.

At the tip of each stem, covered with leaf scales and bases, are cells that differentiate into flower buds in the early autumn. They probably undergo further development throughout the winter except during low temperatures. Early in April buds were seen emerging from the leaf scales. One or more clusters of flowers may develop from each stem or secondary stem. Within 6 to 8 weeks nearly all the fruits have ripened.

## Changes in Fresh and Dry Weights

Growth and development of plants may be measured by determinations of fresh and dry weights of various parts or organs. If taken


Fig. 3.-Total dry weight in grams per 100 plants, 1934-35.


Fig. 4.-Total dry weight in grams per 100 plants, 1935-36.
at close enough intervals such records give at least a rough picture of the seasonal development and performance of a plant.

The general data of the fresh and dry weights of strawberry plants that were set in potted soil in August are recorded in Tables 1-5 and Figures 3 and 4. Examination of Figures 3 and 4 indicate that, beginning early in September, the total dry weights of these plants in both years 1934-35 and 1935-36 increased very rapidly.

Table 1.-Total Fresh Weight in Grams per 100 Plants, 1934-35

|  | Total | Leaves | Roots | Stems |  | Total | Leaves | Roots | Stems |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Aug. 20 | 990.0 | 676.0 | 244.0 | 70.0 | Feb. 9 | 3270.0 | 1403.7 | 1336.0 | 530.5 |
| Sept. 6--- | 1338.0 | 887.0 | 343.5 | 107.5 | Feb. 21 | 2664.0 | 827.0 | 1342.0 | 495.0 |
| Sept. 18--- | 2241.5 | 1376.0 | 704.0 | 167.5 | Mar. 12 | 2017.5 | 580.0 | 952.5 | 485.0 |
| Sept. 25... | 2518.5 | 1463.5 | 851.5 | 203.5 | Mar. 30 | 2408.5 | 916.0 | 913.5 | 579.0 |
| Oct. 2 -..- | 3096.0 3632.5 | 1966.0 | 876.0 950.0 | 254.0 322.5 | Apr. 13 | 3103.0 2763.0 | 1030.5 | 1216.0 | 530.0 |
| Nov. 6 | 4497.0 | 2669.0 | 1287.0 | 541.0 | May 11. | 3476.5 | 1651.0 | 1315.5 | 510.0 |
| Nov. 25 | 4031.0 | 2182.5 | 1361.0 | 487.5 | June 4-2 | 3472.0 | 1951.0 | 890.0 | 631.0 |
| Dec. 12 | 3922.5 | 2025.0 | 1419.0 | 478.5 | June 23- | 3300.0 | 2135.0 | 585.0 | 580.0 |
| Dec. 23 | 3909.0 | 2002.0 | 1430.5 | 476.5 | Aug. 12. | 1563.5 | 1047.5 | 146.0 | 370.0 |
| Jan. 6 | 3677.5 | 1723.5 | 1481.5 | 472.5 |  |  |  |  |  |

Table 2.-Total Fresh Weight in Grams per 100 Plants, 1935-36

|  | Total | Leaves | Roots | Stems |  | Total | Leaves | Roots | Stems |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Sept. ${ }^{15}$ | 1204.8 | 647.4 | 432.4 | 125.0 | Jan. 4 | 1272.2 | 153.6 | 735.0 | 383.6 |
| Sept. 28. | 1138.8 | 532.5 | 483.8 | 122.5 | Feb. 24 | 1645.8 | 508.7 | 756.2 | 380.9 |
| Oct. 12--- | 1451.2 | 710.0 | 551.2 | 190.0 | Mar. 28-.- | 1140.0 | 273.0 | 580.0 | 287.0 |
| Oct. 26-- | 2211.0 | 1367.4 | 543.6 | 300.0 | Apr. 28---- | 2012.0 | 731.6 1110 | 950.4 | 330.0 |
| Nov. 30 | 3895.6 | 1518.4 | 1998.0 | 379.2 | May 28 | 2552.1 | 1458.5 | 781.2 | 312.4 |
| Dec. 15..- | 2233.4 | 411.0 | 1441.2 | 381.2 | July 9....- | 3165.9 | 2278.0 | 511.2 | 376.7 |

Table 3.-Total Dry Weight in Grams per 100 Plants, 1934-35

|  | Total | Leaves | Roots | Stems |  | Total | Leaves | Roots | Stems |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Aug. 20-.- | 305.0 | 208.0 | 69.5 | 27.5 | Feb. 9 | 1210.0 | 561.5 | 431.0 | 217.5 |
| Sept. 6--- | 410.0 | 282.0 | 94.0 | 34.0 | Feb. 21...- | 974.5 | 372.5 | 431.5 | 170.5 |
| Sept. 18-.- | 619.5 | 428.5 | 145.5 | 45.5 | Mar. 12..- | 886.0 | 339.5 | 351.0 | 195.5 |
| Sept. 25--- | 687.5 | 475.0 | 161.0 | 51.5 | Mar. 30..- | 821.0 | 314.5 | 334.0 | 172.5 |
| Oct. ${ }^{\text {Oct. }}$ - | 919.5 1082.5 | 703.0 | 221.5 | 70.5 105.5 | Apr. 13 | 871.0 | 349.5 306.0 | 367.0 267 | 149.5 146.0 |
| Nov. 6 | 1399.5 | 882.0 | 330.0 | 187.5 | May 11.- | 870.0 | 419.5 | 297.5 | 157.0 |
| Nov. 25 | 1327.5 | 727.5 | 412.5 | 187.5 | June 4--- | 942.5 | 528.5 | 248.5 | 165.5 |
| Dec. 12--- | 1289.0 | 675.0 | 4 | 170.5 | June 23. | 930.0 | 595.0 | 160.5 | 174.5 |
| Dec. 23--- | 1346.0 | 665.0 | 507.0 472.5 | 174.0 157.5 | Aug. 12 | 715.0 | 441.0 | 110.5 | 163.5 |

Table 4.-Total Dry Weight in Grams per 100 Plants, 1935-36

| Sept. 15 | Total 301.9 | Leaves $180.0$ | Roots 82.5 | Stems 39.4 | Jan. 4 | $\begin{aligned} & \text { Total } \\ & 636.0 \end{aligned}$ | $\begin{gathered} \text { Leaves } \\ 153.6 \end{gathered}$ | Roots 396.2 | Stems 86.2 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Sept. 28--- | 417.0 | 224.6 | 155.0 | 37.4 | Feb. 24---- | 640.0 | 175.0 | 395.8 | 69.4 |
| Oct. 12 | 673.8 | 337.4 | 272.4 | 64.0 | Mar. 28..- | 594.4 | 172.1 | 336.2 | 86.1 |
| Oct. 26...- | 771.0 | 376.2 | 307.4 | 87.4 | Apr. 28-.-- | 509.4 | 211.2 | 210.2 | 88.0 |
| Nov. 10--- | 1001.8 | 417.4 | 449.2 | 135.2 | May 8--- | 505.2 | 250.0 | 171.2 | 84.0 |
| Nov. 30--- | 948.4 | 406.2 | 432.8 | 109.2 | May 28.-- | 605.5 | 361.0 | 169.2 | 75.3 |
| Dec. 15--- | 930.8 | 411.0 | 396.8 | 121.2 | July 9...- | 984.0 | 675.0 | 143.6 | 165.4 |

Simultaneous with the rapid increase in dry weight, there was an increase also in leaf area (Tables 5 and 6 and Figures 5 and 6) both reaching their maxima each year between October 27 and November 10.

Table 5.-Average Total Leaf Area per Plant

| 1934-35 |  |  | $1935-36$ |  |
| :---: | :---: | :---: | :---: | :---: |
|  | Date | Leaf area sq. cm. | Date | Leaf area $89 . \mathrm{cm}$. |
| Aug. 22. |  | 229.3 |  |  |
| Sepr. 4 |  | 330.4 | Sept. 16-- |  |
| Sept. 20 |  | 596.2 | Sept. 28 | 400.0 |
| Oct. 2 |  | 780.0 | Oct. 12 | 557.0 |
| Oct. 16.- |  | 1136.0 |  |  |
| Oct. 20 |  | 1195.2 | Oct. 26. | 580.0 |
| Oct. 27. |  | 1279.8 |  |  |
| Nov. 6 |  | 837.0 | Nov. 10. | 620.0 |
| Nov. 17 |  | 748.2 |  |  |
| Nov. 24 |  | 463.9 | Nov. 30. | 604.0 |
| De: 13 |  | 455.3 | Dec. 15 | 590.0 |
| Dec. 23. |  | 436.0 |  |  |
| Jan. 6 |  | 302.9 | Jan. 4. | 228.0 |
| Feb. 9- |  | 215.1 |  |  |
| Feb. 21. |  | 103.3 | Feb. 24. | 160.0 |
| Mar. 12 |  | 153.6 |  |  |
| Mar. 30 |  | 162.4 | Mar. 28. | 171.0 |
| Apr. 13. |  | 272.5 |  |  |
| Apr. 27. |  | 399.5 | Apr. 28. | 296.0 |
| May 11. |  | 639.2 | May 8. | 305.0 |
| June 4 |  | 760.2 |  |  |
| June 23. |  | 836.2 |  |  |
| Aug. 12. |  | 280.4 |  |  |

Table 6.-Record of Number and Size of Leaves, Leaf Area, and Dry Weights

| Date | Number of living leaves per plant | Average length of petiole, cm. | Average width of laminae, cm . | Number leaves unfolding | Total leaf area | Number dead leaves | Weight of dead leaves, grams | Weight of living leaves, grams | Total dry weight |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| July 15 | 2-4 | 3-4 | $3 \times 2.5$ | 1 |  | 0.5 |  |  | 28.3 |
| Aug. 20. | 4-6 | 6-7 | $4.5 \times 3.5$ | 1 | 229.3 | 1.0 | 18.4 | 189.6 | 208.0 |
| Sept. 6 | 6-7 | 6-8 | $4.5 \times 5.5$ | 1 | 330.4 | 0.5 | 4.2 | 277.8 | 282.0 |
| Sept. 18 | 7-7.5 | 6-9 | $4.5 \times 5.5$ | 1 | 596.4 | 0.3 | 3.2 | 425.3 | 428.5 |
| Sept. 25 | 7.8-8 | 7-9 | $6.5 \times 7.5$ | 1.1 | 780.0 | 0.1 | 1.6 | 474.4 | 475.0 |
| Oct. 2 | 8-10 | 9-10 | $7.5 \times 9.5$ | 1.9 | 1136.8 | 0.9 | 20.1 | 582.9 | 603.0 |
| Oct. 16 | 12-15 | 9-10 | $8.5 \times 9.5$ | 3.7 | 1279.8 | 0.8 | 19.4 | 756.1 | 775.5 |
| Nov. 6 | 12-15 | 9-10 | $8.5 \times 9.5$ | 6.3 | 837.2 | 2.2 | 74.8 | 807.2 | 882.0 |
| Nov. 25 | 10-12 | 7-8 | $7.5 \times 8.5$ | 5.5 | 463.9 | 4.0 | 146.9 | 581.7 | 727.8 |
| Dec. 12 | 9-10 | 6-7 | $5 \times 7$ | 3.2 | 455.0 | 4-5 | 153.4 | 522.0 | 675.4 |
| Dec. 23 | 6-8 | 4-5 | $4 \times 5$ | 3.0 | 436 | 5-9 | 201.8 | 463.2 | 665.0 |
| Jan. 6 | 3-5 | 3-4 | 3x4.5 | 2.0 | 302.9 | 10-12 | 242.2 | 426.8 | 669.0 |
| Feb. 9 | 2-4 | 3-4 | $2.5 \times 3.5$ | 1.0 | 215.0 | 10-12 | 220.1 | 341.4 | 561.5 |
| Feb. 21 | 1-2 | 3-4 | $2.5 \times 3.5$ | 0.5 | 103 | $10-$ | 212.4 | 160.1 | 372.5 |
| Mar. 12 | 1-2 | 2-3 | $2.5 \times 3.5$ | 0.5 | 153.6 | 8-10 | 208.5 | 131.0 | 339.5 |
| Mar. 30 | 4.5 | 1.5-2.5 | $2.5 \times 3.5$ | 1.0 | 162.4 | 6.0 | 194.5 | 120.0 | 314.5 |
| April 13 | 4.5-5.5 | 2.4 | $2.5 \times 3.5$ | 1.0 | 272.5 | 3-4 | 126.5 | 222.0 | 348.5 |
| April 27 | 5-6 | 5.0 | $3.5 \times 4$ | 1.5 | 399.5 | 2.0 | 64.3 | 242.2 | 306.5 |
| May 11 | 7-7.5 | 6-9 | $4.5 \times 5.8$ | 3-4 | 639.2 | 1.0 | 32.1 | 387.5 | 419.5 |
| June 4- | 7-8 | 7-8 | $4.5 \times 6$ | 3-5 | 760.2 | 1.0 | 33.6 | 494.9 | 528.5 |
| June 23 | 8-9 | 6-8 | $4.5 \times 5.5$ | 2-3 | 836.2 | 0.5 | 18.9 | 576.1 | 595.0 |
| Aug. 12. | 7-8 | 5-8 | $4 \times 5$ | 1-2 | 280.4 | 2.0 | 66.8 | 375.2 | 441.0 |

Excellent weather conditions prevailed in late autumn for the growth and photosynthesis of strawberry plants. Freezing weather occurred on November 10, resulting in a decreased leaf area of 30 per cent or more within a few days. From the date of maximal leaf area (October


Fig. 5.-Total leaf area in sq. cm. per plant, 1934-36.


Fig. 6.-Record of the dry weights of living leaves, dead leaves, total dry weights of leaves, and total leaf area.

26 to November 10) there was a decrease in total dry matter, which was due mostly to loss of leaves through decay (Table 6). Throughout the dormant season (December to February) a continuous loss of dry matter occurred, largely because of death of plant parts and from respiration.

The dry weight of roots increased from August (the beginning of the experiment) to November 10 of one year and to late Deçember of the other. This increase was due, not only to the normal development of the roots, but also to an augmented storage of food reserves there. The dry weight may continue to increase even after the greatest leaf area is reached (October 27) possibly because of the movement of soluble organic substances from the dying leaves. This is a typical autumnal migration of food reserves exhibited by many other perennial plants. ${ }^{28}$

Beginning in March of each year, a sudden drop in total dry matter of roots occurs, which continues until July-August. This is, in general, also true of the percentage of dry matter. Some of the roots may have been lost but no part of the stems was lost, and the same decrease is noted in this organ. The record of leaf development (Figure 6) and dry weights of floral organs (Figures 3 and 4) show that March is also the time of rapid growth of leaves, just preceding the development of floral organs and fruits in April and May. It may be assumed then that the decrease in dry matter which is very rapid in March and April may be partly accounted for in the growth of new leaves and floral organs.

The trend for dry matter of the stems follows very closely that of roots, increasing during the autumn and decreasing during dormancy, spring growth, and fruiting.

Table 7.-Percentage of Total Dry Matter

| 1934-35 |  |  |  | 1935-36 |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Date | Leaves | Roots | Stems | Date | Leaves | Ronts | Stems |
| Aug. 20 | 68.1 | 22.8 | 9.0 |  |  |  |  |
| Sept. 6 | 68.7 | 22.9 | 8.2 |  |  |  |  |
| Sept. 18 | 69.1 | 23.4 | 7.3 | Sept. 15- | 59.6 | 27.3 | 13.1 |
| Sept. 25 | 69.0 | 23.4 | 7.4 | Sept. 28 | 53.8 | 37.1 | 9.1 |
| Oct. 2. | 65.5 | 26.7 | 7.6 | Oct. 12 | 50.0 | 40.4 | 9.6 |
| Oct. 16 | 71.6 | 20.4 | 9.7 | Oct. 26 | 48.8 | 39.8 | 11.4 |
| Nov. 6 | 63.2 | 23.5 | 13.3 | Nov. 10 | 41.6 | 44.8 | 13.6 |
| Nov. 25 | 55.6 | 31.0 | 13.4 | Nov. 30 | 42.8 | 45.6 | 11.6 |
| Dec. 12 | 52.3 | 39.3 | 8.4 | Dec. 15 | 44.1 | 42.8 | 13.1 |
| Dec. 23 | 49.4 | 37.6 | 13.0 |  |  |  |  |
| Jan. 6 | 51.5 | 36.3 | 12.2 | Jan. 4 | 24.1 | 62.2 | 13.7 |
| Feb. 9 | 46.3 | 35.6 | 18.1 |  |  |  |  |
| Feb. 21 | 39.2 | 44.1 | 16.7 | Feb. 24 | 27.3 | 61.8 | 10.9 |
| Mar. 12 | 38.2 | 39.6 | 22.2 |  |  |  |  |
| Mar. 30 | 38.2 | 40.5 | 21.3 | Mar. 28. | 56.5 | 14.6 | ---- |
| Apr. 13- | 38.7 | 37.9 | 23.4 |  |  |  |  |
| Apr. 27 | 37.8 | 33.0 | 29.2 | Apr. 28 | 41.4 | 41.2 | 17.4 |
| May 11 | 46.9 | 34.1 | 19.0 | May 8 | 49.4 | 33.8 | 16.8 |
| June 4 | 56.1 | 26.3 | 17.6 | May 28 | 59.6 | 27.9 | 12.5 |
| June 23 | 64.0 | 17.2 | 18.8 | July 9. | 68.6 | 14.6 | 16.8 |
| Aug. 12....- | 61.6 | 15.3 | 23.1 |  |  |  |  |

In general, the results of our dry weight studies of the strawberry plant are approximately the same as those found by Mann and Ball. ${ }^{20}$ Although the percentages of dry matter and water for a particular tissue do not vary significantly through a season, certain relations are apparent. In Table 7 are presented data that show the distribution of total dry matter in the roots, stems, and leaves at various seasons.

In August and September, when the plants are small, the leaves make up $68 \%$ or more of the total dry matter, the roots only $22-23 \%$. Similar ratios prevail at the time of maximal leaf area, but of course the total dry weight is much greater than in August. There is a decrease in the total dry matter of the leaves and an increase of that of roots and stems until the greatest leaf reduction is reached February 21. Then the leaves make up $39.2 \%$, roots $41.1 \%$ and stems $16.7 \%$, which points to the roots as storage organs of dry matter. During the period of growth of leaves in March the dry matter of roots decreases abruptly, followed by a rapid loss at the time of flowering and fruiting (especially pronounced in 1935).

In general, the data indicate that the strawberry plants behave as perennials, increasing in dry weight the first year of growth and decreasing the succeeding year with the production of new growth, flowers, fruits, and new plants.

## Nitrogen Content

The concentration and total amount of this element, which is relatively abundant and probably the most important constituent in metabolically active as well as more permanent inactive tissue, are expressed in Tables 8-12 and Figures 7 to 10.

Table 8.-Total Nitrogen in Grams per 100 Plants, 1934-35

|  | Total | Leaves | Roots | Stems |  | Total | Leaves | Roots | Stems |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Aug. 22 | 5.97 | 4.45 | 1.16 | 0.36 | Feb. 9 | 22.86 | 8.69 | 8.40 | 5.77 |
| Sept. 6--- | 7.67 | 5.97 | 1.31 | 0.39 | Feb. 21-- | 21.66 | 7.17 | 7.97 | 4.52 |
| Sept. 18-- | 11.91 | 9.20 | 2.06 | 0.65 | Mar. 12. | 18.66 | 6.00 | 7.65 | 5.01 |
| Sept. 26.-- | 14.07 | 10.92 | 2.41 | 0.74 | Mar. 30. | 17.52 | 6.44 | 6.78 | 4.30 |
| Oct. ${ }^{2}$ | 16.78 | 11.27 | 4.20 | 1.31 | Apr. 13-- | 17.08 | 6.10 | 6.85 | 4.13 |
| Oct. 17.. | 21.59 | 16.38 | 3.44 | 1.77 | Apr. 26-- | 15.27 | 6.91 | 4.10 | 4.26 |
| Nov. 6 -- | 24.00 | 17.28 | 4.75 | $\frac{2}{2} .97$ | May 11. | 13.57 |  | 3.32 | 1.69 |
| Nov. 25-- | 23.46 | 13.30 | 6.55 | 3.61 | June 4-- | 14.09 | 10.10 | 2.15 | 1.84 |
| Dec. 12-- | 21.09 | 10.60 | 7.26 | 3.23 | June 23. | 11.85 | 9.25 | 1.20 | 1.41 |
| Dec. 24-.. | 21.26 21.86 | 9.84 9.29 | 7.65 8.68 | 3.77 3.89 | Aug. 12 | 9.95 | 7.74 | 0.91 | 1.30 |

Table 9.-Total Nitrogen in Grams per 100 Plants, 1935-36

|  | Total | Leaves | Roots | Stems |  | Total | Leaves | Roots | Stems |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Sepr. 15 | 5.32 | 3.50 | 1.30 | 0.52 | Dec. 15... | 13.04 | 4.66 | 5.66 | 2.72 |
| Sept. 28 | 4.23 | 1.86 | 1.89 | 0.48 | Jan. 4 | 10.67 | 2.50 | 5.94 | 2.23 |
| Oct. 12 | 12.76 | 8.20 | 3.60 | 0.96 | Feb. 24 | 11.00 | 3.06 | 6.28 | 1.66 |
| Oct. 26 | 12.26 | 7.66 | 3.38 | 1.22 | Mar. 28. | 11.50 | 3.30 | 6.24 | 1.96 |
| Nov. 10-.- | 15.56 | 9.00 | 4.54 | 2.02 | Apr. 28...- | 9.58 | 4.24 | 2.38 | 2.96 |
| Nov. $30 .-$ | 17.54 | 8.12 | 6.88 | 2.54 | May 8.-. | 7.14 | 3.64 | 1.70 | 1.80 |

Table 10.-Total Nitrogen in Percentages of Dry Weight, 1934-35

|  | Leaves | Roots | Stems |  | Leaves | Roots | Stems |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| ${ }_{\text {Aug. }} 22$ | 2.13 | 1.69 | 1.34 | Feb. 9 - | 1.55 | 1.95 | 2.66 |
| Sepu. 6 | 2.12 | 1.40 | 1.16 | Feb. 21 | 1.55 | 1.85 | 2.66 |
| Sept. 18 | 2.15 | 1.42 | 1.45 | Mar. 12 | 1.77 | 2.18 | 2.57 |
| Sept. 25 | 2.30 | 1.50 | 1.48 | Mar. 30 | 2.05 | 2.03 | 2.47 |
| Oct. 17 | 1.87 2.17 | 1.71 | 1.87 | Apr. 13 | 2.19 | 2.01 | 2.31 |
| Nov. 6 | 1.96 | 1.44 | 1.59 | May 11 | 2.04 | 1.12 | 1.18 |
| Nov. 25 | 1.83 | 1.59 | 1.93 | June 4 | 1.92 | 0.87 | 1.12 |
| Dec. 12 | 1.57 | 1.64 | 1.90 | June 23 | 1.56 | 0.75 | 0.81 |
| Dec. 24 | 1.48 | 1.51 | 2.17 | Aug. 12 | 1.53 | 0.82 | 0.80 |
| Jan. 6 | 1.40 | 181 | 2.48 |  |  |  |  |

Table 11.-Total Nitrogen in Percentages of Dry Weight, 1935-36

|  | $\underline{\text { Leaves }}$ | Roots | Stems |  | Leaves | Roots | Stems |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Sept. 15-1 | 1.95 | 1.77 | 1.42 | Dec. 15 | 2.01 | 1.42 | 2.25 |
| Sept. 28 | 1.82 | 1.22 | 1.30 | Jan. 4 | 1.62 | 1.50 | 1.93 |
| Oct. 12 | 2.43 | 1.32 | 1.54 | Feb. 24 | 1.75 | 1.59 | 2.39 |
| Oct. 26 | $\frac{2}{2} .04$ | 1.10 | 1.41 | Mar. 28 | 1.92 | 1.86 | 2.27 |
| Nov. 10 | 2.16 | 1.01 | 1.53 | Apr. 28 | 2.12 | 1.19 | 1.48 |
| Nov. 30. | 2.00 | 1.19 | 2.33 | May 8 | 1.82 | 0.85 | 0.90 |

Although the graphs showing changes in nitrogen content for 193536 (Figures 8 and 10) are in part more irregular than those for 1934-35 (Figures 7 and 9), they are in general quite similar, indicating that nitrogen reserve are built up in the plant as a whole in the autumn and depleted in the spring. At the time of greatest leaf developmnt (October 27 to November 10), when leaves show 2.0 to $2.4 \%$ nitrogen, 60 to $75 \%$ of the total nitrogen of the plant is contained in these organs (Tables 8 and 9 ). At the time of fruit setting of the strawberry (AprilMay), 45 to $70 \%$ of the total nitrogen may be in the leaves, again indicating the importance of nitrogen in the food manufacturing organs.

Further studies of the tables and of Figures 7 to 10 should make it clear that from October 27 to November 10 there was a general decrease in the percentage of nitrogen in leaves. This began even before yellowing was apparent and continued till January. Approximately one-half the nitrogen was removed from the leaves before death. Through the dormant season (December to February) dead leaves have progressively less nitrogen till the time when spring growth begins (March).

During the period of minimal leaf area (January and February), leaves contain only 1.4 to $1.6 \%$, or 20 to $30 \%$ of the total amount of this element in the whole plant. But early in the spring (March), nitrogen increases rapidly to the amount of 1.9 to $2.1 \%$.

Table 12.-Nitrogen and Carbohydrate Content of Flowers-Fruits, 1935-36

| Date | Tissue | Dry Weight |  | Fresh Weight |  | Nitrogen |  |  | Reducing Sugars |  |  | Total Sugars |  |  | Starch |  |  | Hemicellulose |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | \% | Gms. | \% | Gms. | Per cent |  | Gms. | Per cent |  | Gms. | Per cent |  | Gms. | Per cent |  | Gm8. | Per cent |  | Gms. |
|  |  |  |  |  |  | $\begin{gathered} \text { Fresh } \\ \text { wt. } \end{gathered}$ | $\begin{gathered} \text { Dry } \\ \text { wt. } \end{gathered}$ |  | Fresh wt. | $\begin{aligned} & \text { Dry } \\ & \text { wt. } \end{aligned}$ |  | Fresh wt. | $\begin{aligned} & \text { Dry } \\ & \text { wt } \end{aligned}$ |  | Fresh wt. | $\begin{aligned} & \text { Dry } \\ & \text { wt. } \end{aligned}$ |  | Fresh wt. | $\begin{aligned} & \text { Dry } \\ & \text { wt. } \end{aligned}$ |  |
| $\begin{gathered} 1935 \\ \text { Apr. } 13 \end{gathered}$ | Buds | 23.6 | 30.0 | 76.4 | 127.0 | 0.76 | 3.20 | 0.96 | 0.34 | 1.45 | 0.43 | 0.79 | 3.35 | 1.00 | 0.81 | 3.42 | 1.02 | 1.75 | 7.42 | 2.22 |
| Apr. 27. | Flowers.- | 22.3 | 89.5 | 77.7 | 398.0 | 0.62 | 2.76 | 2.45 | 0.52 | 2.31 | 2.07 | 0.87 | 3.90 | 3.5 | 0.67 | 3.00 | 2.68 | 1.54 | 6.90 | 6.15 |
| May 11. | Pedicels <br> Fruits. | $\begin{aligned} & 16.4 \\ & 22.6 \end{aligned}$ | $\begin{array}{r} \overline{67.5} \\ 120.0 \end{array}$ | $\begin{aligned} & 83.6 \\ & 77.4 \end{aligned}$ | $\begin{aligned} & 395.0 \\ & 524.0 \end{aligned}$ | $\begin{aligned} & 0.49 \\ & 0.61 \end{aligned}$ | $\begin{aligned} & -3.72 \\ & 2.16 \end{aligned}$ | 2.50 2.07 | 0.49 0.30 | $\begin{aligned} & 3.0 \\ & 3.05 \end{aligned}$ | $\frac{2.02}{3.66}$ | 0.74 1.10 | 3.3 3.6 | 2.9 4.3 | 0.53 0.72 | 3.10 3.30 | 2.09 3.96 | 1.37 1.73 | 8.07 7.87 | $\begin{aligned} & 5.40 \\ & 9.44 \end{aligned}$ |
| June 4-- | Pedicels.. Fruits | $\begin{array}{r} 20.9 \\ 9.5 \end{array}$ | $\begin{array}{r} 88.5 \\ 370.0 \end{array}$ | $\begin{aligned} & 79.1 \\ & 90.5 \end{aligned}$ | $\begin{array}{r} 41.0 \\ 3400.0 \end{array}$ | $\begin{aligned} & 0.13 \\ & 0.23 \end{aligned}$ | $\begin{aligned} & 1.16 \\ & 1.45 \end{aligned}$ | 1.22 5.15 | $\begin{aligned} & 0.63 \\ & 0.30 \end{aligned}$ | 2.8 5.8 | 21.48 21.46 | $\begin{aligned} & \overline{0.77} \\ & 1.30 \end{aligned}$ | $\begin{aligned} & 3.7 \\ & 6.7 \end{aligned}$ | 3.3 24.79 | 0.75 | 3.59 3.09 | $12.9{ }^{2.94}$ | 1.53 1.08 | 7.30 5.10 | 6.46 <br> 18.5 |
| $\begin{gathered} 1936 \\ \text { Apr. } 28 . \end{gathered}$ | Flowers.- | 21.9 | 45.0 | 78.1 | 204.7 | 0.53 | 2.41 | 1.08 | 0.39 | 1.80 | 0.81 | 0.96 | 4.4 | 1.98 | 1.18 | 5.4 | 2.43 | 3.65 | 16.71 | 7.50 |
| May 8_- | Flowers. . <br> Pedicels_- <br> Fruits | $\begin{aligned} & 21.8 \\ & 12.5 \\ & 163 \end{aligned}$ | $\begin{aligned} & 22.4 \\ & 25.0 \\ & 58.8 \end{aligned}$ | $\begin{aligned} & 78.2 \\ & 87.5 \\ & 83.7 \end{aligned}$ | $\begin{aligned} & 102.4 \\ & 200.0 \\ & 358.8 \end{aligned}$ | $\begin{aligned} & 0.19 \\ & 0.15 \\ & 0.39 \end{aligned}$ | $\begin{aligned} & 0.88 \\ & 1.23 \\ & 2.42 \end{aligned}$ | 1.96 0.50 1.42 | $\begin{aligned} & 0.28 \\ & 0.25 \\ & 0.34 \end{aligned}$ | $\begin{aligned} & 1.30 \\ & 2.00 \\ & 2.10 \end{aligned}$ | 0.29 0.45 1.22 | 0.39 0.39 0.78 | $\begin{aligned} & 1.80 \\ & 3.2 \\ & 4.78 \end{aligned}$ | $\begin{aligned} & 0.40 \\ & 0.80 \\ & 7.81 \end{aligned}$ | 0.74 0.50 0.18 | 3.40 4.00 1.10 | 0.76 1.00 0.65 | $\begin{aligned} & 2.87 \\ & 1.59 \\ & 2.40 \end{aligned}$ | $\begin{aligned} & 13.2 \\ & 12.8 \\ & 14.7 \end{aligned}$ | 2.96 3.20 8.60 |
| May 28. | Pedicels_ Fruits.-- | $\begin{aligned} & 22.2 \\ & 11.0 \end{aligned}$ | $\begin{aligned} & 44.0 \\ & 62.1 \end{aligned}$ | $\begin{aligned} & 77.8 \\ & 89.0 \end{aligned}$ | $\begin{aligned} & 197.8 \\ & 566.1 \end{aligned}$ | ----- | ----- | -- | $\begin{aligned} & 0.60 \\ & 1.62 \end{aligned}$ | 2.72 14.6 | $\begin{aligned} & 1.19 \\ & 9.15 \end{aligned}$ | 0.92 1.67 | 4.15 15.1 | 1.83 9.46 | 0.84 0.36 | 3.8 3.3 | 1.67 2.07 | 4.37 1.49 | $\begin{aligned} & 19.67 \\ & 13.52 \end{aligned}$ | $\begin{aligned} & 8.65 \\ & 8.47 \end{aligned}$ |



Fig. 7.-Total nitrogen in grams per 100 plants, 1934.35.


Fig. 8.-Total nitrogen in grams per 100 plants, 1935-36.


Fig. 9.-Total nitrogen in percentage of dry weight, 1934-35.


Fig. 10.-Nitrogen in percentage of dry weight, 1935-36.

In an endeavor to account for all the nitrogen in a plant during leaf senescence and dormacy, the following data may be of interest. They are expressed in grams per 100 plants.


Disconsidering a possible experimental error, it would seem that in 1934, 4.87 grams of nitrogen migrated to roots and stems from leaves with only .14 grams lost or unaccounted for. In 1935, however, only 1.38 grams of nitrogen migrated to roots and stems, with 1.18 grams lost or unaccounted for, thus showing marked season differences in this respect.

Roots are the principal storage organs of nitrogen in winter, not necessarily because of its high concentration there, but because of their spread and high total weight. In studying the graphs for nitrogen content (Figures 7 to 10 ), it is apparent that nitrogen increases during the autumn as judged both by percentage of dry weight and by total amounts in grams, and decreases during the spring, but particularly so at the time of flowering and fruit. In winter $30-40$ per cent of the nitrogen is in the roots. Some increase in roots and stems is noted during leaf death, indicating that nitrogen "migrates" to these organs or that it is absorbed from the soil.

An inspection of the data, especially those for the period of October 17, 1934 to February 21, 1935, will show that the total amount of nitrogen contained in the plant varied within the limits of a few grams. There was a considerable decrease of nitrogen in leaves due to death from freezing, with a concurrent large increase in roots and stems. This emphasizes once more the fact that nitrogen moves from leaves to the storage organs, primarily the roots.

To illustrate the reverse movement of nitrogen, from the storage organs to the leaves, the following facts may be cited. When active spring growth is in progress (March), the leaf area may be doubled, growth being at the expense of food reserves. At the same time the nitrogen content of the roots and stems decreased from 7 to 11 grams
in February to 4 to 8 grams in April. In June approximately 77 per cent of the total nitrogen was concentrated in the leaves, and only 22 per cent in the storage organs.

All of the nitrogen that is removed from the roots and stems is not used in leaf development, because an additional demand is made by organs associated with sexual reproduction (Table 12). Considering our studies of the nitrogen content of flowers and fruits, attention must be directed to the work of 1934-35, since in 1935-36 samples were not taken at very frequent intervals. The buds, flowers, or fruit samples contained also the small green leaf-like organs just beneath and surrounding the flower or fruit. In an attempt to explain the heavy drain made upon stored nitrogen reserves referred to previously, buds when just large enough to be dissected without the aid of lenses, held 3.2 per cent nitrogen on dry weight basis. . Two weeks later, this percentage was 2.76, although the total nitrogen in grams was nearly three times as great. By May 11, the pedicels, which held 3.72 per cent nitrogen, had elongated so that their separation from the flowers was practical. The nitrogen content of flowers was 2.16 per cent. By June 4, when the fruits had formed, nitrogen in the pedicels had decreased from 2.16 to 1.16 per cent, with a similar decrease in flowers. Not only did the per cent of nitrogen in the pedicels decrease, but the total amount also decreased to one-half while in the fruits it had doubled.

In general then, in the autumn the percentage and total amount of nitrogen increases rapidly in all organs, reaching a maximum at the peak of leaf growth (October 27 to November 10) when three-fourths of the nitrogen is held in the leaves. During leaf senescence (November 20 to December 15) nitrogen in the leaves decreases rapidly while at the same time it increases in the roots and stems, which are the principal storage organs of the strawberry. There is little fluctuation of this element in the roots and stems during the dormant season (December to February). In the spring (early March), there is a great demand for nitrogen for the development of leaves, elongation of pedicels, formation of flowers, and the growth of fruit. To meet this demand nitrogen is moved from the storage organs which show the greatest depletion of this element in early summer (May-June). A further demand upon the reserve nitrogen is made for runner production (July-August).

## Carbohydrates

Total Sugars.-The concentration and total amount of sugars are recorded in Tables 13 to 16 and presented graphically in Figures 11 to 14 .

Table 13.-Total Sugars in Grams per 100 Plants, $1934-35$

|  | Total | Leaves | Roots | Stems |  | Total | Leaves | Roots | Stems |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Aug. 20... | 36.68 | 16.32 | 19.80 | 0.56 | Feb. 2 | 101.16 | 19.09 | 62.5 | 19.57 |
| Sept. 6... | 19.29 | 16.92 | 2.02 | 0.35 | Feb. 21 | 90.06 | 8.57 | 60.41 | 11.08 |
| Sept. 18..- | 33.7 | 30.17 | 2.75 | 0.78 | Mar. 12-- | 68.21 | 20.2 | 35.8 | 12.21 |
| Sept. 25...- | 40.17 | 34.43 | 4.42 | 1.32 | Mar. 30.. | 48.25 | 15.56 | 26.05 | 6.64 |
| Oct. 2 | 54.16 | 42.51 | 9.47 | 2.18 | Apr. 13-- | 104.8 | 28.3 | 64.29 | 12.20 |
| Oct. 16 | 70.96 | 57.0 | 9.40 | 4.56 | Apr. 27. | 86.95 | 14.07 | 65.0 | 7.88 |
| Nov. 6 | 93.53 | 67.03 | 16.50 | 10.00 | May 11. | 40.45 | 22.23 | 12.20 | 6.02 |
| Nov. 25...- | 75.22 | 51.98 | 12.40 | 10.84 | June 4.- | 40.81 | 29.07 | 3.8 | 7.94 |
| Dec. 12--- | 101.1 | 42.18 | 44.30 | 14.53 | June 23.- | 75.2 | 64.25 | 4.17 | 6.78 |
| Dec. 23--- | 80.9 | 28.26 | 34.98 | 17.66 | Aug. 16.- | 42.82 | 33.5 | 5.07 | 4.25 |
| Jan. 6.... | 96.97 | 27.44 | 51.03 | 18.5 |  |  |  |  |  |

Table 14.-Total Sugars in Grams per 100 Plants, 1935-36

|  | Total | Leaves | Roots | Stems |  | Total Leaves |  | Roots | Stems |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Sept. 15-- | 12.68 | 8.64 | 2.46 | 1.58 | Jan. 4 | 58.32 | 11.50 | 36.14 | 10.68 |
| Sept. 28... | 15.82 | 8.68 | 4.18 | 2.96 | Feb. 24 | 38.54 | 5.88 | 29.24 | 3.42 |
| Oct. 12... | 31.48 | 16.74 | 11.82 | 2.92 | Mar. 28 | 44.30 | 4.72 | 26.76 | 12.82 |
| Oct. 26... | 43.86 | 32.72 | 7.38 | 3.76 | Adr. 28. | 21.86 | 10.14 | 9.66 | 2.06 |
| Nov. 10. | 57.40 | 29.22 | 24.70 | 3.54 | May 8. | 19.14 | 10.50 | 9.26 | 5.38 |
| Nov. 30.. | 57.98 | 24.4 | 28.56 | 5.02 | May 28. | 18.04 | 12.82 | 2.44 | 2.78 |
| Dec. 15 ... | 70.00 | 19.44 | 27.10 | 22.46 | July 9, | 26.80 | 21.60 | 1.97 | 3.23 |

Table 15.-Total Sugar in Percentage of Dry Weight, 1934-35


Table 16.-Total Sugar in Percentage of Dry W'eight, 1935-36


Due to many variable environmental factors, especially the amount of light obtained previous to sampling, no consistent conclusions can be drawn from the study of the data for leaves. It can be stated, however, that the concentration of sugars (in percentage of dry weight) may vary from as little as $2.3 \%$ to as much as $12.4 \%$. Comparable concentrations of sugar in apple leaves in October were found by Murneek ${ }^{24}$ (apple leaves $7.3 \%$, strawberry leaves $7-8.7 \%$ ). Similarly in the spring (March to June) strawberry leaves contained 4 to $7.8 \%$ sugar, and apple leaves, 4 to $6 \%$, indicating a close similarity between strawberry leaves and those of a woody plant. ${ }^{25}$ At the time of maximal leaf area (October 27 to November 10) 50 to $70 \%$ of the total sugars were present in the leaves, suggesting an intensive photosynthetic


Fig. 11.-Total sugars in grams per 100 plants, 1934-35.


Fig. 12.-Total sugars in grams per 100 plants, 1935-36.


Fig. 13.-Total sugars in percentage of dry weight, 1934-36.


Fig. 14.-Total sugars in percentage of dry weight, 1935-36
activity at that time. During leaf senescence (November to December) there may be a sharp decrease in sugars.

In the autumn (September to November) a rapid flow of soluble carbohydrates to the roots and stems took place, resulting in an increase there, not only of sugars, but also starch and hemicelluloses. Of the total sugars contained in the strawberry plant, 40 per cent was found in the roots in December and approximately 70 per cent in February. Similar high concentrations of sugars have been noted also in apple roots. ${ }^{26}$ In view of the fact that starch and hemicellulose were present in the lowest amounts at this time, it is possible that these insoluble carbohydrates were hydrolyzed into soluble sugars ${ }^{22,23}$ as a result of the low winter temperatures. In the year 1935, a high concentration of sugars in the roots was obtained in April with a rapid depletion thereafter. A similar reduction was found in 1936, but it was not preceded by an increase, as exhibited in the preceding year. This may be due to the fact that samples were not analyzed often enough in 1936 to "catch" the high concentration. ${ }^{25}$

The floral organs of the strawberry are high in sugar content (from $3.35 \%$ in buds to $6.7 \%$ in fruits). Similar concentrations of sugar have been reported by Howlett ${ }^{12}$ and Murneek ${ }^{25}$ for the apple flower. A very large per cent of the total sugars of flowers and fruits is of the reducing type. There appears to be a heavy demand for soluble carbohydrates, not only for the development and growth of new leaves, but also for formation and ripening of fruits. ${ }^{25}$ The reserve sugars in roots and stems seem to be used up for this purpose, resulting in a decrease of 75 per cent in these organs. At similar periods Hooker ${ }^{11}$ found minimal quantities and Murneek ${ }^{25}$ a decrease in sugars in apple spurs.

The above evidence would seem to permit the following summary: There is a rapid flow of soluble carbohydrates to the roots and stems of the strawberry plant during the autumn. This reserve reaches a concentration of $60-80 \%$ of the total sugars present during periods of low temperatures in the winter. A large proportion of the sugars undoubtedly comes from the hydrolysis of starch and hemicelluloses as these carbohydrates reach low amounts during the winter. During the spring, the stored sugars are almost completely depleted due to the great demand by the young leaves, floral organs and growing fruits. A further need for runner production in July and August exhausts still further these reserves.

Starch.-Although the presence of starch at certain seasons in the strawberry has been noted before, ${ }^{19}$ only recently this storage carbohy-
drate has been measured quantitatively in this plant throughout all seasons (Long ${ }^{17}$ ).

The records of starch analyses are found in Tables 17-20 and Figures 15 to 18 . As in the case of sugars, there was a considerable fluctuation of starch in the leaves, varying from less than $1 \%$ to $6 \%$, due no doubt to variations in light exposure previous to sampling. Thirty per cent or more of the total starch may be found in the leaves in October or November. Yellowing leaves may contain $3 \%$ or more starch in December. While dead leaves occasionally have as much as $7 \%$ starch, the amount present is usually much less, especially in midwinter. Starch has been found in the dead leaves of other plants, ${ }^{32,}{ }^{34}$

Table 17.-Total Starch in Grams per 100 Plants, 1934-35

|  | Total | Leaves | Roots | Stems |  | Total | Leaves | Roots | Stems |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Aug. 22.-- | 15.67 | 10.4 | 3.26 | 2.01 | Feb. ${ }^{2}$--- | 59.46 | 21.34 | 28.88 | 9.24 |
| Sept. 6-.- | 11.7 | 4.78 | 4.44 | 2.48 | Feb. 21-.-- | 62.69 | 17.13 | 39.48 | 6.08 |
| Sept. 18-..- | 32.49 | 20.97 | 7.61 11.32 | 3.91 | Mar. 12--- | 46.39 | 9.16 | 30.19 | 7.04 |
| Sept. 25--- | 25.18 49.05 | ${ }_{26.3}^{10.11}$ | 11.32 17.22 | 3.75 5.50 | Mar. 30...- | 37.66 31.46 | 7.54 4.72 | 23.05 18.2 | 7.07 8.54 |
| Oct. 16. | 43.18 | 32.84 | 6.52 | 3.81 | Apr. 28 | 21.59 | 5.71 | 12.01 | 3.87 |
| Nov. 6--- | 90.12 | 31.13 | 42.83 | 16.26 | May 11--- | 13.93 | 4.07 | 4.02 | 5.84 |
| Nov. 25--- | 116.47 | 25.66 |  | 17.07 | June 4--- | 22.49 | 12.42 | 5.27 | 4.80 |
| Dec. 12--- | 91.51 89.03 | 27.33 23.14 | 51.96 55.66 | 12.20 | June 23--- | 39.01 | 26.38 | 5.13 | 7.5 |
| Jan. 6---- | 67.13 | 43.18 | 21.27 | 2.68 | Aug | 29.7 | 17.2 | 3.75 | 8.65 |

Table 18.-Total Starch in Grams per 100 Plants, 1935-36

|  | Total | Leaves | Roots | Stems |  | Total | Leaves | Roots | Stem |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Sept. 15-.- | 6.04 | 4.50 | 1.06 | 0.48 | Jan. 4 | 10.10 | 2.54, | 5.54 | 2.02 |
| Sept. 28.-- | 15.92 | 2.52 | 12.4 | 1.04 | Feb. 24 --- | 26.36 | 2.48 | 18.45 | 5.48 |
| Oct. 12 | 50.40 | 27.01 | 16.88 | 6.52 | Mar. 28.-- | 18.84 | 4.98 | 10.82 | 3.84 |
| Oct. 26. | 29.00 | 10.07 | 14.84 | 4.20 | Apr. 28--- | 16.04 | 6.12 | 4.34 | 5.58 |
| Nov. 10. | 71.74 | 18.66 | 38.62 | 14.46 | May 8 | 14.12 | 7.50 | 4.52 | 2.10 |
| Nov. 30. | 51.88 | 6.76 | 39.90 | 5.22 | May 28.-. | 14.55 | 9.27 | 2.71 | 2.57 |
| Dec. 15..- | 60.88 | 14.90 | 37.46 | 8.52 | July 9...- | 51.70 | 33.75 | 4.69 | 13.26 |

Table 19.-Starch in Percentage of Dry Weight, 1934-35

|  | Leaves | Roots | Stems |  | Leaves | Roots | Stems |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Aug. 22. | 5.0 | 4.70 | 7.33 | Feb. 2 | 3.8 | 6.7 | 4.25 |
| Sept. 6 | 1.98 | 4.73 | 7.30 | Feb. 21 | 4.6 | 9.15 | 3.57 |
| Sept. 18 | 4.90 | 5.25 | 8.70 | Mar. 12. | 2.7 | 8.6 | 3.6 |
| Sept. 25 | 2.13 | 7.08 | 7.35 | Mar. 30 | 2.04 | 6.9 | 4.1 |
| Oct. 2 | 3.93 | 7.00 | 7.80 | April 13 | 1.35 | 5.32 | 4.95 |
| Oct. 16 | 4.35 | 2.95 | 3.65 | April 27 | 1.90 | 4.5 | 2.65 |
| Nov. 6 | 3.53 | 12.95 | 8.70 | May 11. | 0.97 | 1.35 | 3.72 |
| Nov. 28. | 3.53 | 17.90 | 9.13 | June 4 | 2.35 | 2.12 | 2.9 |
| Dec. 12 | 4.05 | 11.73 | 7.18 | June 23 | 4.4 | 3.4 | 4.3 |
| Dec. 23 | 3.33 | 10.98 | 5.88 | Aug. 12 | 3.9 | 3.4 | 5.3 |
| Jan. 6. | 6.45 | 4.5 | 1.7 |  |  |  |  |

Table 20.-Starch in Percentage of Dry Weight, 1935-36

|  | Leaves | Roots | Stems |  | Leaves | Roots | Stems |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Sept. 15 | 2.53 | 1.35 | 1.26 | Jan. | 1.73 | 1.43 | 2.35 |
| Sept. ${ }^{28}$ | 1.14 | 0.84 | 2.75 | Feb. 24 | 1.42 | 4.65 | 7.91 |
| Oct. 12 | 0.89 | 4.22 | 1.05 | Mar. 28 | 2.43 | 3.22 | 4.46 |
| Oct. 28 | 2.65 | 6.92 | 4.82 | Apr. 28 | 2.90 | 2.07 | 6.35 |
| Nov. 10 | 4.47 | 8.64 | 10.76 | May 8 | 2.95 | 2.64 | 2.5 |
| Nov. 30 | 2.65 | 9.22 | 6.05 | May 28. | 2.57 | $1.6{ }^{3}$ | 3.42 |
| Dec. 15...-.-. | 4.17 | 9.45 | 4.75 | Julv 9 | 5.00 | 3.27 | 8.02 |



Fig. 15.-Total starch in grams per 100 plants, 1934-35.


Fig. 16.-Total starch in grams per 100 plants, 1935-36.


Fig. 17.-Total starch in percentage of dry weight, 1934-35.


Fig. 18. - Starch in percentages of dry weight, 1935-36.
which may be due to their inability to remove all of it during senescence because of inactivation of diastase by low temperature or for some other reason. ${ }^{9}$

When the leaves yellow there is a rapid accumulation of starch in the more permanent organs, reaching a maximum of $50-75 \%$ of the plant's total amount in roots in late November, $10-20 \%$ in the stems, with only $20 \%$ in the leaves, compared with $30 \%$ in leaves in October. Soon after the beginning of leaf senescence, there is a sharp decrease in starch in all organs with a minimum in January. Simultaneously, there is a similar increase in total sugars. A reciprocal relationship, therefore, seems to exist between the sugars and starch during the period of low temperatures. A new maximum of starch was noted each year in February, just before the beginning of active spring growth, which is followed by an almost complete depletion later in the spring. ${ }^{19}$

The floral organs of strawberries contain a considerable amount of starch (Table 12) : buds, about $3.4 \%$; flowers $3.0 \%$; pedicels $3.1 \%$ to $3.6 \%$; and fruits $3.0 \%$. These figures are similar to those given by Murneek ${ }^{25}$ for the apple. On account of the small leaf area in the spring much of the starch of roots and stems must be used to supply the demand for carbohydrates by the flowers and fruits. In both years, the roots were depleted at this time of starch. A further demand on the reserve carbohydrates is made during the period of runner formation (July to August).

In conclusion, strawberry plants behave as woody plants usually do in that there is a double starch maximum (November to February) and a double minimum (October to January). The maxima occur when leaf senescence is in progress, and just before spring growth begins; the minima occur in October at the height of leaf area, and during the period of low temperatures (January to February). ${ }^{11}$ A third minimum occurs during fruiting and runner production.

Hemicelluloses.-The concentration and total amounts of these complex acid-hydrolyzable substances are presented in Tables 21-24 and Figures 19-22. The general seasonal trend in their content is the same whether it is expressed in terms of percentage or grams; namely, an increase in the autumn, with a general decrease in winter and spring.

Strawberry leaves contain 14-20\% hemicellulose on the dry weight basis, equalling young apple leaves in this respect. ${ }^{25}$ Considerable hemicellulose still remains in yellowing and dead leaves.

There is a general increase in hemicellulose in the roots and stems in the autumn. While starch may constitute $10-17 \%$ of the roots,

Table 21.-Total Hemicellulose in Grams per 100 Plants, 1934-35

|  | Total | Leaves | Roots | Stems |  | Total | Leaves | Roots | Stems |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Aug. 22--- | 60.58 | 42.28 | 13.06 | 5.24 | Feb. 2 | 98.82 | 50.25 | 34.57 | 14.00 |
| Sept. 6--- | 79.40 117.61 | 55.78 85.51 | 17.10 25.15 | 6.24 6.05 | Feb. 21 | 78.45 68.89 | 31.30 | 33.44 | 13.72 |
| Sept. 25- | 127.33 | 87.30 | 31.52 | 8.85 | Mar. ${ }_{\text {Mar. }} 12$ | 68.89 63.77 | 27.74 | 26.68 | 14.47 |
| Oct. 2--- | 170.62 | 112.33 | 44.65 | 13.64 | Apr. 13 | 60.72 | 24.22 | 26.79 23.6 | 12.76 11.94 |
| Oct. 16..-- | 168.17 | 108.19 | 39.56 | 20.42 | Apr. 28 -- | 48.46 | 15.76 | 21.9 | 11.94 |
| Nov. 6-.- | 254.69 | 168.02 | 53.95 | 32.72 | May 11. | 72.35 | 33.01 | 26.83 | 12.51 |
| Nov. 25 | 261.62 260 | 152.52 | 78.19 | 30.91 | June 4- | 73.67 | 39.64 | 21.62 | 12.41 |
| Dec. 27 | 217.35 | 144.30 | 84.08 43.6 | 39.45 <br> 1 | Aune 16 | 34.47 | 8.9 | 13.87 | 11.7 |
| Jan. 6. | 138.02 | 81.0 | 37.8 | 19.22 | Aug. | 75.12 | 53.9 | 8.80 | 12.42 |

Table 22.-Total Hemicellulose in Grams per 100 Plants, 1935-36

|  | Total | Leaves | Roots | Stems |  | Total | Leaves | Roots | Stems |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Sept. 15--- | 32.77 | 19.62 | 9.40 | 3.75 | Jan. 4 | 64.70 | 28.22 |  |  |
| Sept. 28--- | 62.42 | 46.62 | 10.08 | 5.72 | Feb. $24 .-$ | 64.10 | 24.04 | 23.76 25.12 | 12.72 2.94 |
| Oct. ${ }_{\text {Oct. }}$ 26-.-- | 90.36 111.68 | 51.92 56.24 | 30.2 46.36 | 8.24 9.08 | Mar. 28--- | 82.28 | 26.82 | 51.42 | 2.94 4.04 |
| Nov. $10 .-$ | 149.86 | 66.84 | 46.36 66.02 | 17.04 | ${ }^{\text {Apr. }}$ May 8. | 72.82 73 | 33.80 | 30.48 | 8.54 |
| Nov. 30--- | 130.66 | 58.50 | 60.16 | 12.00 | May 28--- | 73.98 | 37.50 | 22.08 | 14.40 |
| Dec. 15..- | 102.64 | 52.00 | 23.92 | 26.72 | July 9---- | 161.6 | 113.7 | 22.4 | 11.5 |

Table 23.-Hemicellulose in Percentage of Dry Weight, 1934-35

|  | Leaves | Roots | Stems |  | Leaves | Roots | Stems |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Aug. 22. | 20.33 | 18.80 | 19.08 | Feb. ${ }^{2}$ | 8.95 |  |  |
| Sept. ${ }^{6}$ | 19.78 19.98 | 18.20 | 19.18 | Feb. 21 | 8.95 8.4 | 7.75 | 6.9 8.05 |
| Sept. ${ }^{\text {Sep }}$ 25- | 19.98 18.38 | 17.35 19.70 | 15.45 16.70 | Mar. 12 | 8.17 | 7.6 | 7.4 |
| Oct. 2. | 18.63 | 18.15 | 19.35 | Apr. ${ }^{\text {Mar. }}$ | 7.7 6.92 | 8.02 | 7.4 |
| Oct. 16 | 14.33 | 17.90 | 19.45 | Apr. 27 | 6.92 5.15 | 6.9 | 6.65 |
| Nov. 6 - | 19.05 | 16.35 | 17.50 | May 11 | 7.87 | ${ }_{9}{ }^{8 .}{ }^{2} 2$ | 7.40 |
| Nov. 25 | 20.98 | 18.98 | 16.53 | June 4 | 7.5 | 8.7 | 7.97 |
| Dec. ${ }^{12}$ | 21.53 21.70 | 18.98 8.60 | 16.63 | June 23 | 1.5 | 7.4 | 6.5 |
| Jan. 6. | 12.1 | 8.0 | 12.2 | Aug. 12 | 12.92 | 8.0 | 7.6 |

Table 24.- Hemicellulose in Percentage of Dry Weight, 1935-36

|  | Leaves | Roots | Stems |  | Leaves | Roots | Stems |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Sept. 15- | 10.91 | 11.41 | 8.96 | Jan. |  |  |  |
| Sepr. 28. | 20.42 15.41 | 6.54 | 15.37 | Feb. 24 | 20.02 13.16 | 6.05 14.15 | 14.80 13.96 |
| Oct. 26 | 14.95 | 15.45 | 13.38 10.42 | Mar. 28 | 15.67 | 15.25 | 13.64 |
| Nov. 10 | 16.04 | 14.76 | 12.63 | Apr. ${ }^{\text {May }} 8$ | 15.95 15.0 | 14.5 | 9.7 |
| Nov. 30 | 14.43 | 13.93 | 13.91 | May 28 | 15.20 | 12.85 | 17.15 |
| Dec. 15 | 17.12 | 12.64 | 12.45 | July 9 | 16.85 | 15.90 15.60 | 15.27 15.42 |

hemicellulose is slightly higher. It is of interest that in December these complex substances decreased by about 50 per cent. As the sugars increased in concentration at this time, a reciprocal relationship seems to exist between hemicellulose and sugar as well as between starch and sugar as was pointed previously. ${ }^{23}$ A new low concentration of hemicellulose in both roots and stems is exhibited in April.

Of the floral organs of strawberries, buds contained $7.42 \%$ hemicellulose, pedicels $8-12 \%$, flowers $7-13 \%$, and fruits $5-14 \%$. The concentration of hemicellulose does not increase materially during runner production.


Fig. 19.-Total hemicellulose in grams per 100 plants, 1934-35.


Fig. 20.-C'otal hemicellulose in grams per 100 plants, 1935-36.


Fig. 21.--Hemicellulose in percentage of dry weight, 1934-35.


Fig. 22.-Hemicellulose in percentage of dry weight, 1935-36.

It is evident from these records that, in addition to starch, strawberry plants contain other complex insoluble carbohydrates that serve as reserve substances in roots and stems, especially the former. They are built up rapidly during the autumn, are hydrolyzed into sugars during cold weather, and are nearly depleted during flowering.

General Distribution of Carbohydrates and Nitrogen in the Strawberry Plant-A Summary

For reasons of better visualization of the main seasonal changes in dry weight and nitrogen and carbohydrate distribution, all the preceding data are presented herewith in a summarized form (Tables 25 and 26 and Figures 23 and 24). Only certain critical developmental stages, such as the time of greatest leaf development, leaf senescence, dormancy, early spring growth and fruiting have been taken into account, as these are sufficient to illustrate the general trends.

At the height of autumnal growth (November 10), also the time of maximal leaf area and greatest dry weight, $3 \%$ of the plant is sugar, $7 \%$ starch, $15 \%$ hemicellulose, $28 \%$ total carbohydrates, and $1 \%$ nitrogen. Closer examination shows that one-half of the sugar is in the leaves, one-half the starch is in the roots, and over $50 \%$ of the nitrogen is in the leaves. Three weeks later, after several freezes had occurred, and during leaf senescence, $50 \%$ of the sugars are in the roots, nearly $80 \%$ of the starch is also there compared with $50 \% 3$

Table 25.-Quantitative Distribution of Carbohydrates and Nitrogen in the Strawberry Plant-in Grams per 100 Plants; 1934-35

| Date | Material | Fresh weight, grams | Dry weight, grams | Sugars, grams | Starch, grams | $\begin{gathered} \text { Hemi- } \\ \text { cellu- } \\ \text { lose } \end{gathered}$ | Total carbohydrates | Total nitrogen |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Nov. 6 $\qquad$ Autumnal maximum growth of leaves. | Leaves | 2669.0 | 882.0 | 67.03 | 31.13 | 168.02 | 266.16 | 17.28 |
|  | Roots.. | 1287.0 | 330.0 | 16.50 | 42.83 | 53.95 | 113.28 | 4.75 |
|  | Stems.---- | 541.0 | 187.5 | 10.00 | 16.26 | 32.72 | 58.98 | 25.97 |
|  | Total.---- | 4497.0 | 1399.5 | 93.53 | 90.22 | 254.69 | 439.42 | 25.00 |
| Nov. 25 $\qquad$ Leaf senescence. | Leaves | 2182.5 | 727.5 | 51.98 | 25.66 | 152.52 | 230.16 | 13.30 |
|  | Roots | 1361.0 | 412.5 | 12.40 | 73.74 | 78.19 | 164.33 | 6.55 |
|  | Stems | 487.5 | 187.5 | 10.84 | 17.07 | 30.91 | 58.82 | 3.61 |
|  | Total. | 4031.0 | 1327.5 | 77.22 | 116.47 | 261.61 | 453.31 | 23.46 |
| Feb. 2--.-.-.-.-.-.-. Winter minimum of leaf growth. | Leaves | 1403.75 | 561.5 | 19.09 | 21.34 | 50.25 | 90.63 | 8.69 |
|  | Roots | 1336.0 | 431.0 | 62.5 | 28.88 | 34.57 | 125.98 | 8.4 .7 |
|  | Stems. | 530.5 | 217.5 | 19.57 | 9.24 | 14.00 | 42.81 | 5.77 |
|  | Total. | 3270.25 | 1210.0 | 101.16 | 59.46 | 98.82 | 259.37 | 22.86 |
| April 27 $\qquad$ Beginning of growth. | Leaves | 1017.5 | 306.0 | 24.07 | 5.71 | 15.76 | 45.54 | 6.91 |
|  | Roots. | 1216.0 | 267.0 | 65.0 | 12.01 | 21.9 | 98.91 | 4.10 |
|  | Stems. | 530.0 | 146.0 | 7.88 | 3.87 | 10.94 | 22.69 | 4.26 |
|  | Total.----- | 2763.5 | 719.0 | 96.95 | 21.59 | 48.60 | 177.14 | 15.27 |
| June 23 $\qquad$ After fruiting. | Leaves.--- | 2135.0 | 595.0 | 64.25 | 26.38 | 8.97 | 99.53 | 9.25 |
|  | Roots.-.-- | 585.0 | 160.5 | 4.17 | 5.13 | 13.87 | 23.17 | 1.20 |
|  |  | 580. | 174. | 6.78 | 7.50 | 11.7 | 25.98 149 | 11.41 |
|  | Total..--- | 3300.0 | 930.0 | 75.20 | 39.01 | 34.47 | 149.68 | 11.86 |

Table 26.-Quantitative Distribution of Carbohydrates and Nitrogen in 100 Strawberry Plants-Grams; 1935-36

| Date | Material | Fresh weight | $\begin{gathered} \text { Dry } \\ \text { weight } \end{gathered}$ | Sugars | Starch | $\begin{aligned} & \text { Hemi- } \\ & \text { cellu } \\ & \text { lose } \end{aligned}$ | Total Carbohydrates | Total <br> Nitrogen |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Nov. 10.-.--- | Leaves.-.- | 890 | 417 | 29.2 | 18.6 | 66.8 | 114.6 | 9.0 |
|  | Roots----- | 1505 | 449 | 24.7 | 38.6 | 66.0 | 129.3 | -4.5 |
|  | Stems.-.-- | 329 | 135 | - 3.5 | 14.5 | 17.0 | 35.0 | $-2.0$ |
|  | Total-.--- | 2724 | 1001 | 57.5 | 71.7 | 149.8 | 278.9 | 15.5 |
| Nov. 30 | Leaves...- | 1518 | 4116 | $2+.4$ | 6.76 | 58.5 | 89.6 | 8.1 |
|  | Roots.-.-- | 1998 | 432 | 28.5 | 39.9 | 60.1 | 128.4 | 6.9 |
|  | Stems.-.-- | 379 | 109 | 5.0 | 5.2 | 12.0 | 22.2 | 2.5 |
|  | Total...-- |  | 948 | 57.9 | 51.9 | 130.6 | 240.4 | 17.5 |
| Feb. 24 | Leaves.--- | 508 | 175 | 5.8 | 2.5 | 24:0 | 32.3 | 3.0 |
|  | Roots....- | 756 | 395 | 29.2 | 18.4 | 25.1 | 72.7 | 6.3 |
|  | Stems.---- | 380 | 69 | 3.4 | 5.5 | 2.9 | 11.8 | 1.6 |
|  | Total-.-- | 1645 | 640 | 38.5 | 26.4 | 52.1 | 117.0 | 11.0 |
| Apr. 28. | Leaves_--- | 273 | 211 | 10.1 | 6.12 | 33.8 | 50.0 | 4.2 |
|  | Roots.-..- | 580 | 210 | 9.6 | 4.34 | 30.5 | 44.4 | 2.4 |
|  | Stems----- | 287 | 88 | 2.0 | 5.58 | 8.5 | 16.0 | 2.9 |
|  | Total.---- | 2012 | 509 | 21.8 | 16.0 | 72.8 | 110.4 | 9.6 |
| May 8. | Leaves-.-- | 1110 | 250 | 10.5 | 7.5 |  |  |  |
|  | Roots...-- | 827 | 171 | 3.2 | 4.5 | 22.1 | 29.8 | 1.7 |
|  | Stems...-- | 316 | 84 | 5.4 | 2.1 | 14.4 | 21.9 | 1.8 |
|  | Total. .-.- | 2253 | 505 | 19.0 | 14.1 | 73.9 | 107.0 | 7.1 |

weeks previously, and $50 \%$ of the nitrogen as against $30 \% 21$ days earlier. Also over half the hemicellulose is now in the roots.

During dormancy, just as the period of low temperatures ceased, almost $70 \%$ of the sugars and $40-50 \%$ of nitrogen are in the roots, the starch is not quite as low as in Jantary, the hemicellulose continues to decrease.

On April 28, one-half the nitrogen and $30 \%$ of the sugars were in the leaves, while the starch in the roots had decreased from 18.4 grams on February 24 to 4.34 grams on April 28. Little change took place from April 28 to May 8.

In general then, the nitrogen and carbohydrate reserves which accumulate in the autumn, diminish to one-half or less by fruiting time. Much of the carbohydrates is lost in respiration, in dead tissues, and in the formation of floral organs which were not included in the analyses. Nitrogen is stored largely in the roots from which place it is drawn upon for new leaf growth, flower development and runner production. The typical redistribution of these substances emphasizes once more the physiological similarity of the strawberry to a perennial plant.


Fig. 23.-Summation curves, 1934-35.


Fig. 24.-Summation curves, 1935-36.

## THE EFFECTS OF APPLICATION OF NITROGEN FERTILIZERS UPON THE NITROGEN AND CARBOHYDRATE CONTENT, AND FLOWER AND FRUIT PRODUCTION

The tabulated data and preceding discussion show that the strawberry plant behaves somewhat as a perennial in that nitrogen and carbohydrate reserves accumulate during the summer and autumn and decrease during the period of leaf growth, fruit and runner production. Flower and fruit formation of the strawberry have been correlated with the leaf area and nitrogen content of plants during the season of flower bud formation. Within limits, the more nitrogen and leaf area a plant has, the more flowers and fruits are produced.

In view of the unsatisfactory results that have been obtained from fertilization of strawberries, it is believed that an increased knowledge of the physiology, especially the distribution and utilization of certain organic food reserves as affected by fertilizers, would be of value.

An organic and an inorganic nitrogen fertilizer, singly and in combination, were used in this investigation. Organic sources of nitrogen such as dried blood, tankage, and cottonseed meal have proved beneficial in strawberry culture, ${ }^{2,16}$ while inorganic nitrogen such as sodium nitrate and ammonium sulphate have been often used. ${ }^{16,30}$ In some experimental work, a combination of an organic source of nitrogen and an inorganic has been found of the greatest value. ${ }^{16}$ In this investigation, dried blood (supplying organic nitrogen), ammonium sulphate (the inorganic source) and both dried blood and ammonium sulphate (as the combination) were used.

## MATERIALS AND METHODS

The following mixture was employed as the medium to which the fertilizers were added, and in which the control or check plants also grew:

Clay soil of low nitrogen content-4 parts River sand-1 part
About one quart each of superphosphate and sulphate of potash were added to each wheelbarrow load of the above mixture to prevent a deficiency of phosphorus and potassium.

The plants were produced asexually in a propagation bed as previously described, transplanted to 5 -inch pots containing the above mixture, and bedded in the open in a very poor clay loam. They were watered as needed. At the approach of very low temperatures the
plants were removed from the pots and placed in the vacated space without disturbing the root system. A mulch of wheat straw, which covered the plants during the winter, was removed at the beginning of spring growth.

The applications of nitrogen were begun on September 1, according to the following plan:

| Series | Treatment |
| :---: | :--- |
| A | Dried Blood |
| B | Dried Blood and Ammonium Sulphate |
| C | Ammonium Sulphate |
| D | Check (no treatment) |

At intervals of 10 days to 2 weeks, to prevent nitrogen burning, a treatment of 0.5 gram of $\left(\mathrm{NH}_{4}\right)_{2} \mathrm{SO}_{4}$ in solution, or one small dipper of dried blood, or a combination of the two, was made until 1.5 to 2.0 grams nitrogen had been given to each plant. No applications were made after October 15.

## RESULTS OF FERTILIZER STUDIES

## Effects of Fertilizers on Dry Weight and Distribution of Nitrogen and Carbohydrates

Little difference could be detected between the dry weights of fertilized plants at any particular time, but wherever sulphate of ammonia was added, the plants grew more rapidly. Although the control plants weighed only about one-third of the fertilized ones, they exhibited the same tendency to increase in dry weight during the fall and to decrease in winter (Table 27 and Figure 25).

Table 27-Total Dry Weight in Grams Per 100 Plants 1935-36.

|  | Dried blood | Dried blood and ammonium sul. phate | Ammonium su!phate | Check <br> clay <br> soi! |  | Dried blood | Dried <br> blood and ammonium sulphate | Ammonium sulphate | Check clay soil |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Sept. 15 | 283.4 | 376.2 | 242.9 | 160.0 | Dec. 15 | 687.9 | 840.50 | 880.1 | 276.3 |
| Sept. 28...- | 337.2 | 426.3 | 397.0 | 268.0 | Jan. 4-.-- | 555.5 | 695.6 | 721.7 | 249.3 |
| Oct. 12 | 507.1 | 620.1 | 476.2 | 302.6 | Feb. 24-- | 562.5 | 627.4 | 582.5 | 142.5 |
| Oct. 26. | 767.4 | 839.5 | 747.9 | 333.6 | Mar. 28. | 592.1 | 670.9 | 721.2 | 297.6 |
| Nov. 10--- | 919.6 | 904.2 | 964.2 | 390.8 | Apr. 28.-. | 729.8 | 576.8 | 919.6 | 267.1 |
| Nov. 30-.-- | 894.3 | 843.0 | 919.5 | 338.2 | May 8... | 677.1 | 756.3 | 834.3 | 269.3 |

All groups of plants had formed the greatest leaf area in November, though the growth of leaves in the series receiving dried blood was somewhat slower (Table 28 and Figure 26). This difference in


Fig. 25.-Total dry weight in grams per 100 plants, 1935-36. (a) Dried blood. (b) Dried blood and $\left(\mathrm{NH}_{4}\right)_{2} \mathrm{SO}_{4}$. (c) $\left(\mathrm{NH}_{4}\right)_{2} \mathrm{SO}_{4}$. (d) Check clay soil.


Fig. 26.-Total leaf area per plant.

Table 28.-Fertilizer Treatments and Leaf Area per Plant, SQ. Cm.

| . | Dried blood | $\begin{aligned} & \text { Dried } \\ & \text { blood } \\ & \text { and } \\ & \text { a mmo- } \\ & \text { nium } \\ & \text { sul- } \\ & \text { phate } \end{aligned}$ | Ammonium sulphate | Check <br> clay <br> soil |  | Dried blood | Dried blood and a mmo$\underset{\text { nium }}{\text { sul- }}$ phate | Ammonium sulphate | Check <br> clay <br> soil |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Sept. 16..- | 373.5 | 418.6 | 302.6 | 161.5 | Dec. 15-.- | 463.4 | 468.6 | 578.5 | 168.2 |
| Sept. 28--- | 212.4 | 420.8 | 620.3 | 211.3 | Jan. 4-- | 342.0 | 354.0 | 402.0 | 150.8 |
| Oct. 12-..- | 338.3 | 662.3 |  | 219.3 | Feb. 24-..- | 196.7 | 209.6 | 239.8 | $113: 2$ |
| Oct. 26...- | 617.5 | 675.8 | 715.3 | 243.5 | Mar. 28. | 216.4 | 247.0 | 315.0 | 61.3 |
| Nov. 10... | 759.2 | 769.7 | 763.9 | 292.2 | Aor. 28. | 348.0 | 400.0 | 613.3 | 137.3 |
| Nov. 30... | 661.3 | 669.4 | 657.0 | 188.8 | May 8.- | 416.0 | 453.0 | 628.0 | 138.6 |

Table 29.-Total Nitrogen in Grams per 100 Plants, 1935-36

|  | Dried blood | Dried blood and 2 mmo nium sulphate | Ammonium sulphate | Check <br> clay <br> soil |  | Dried blood | $\begin{aligned} & \text { Dried } \\ & \text { blood } \\ & \text { and } \\ & \text { ammo- } \\ & \text { nium } \\ & \text { sul- } \\ & \text { phate } \end{aligned}$ | Ammo- $\begin{gathered}\text { nium } \\ \text { sul- } \\ \text { phate }\end{gathered}$ | Check <br> clay <br> soil |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Sept. 15--- | 6.72 | 9.77 | 5.34 | 3.19 | Dec. 15 | 14.29 | 17.13 | 18.61 | 3.13 |
| Sept. 28--- | 8.32 | 12.32 | 9.92 | 7.28 | Jan. 4 | 11.86 | 15.99 | 17.12 | 3.91 |
| Oct. 12---- | 11.89 | 16.41 | 13.21 | 4.91 | Feb. 24 | 11.98 | 15.30 | 15.07 | 4.03 |
| Oct. 26---- | 14.24 | 19.17 | 17.48 | 4.56 | Mar. 28. | 13.35 | 15.42 | 18.49 | 4.93 |
| Nov. 10--- | 17.84 | 18.91 | 21.10 | 5.57 | Aor. 28. | 12.20 | 10.48 | 14.02 | 3.30 |
| Nov. 30..- | 16.25 | 18.67 | 20.64 | 4.78 | May 8. | 8.87 | 11.21 | 11.58 | 3.02 |

rate of growth no doubt indicates a difference in availability of nitrogen, as the plants absorbed and utilized it more quickly from sulphate of ammonia than from dried blood. There was a greater leaf development in proportion to root growth in all fertilized plants. The fact that the leaf area increased so rapidly from March 28 to May 8 in all fertilized plants points to the value of nitrogen in development of the foliage.

The addition of nitrogen fertilizers did not affect greatly the basic seasonal cycle of variation in nitrogen concentration of the strawberry plant. Changes in nitrogen content of the check plants exhibited the following major differences: The total quantity of nitrogen present reached a maximum at the end of September or 6 weeks earlier than in the fertilized plants (Table 29 and Figure 27). This increase is most noticeable in the leaves but less so in the roots. On percentage basis there do not appear to be any great seasonal differences, excepting that in the check plants nitrogen was always lower than in those fertilized.

There is some evidence that leaves with a high nitrogen content may not release as much of this element during leaf senescence as do plants that have a lower initial nitrogen concentration. ${ }^{30}$ For example, check plants with leaves containing $2.02 \%$ nitrogen on November 10 retained only $1.76 \%$ on November 30, while those of the sulphate of


Fig. 27.-Total nitrogen in grams per 100 plants, 1935-36.
ammonia series with $2.5 \% \mathrm{~N}$ on this date retained $2.4 \%$ and others with $2.48 \% \mathrm{~N}$ (series receiving both dried blood and sulphate of ammonia) had the same nitrogen content ( $2.48 \%$ ) on November 30 (Table 30).

Fertilized plants had floral organs and fruit with a higher concentration of nitrogen than non-fertilized ones, and those receiving sulphate of ammonia produced flowers and fruits with a higher nitrogen content than plants receiving only dried blood (Table 32).

Irrespective of the fertilizers used all series of plants exhibit the usual seasonal trend in concentration and distribution of soluble carbohydrates: An autumnal increase followed by a decrease during the dormant season (December to February), the period of spring growth (March and April) and at flowering and fruiting (May and June). The control plants contained approximately 50 per cent as much of the total sugars as the fertilized plants (Table 31).

It would seem that when plants have less nitrogen (controls), starch will accumulate earlier in the season than when ample nitrogen is provided. ${ }^{2}$ Fertilized plants seem to utilize their carbohydrate reserves more rapidly and more completely than non-fertilized ones. The floral organs and fruits of plants supplied with nitrogen were slightly higher in starch than those of plants not receiving nitrogen.

Table 30.-Nitrogen in Percentages of Dry Weight, 1935-36


Table 31.-Quantitative Distribution of Carbohydrates and Nitrogen in 100 Strawberry Plants-Grams

| Treatment |  | Dried Blood |  |  | Dried Blood and Ammonium Sulphate |  |  | Ammonium Sulphate |  |  | Check (Clay Soil) |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Date | Tissue | Roots | Stems | Leaves | Roots | Stems | Leaves | Roots | Stems | Leaves | Roots | Stems | Leaves |
| Nov. 10_..- | Dry Weight...- | -402 | 94 | 422 | 346 | 106 | 451 | 374 | 107.0 | 481 | 179 | 53 | 157 |
|  | Sugars....-.-.- | 23.5 | 2.4 | 29.3 | 18.1 | 3.2 | 24.8 | 19.5 | 2.5 | 14.0 | 11.3 | 1.6 | 8.6 |
|  | Starch --..--- | 37.0 | 6.8 | 19.6 | 30.9 | 7.4 | 19.9 | 31.5 | 7.4 | 9.6 | 13.6 | 5.4 | 3.1 |
|  | Hemicellulose-- | 65.3 | 4.2 | 71.8 | 51.6 | 15.3 | 57.8 | 48.3 | 14.4 | 74.1 | 26.0 | 7.2 | 13.7 |
|  | Nitrogen.-.--- |  | 1.9 |  | 5.8 | 2.0 | 11.1 | 7.0 | 2.0 | 12.0 | 1.6 | 0.75 | 3.2 |
| Nov. 30...- | Dry Weight..... | 433 | 106 | 354 | 346 | 122 | 374 | 393 | 106 | 419 | 166 | 43 | 128 |
|  | Sugars | 40.7 | 5.5 3 | 37.6 | 28.6 | 7.6 | 26.9 | 35.0 | 4.0 | 31.4 | 18.0 | 2.9 | 10.4 |
|  | Starch.-.-.-.- | 35.4 | 3.9 | 4.9 | 15.6 | 6.5 | 9.7 | 31.8 | 3.0 | 6.7 | 10.1 | 2.7 | 3.5 |
|  | Hemicellulose.- | 49.3 6.7 | 11.6 2.3 | 53.6 7.2 | 37.7 6.9 | 17.4 2.4 | 53.9 9.3 | 51.6 | 14.8 | 49.9 | 25.3 | 6.3 | 19.5 |
| Jan. 4-.---- | Dry Weight.... | 240 | 80 | 234 | 268 | 100 | 326 | 286 | 103 | 331 |  |  |  |
|  | Sugars_--...-. | 43.0 | 8.4 | 14.8 | 71.7 | 2.0 | 19.5 | 47.2 | 12.9 | 24.6 | 21.0 | 16.7 | 92.0 |
|  | Starch.-.-...- | 13.2 | 2.8 | 5.6 | 23.0 | 2.3 | 9.0 | 15.5 | 1.6 | 8.7 | 5.4 | 0.2 | 1.8 |
|  | Hemicellulose-- | 34.9 | 12.5 | 39.2 | 61.8 | 15.5 | 47.5 | 43.9 | 14.9 | 59.4 | 16.4 | 3.6 | 10.2 |
|  | Nitrogen.-...-- | 4.7 | 2.7 | 4.5 | 6.3 | 2.6 | 7.0 | 7.0 | 2.9 | 7.2 | 1.7 | 0.7 | 1.5 |
| Mar. 28.... | Dry Weight....- | 318 | 81.5 | 192 | 332 | 77 | 261 | 336 | 92 | 292 | 168 | 43.2 | 86.6 |
|  | Sugars.-.-..... | 32.1 | 1.8 | 7.9 | 34.2 | 3.1 | 19.4 | 35.3 | 1.7 | 10.9 | 10.2 | 1.9 | 3.7 |
|  | Starch---.--- | 11.8 | 2.2 | 4.4 | 11.5 | 2.9 | 9.1 | 9.7 | 6.3 | 13.4 | 4.8 | 1.9 | 2.0 |
|  | Hemicellulose_- Nitrogen..--. | 46.0 5.9 | 14.2 2.2 | 32.4 | 45.0 7.0 | 13.7 2.0 | 41.4 6.4 | 46.6 8.5 | 16.3 2.3 | 51.7 7.7 | 25.5 2.0 | 7.5 0.95 | 9.5 1.98 |
| May 8....... | Dry Weight.... | 214 | 111 | 353 | 260 | 128 | 367 | 253 | 144 | 436 |  | 53 |  |
|  | Sugars.-....... | 4.6 | 4.3 | 9.8 | 5.2 | 3.7 | 7.3 | 10.2 | 7.9 | 40.2 | 2.0 | 1.6 | 2.3 |
|  | Starch.-........- | 4.2 | 4.9 | 10.2 | 2.8 | 5.0 | 7.7 | 4.3 | 5.8 | 9.1 | 2.0 | 3.2 | 6.0 |
|  | Hemicellulose-- | 31.1 | 18.1 | 54.5 |  | 18.7 | 60.6 | 44.0 | 15.8 | 60.0 | 11.6 | 7.6 | 15.8 |
|  | Nitrogen...-.- | 2.1 | 1.0 | 5.7 | 2.9 | 1.2 | 7.0 | 2.7 | 1.5 | 7.3 | 0.75 | 0.44 | 1.8 |

Plants with low nitrogen content had a wider nitrogen starch ratio (1:4), while those high in nitrogen, a narrow one (1:2).

There is no indication that the nitrogen fertilizers used affected the percentage of hemicellulose, although the total amount in the fertilized plants was considerably larger due to the added dry weight.

## A Comparison of Plants Fall Fertilized, and Fall Plus Spring Fertilized

Data showing the chemical composition of plants fall fertilized and fall plus spring fertilized are recorded in Tables 32, 33, and 34.

A comparison of the dry weights of roots, stems, and leaves indicates that the most significant result was an increment in dry weight of leaves in nearly every case where a spring application of nitrogen was made. Plants supplied with dried blood only show a decreased nitrogen content, due no doubt in part to a lack of availability of the nitrogen in dried blood, but possibly also as a result of non-uniformity in samples used for analysis. Fertilized plants produced a $30-100 \%$ increase in leaf growth over non-fertilized ones.

Although the dry weight of the roots and stems was not changed much, the percentage of nitrogen increased from 0.99 to 2.32 in roots of dried blood treated plants and from 1.51 to 2.91 per cent in leaves of controls. In other words, the plants that were spring fertilized in addition to the fall fertilization contained twice as much nitrogen as the fall only fertilized plants.

The total quantity of sugars in the leaves varied both in concentration and in total amount. In general, the leaves of spring fertilized plants had a higher concentration of sugars on the percentage basis. In addition the total dry weight of the spring fertilized plants is greater. Therefore, the total amount of sugars present was two or more times as great as in the fall only fertilized plants. Starch was much less evident in plants with an abundant supply of nitrogen. There were little differences in hemicellulose content of plants of the various groups.

Floral organs and fruits of plants fall and spring fertilized had a higher nitrogen content than those of plants fall fertilized only. Little difference, however, was noted in their respective dry weights. There was about twice as much nitrogen in the flowers and pedicels of plants with the additional spring application of fertilizer, but no great difference in nitrogen content of the whole fruit.

In most cases, plants receiving an additional nitrogen application in the spring did not contain as much sugar as those receiving nitrogen only in the fall. Little difference was noted in the dry weights of fruits of the various series except a large increase in the controls that received an application of nitrogen in the spring.

Table 32.-Nitrogen and Carbohydrate Content of Flowers-Fruits of Plants Fall Fertilized, and Fall and Spring Fertilized

| Treatment | Tiss | Nitrogen |  | Reducing Sugars |  | Total Sugars |  | Starch |  | Hemicellulose |  | $\begin{gathered} \text { Dry } \\ \text { weight, } \\ \text { grams } \end{gathered}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | $\underline{\text { Per cent }}$ | Total | Per cent | Total | Per cent | Total | Per cent | Total | Per cent | Total |  |
| Dried Blood. | Flowers | 1.75 | 0.51 | 1.36 | 0.39 | 3.12 | 0.91 | ${ }^{4.72}$ | 1.29 | 12.72 | 3.68 | 29.0 |
|  |  | 1.90 <br> 1.29 <br> 1.0 | 1.25 0.85 | 2.90 <br> 1.45 | 1.91 0.96 | 5.55 <br> 2.45 | 3.66 1.62 | 2.17 2.37 | 1.43 1.56 | 18.20 15.40 | 12.08 10.16 | 66.0 66.0 |
|  | Flowers.-..- | 1.09 | 0.24 | 1.37 | 0.30 | 3.14 | 0.68 |  |  |  |  |  |
|  | Fruits_..... | ${ }_{2}^{2.36}$ | 1.64 | ${ }_{2}^{1.55}$ | 1.07 | 3.10 | 2.15 | 4.85 | 3.36 | ${ }_{15} 12.42$ | ${ }_{10.68}^{2.65}$ | 21.8 69.3 |
| Dried Blood andAmmonium Sulphate. |  |  |  |  |  |  |  | 2.5 | 1.56 | 12.15 | 7.43 | 61.4 |
|  | Flowers ${ }_{\text {Fruits }}$ |  | 0.72 | 1.53 | 0.39 | 3.46 | 0.89 | 6.72 | 1.73 | 11.64 |  |  |
|  | Fruits-....- | 2.25 2.57 | 2.36 <br> 1.83 | 1.92 2.17 | 2.02 <br> 1.55 | 2.80 4.20 | 2.94 2.30 | 3.20 3.20 3.37 | 3.36 <br> 3.06 | $\begin{array}{r}13.80 \\ 14.87 \\ \hline\end{array}$ | $\begin{array}{r}14.99 \\ 10.59 \\ \hline 10.55\end{array}$ | 105.0 11.3 |
|  | Flowers | 2.51 | 0.71 | 1.60 | 0.45 | 3.90 | 1.11 |  |  |  |  |  |
|  | ${ }_{\text {Pruits }}{ }_{\text {Pedicels }}$ | 2.73 <br> 1.96 | 2.56 1 | 1.65 1.70 | 1.17 | 3.90 <br> 3.10 | 3.00 | 10.65 4.70 | 3. 40 | 10.50 12.15 | 2.98 12.34 | 28.4 93.7 |
| AmmoniumSulphate. |  |  |  |  |  |  | 1.49 |  |  | 17.35 |  |  |
|  | Flowers <br> Fruits. | 1.90 2.13 | 0.73 | 1.40 2.00 | 0.53 1.80 1 | 1.70 | 0.64 | 5.70 | 2.14 | 13.97 | 5.26 | 37.6 |
|  | Pedicels....-- | 1.40 | 1.23 | 2.17 | 1.91 | 3.40 | 4.61 2.99 | 4.20 1.70 | 3.76 <br> 1.50 | 14.07 11.48 | 12.53 10.10 | 89.8 88.0 |
|  | Flowers | 2.32 <br> 2.65 | 0.73 | 1.37 | 0.43 | 2.20 | 0.69 | 4.00 | 1.25 | 13.90 |  |  |
|  | ${ }^{\text {Fruits-1...- }}$ | ${ }^{2.65}$ | 1.92 <br> 2.04 | 1.95 <br> 2.35 | 1.41 <br> 1.90 | 2.00 2.76 | 0.73 <br> 2.43 | 0.75 2.35 | 0.54 1.90 | 14.20 | $\begin{array}{r}10.28 \\ \\ \hline\end{array}$ | ${ }_{82} 7.4$ |
| Check Clay Soil. |  |  |  |  |  |  |  |  |  |  |  |  |
|  | Fruits------- | 1.72 | 0.50 | ${ }_{2}^{1.26}$ | 0.083 0.68 | 1.42 2.50 | 0.94 0.73 | 3.24 <br> 4.75 | 2.14 1.38 | 11.43 12.67 | 7.54 3.67 | ${ }^{6.6}$ |
|  | Pedicels | 1.15 | 0.21 | 2.17 | 0.40 | 2.67 | 0.49 | ${ }_{2}$ | 1.38 0.38 | 12.67 14.65 | 3.67 <br> 2.70 | 29.0 18.5 |
|  | Flowers-.--- |  | 0.28 |  |  |  |  |  |  |  |  |  |
|  | $\xrightarrow{\text { Fruits--...-- }}$ | 3.00 2.46 | 1.96 | ${ }_{2}^{1.57}$ | ${ }^{1.10}$ | ${ }_{2}^{2.42}$ | 1.69 | 3.67 | 2.17 | 11.72 11.72 | 88.21 | 12.5 70.0 |
|  |  |  |  |  |  |  | 0.77 | 3.30 | 0.87 | 16.37 | 4.33 | 26.4 |

Table 33.-Nitrogen and Carbohydrate Content at Fruiting of Plants Fall Fertilized, and Fall and Spring Fertilized

*A-Applications of fertilizer in fall only.
$\dagger$ B-Applications of fertilizer in fall and spring.

Table 34.-Nitrogen and Carbohydrate Content of Flowers-Fruits: Fertilizer Treatments


The above records would seem to indicate that proper nutritive conditions in the autumn are of far greater importance than in the spring. It appears that if strawberry plants make a fairly good growth in the autumn (have a leaf area of $300-500 \mathrm{sq} . \mathrm{cm}$. per plant, containing $2-2.5 \%$ nitrogen, or about 0.11 to 0.16 grams per plant), then any additional amount of nitrogen added in the spring will increase the leaf area and nitrogen content of the roots and stems, but will not enlarge their dry weights and will not increase fruit production. Only in one instance was there a substantial increase in amount of fruits formed as a result of nitrogen application in the spring; namely, the controls. Table 36 shows that these plants had a leaf area of only $219 \mathrm{sq} . \mathrm{cm}$. per plant with a total nitrogen content of .049 grams which was less than one-half in the plants that produced the maximum number of flowers. When fertilizers were applied in the spring to these "controls" the number of clusters was doubled, and flower and fruit production was increased by 20 per cent. This would seem to indicate that the control plants did not contain enough organic substances, including those containing nitrogen, to "develop" the flowers differentiated in the fall.

The spring application of fertilizers to strawberry plants that have made "good" growth, measured in terms of leaf area and nitrogen content, does not seem to be desirable. It results only in a greater leaf area, and more nitrogen concentration in tissues throughout the plant. Under some conditions, however, an increased leaf area may increase the size of fruits. If plants do not have favorable nutritive conditions in the autumn, as measured in terms of leaf growth and nitrogen content, then an early spring application of fertilizers would be desirable.

It seems to be better to get the nitrogen into the strawberry plant in the autumn to serve as a reserve for spring growth than to depend on a quickly acting fertilizer. Strawberries in a poor nutritive condition respond more favorably to spring fertilizers. A satisfactory nutrition of the plant is especially desirable during the period of fruit bud formation.

## Relation of Leaf Area and Nitrogen Content to Flower and Fruit Production

In Tables 35 and 36 are recorded the leaf areas in square centimeters per plant at specified dates, the total nitrogen content and the number of flowers and fruits formed.

A fact of some importance concerning leaf area and the fertilizer treatments used is that leaf growth of plants receiving sulphate of ammonia was more rapid and more abundant than on plants not receiving this substance. The control plants show a very limited amount of leaf development. It will be noted that the nitrogen content of

Table 35.-Relation of Leaf Area, and Flowers and Fruits

| Treatment | Leaf area per plant (sq. cm.) |  |  |  |  | Number of |  |  | $\begin{gathered} \text { per } \\ \text { cent } \\ \text { set } \end{gathered}$ | Wt. fruits grams per plant |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | $\begin{aligned} & \text { Sept. } \\ & 28 \end{aligned}$ | $\begin{gathered} \text { Oct. } \\ 16 \end{gathered}$ | $\begin{gathered} \text { Oct. } \\ 26 \end{gathered}$ | ${ }_{28}$ | $\underset{8}{\text { May }}$ | Clusters per plant | Fl'rs | Fruits |  |  |
| Dried Blood: <br> Fall only <br> Fall and Spring | 212 | 338 | 617 | $\begin{array}{r}348 \\ 386 \\ \hline\end{array}$ | 416 <br> 457 | 4.4 5.0 | $23 . \frac{2}{7}$ | 16.2 | $\begin{aligned} & 69.8 \\ & 41.9 \end{aligned}$ | $\begin{aligned} & 35.4 \\ & 34.4 \end{aligned}$ |
| Dried Blood and Ammonium Sulphate: Fall only <br> Fall and Spring | 420 | 662 | 675 | $\begin{array}{r}400 \\ 460 \\ \hline\end{array}$ | $\begin{array}{r}453 \\ 523 \\ \hline\end{array}$ | 4.6 <br> 5.5 | 23.2 <br> 18.1 | $\begin{aligned} & 16.7 \\ & 12.5 \end{aligned}$ | $\begin{array}{r} 72.0 \\ 69.5 \end{array}$ | $\begin{aligned} & 49.4 \\ & 56.1 \end{aligned}$ |
| Ammonium Sulphate: Fall only Fall and Spring | 620 | 678 | 715 | 613 <br> 688 | 628 <br> 742 | 5.8 4.0 | 24.8 17.6 | 17.1 14.1 | 69.1 80.4 | 42.6 36.3 |
| Check, Clay Soil: <br> No Treatment <br> Spring Fertilized | 211 | 219 | 243 | 137 <br> 144 | 139 164 | 1.4 3.4 | $\begin{array}{r}9.7 \\ 11.1 \\ \hline\end{array}$ | 6.7 8.9 | 68.9 80.6 | 14.0 <br> 35.4 |
| Rich Loam <br> No Treatment <br> $\left(\mathrm{NH}_{4}\right)_{2} \mathrm{SO}_{4}$ in Spring-.- | 1136 | 1195 | 1280 | 399 418 | 639 766 | 3.6 3.0 | $\begin{aligned} & 30.1 \\ & 34.4 \end{aligned}$ | $\begin{aligned} & 18.2 \\ & 18.6 \end{aligned}$ | $\begin{aligned} & 54.4 \\ & 54.0 \end{aligned}$ | $\begin{aligned} & 34.0 \\ & 47.6 \end{aligned}$ |

plants given sulphate of ammonia was not only greater, but reached a peak more quickly than in plants receiving other fertilizers. This undoubtedly was due to the fact that the nitrogen from sulphate of ammonia was more quickly available than from an organic source, such as dried blood. The control plants, which contained only .072 gram continued to lose nitrogen through death of the plant parts. Furthermore, the leaf area of these plants remained at a minimum with but a slight increase.

Another fact that may be of interest is that the total leaf area of plants that grew in rich loam was nearly double that of plants that received both organic and inorganic nitrogen. When fertilizers were applied in the spring in addition to fall, the leaf increments were approximately the same in all series.

The period of flower bud differentation extended probably from September 20 to October 15 on average strawberry plants that were growing under fairly normal conditions. Therefore, the total leaf area and the nitrogen content per plant are recorded for this period (September 28 to October 26). A correlation between these two factors may be of interest. On September 28, the leaf area of plants that received dried blood as well as that of control plants was practically the same (211 and $212 \mathrm{sq} . \mathrm{cm}$. per plant), while the leaf area of plants receiving sulphate of ammonia was 3 times larger. Yet the nitrogen content did not differ greatly in plants of these three groups. There was, however, a marked difference in the number of flowers produced, the control plants having only 9.7 while those fertilized carried 23.0 to 24.0 per plant.

Table 36.-Leaf Area, Total Nitrogen per Plant, and Flowers and Fruits

|  | Leaf Area per Plant-Sq. Cm. |  |  |  |  | Nitrogen Content per Plant-Grams |  |  |  |  | Number of-per Plant |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Sept. 28 | Oct. 16 | Oct. 26 | Apr. 28 | May 8 | Sept. 28 | Oct. 16 | Oct. 26 | Apr. 28 | May 8 | Clusters | Flowers | Fruits |
| Dried Blood: <br> $\stackrel{\text { Fall Only }}{\text { Fall and Spring-...... }}$ | 212 | 338 | 617 | 348 | 416 | 0.083 | 0.118 ---1 | 0.142 | 0.122 | $\begin{aligned} & 0.088 \\ & 0.14 \end{aligned}$ | 5.4 | $\begin{array}{r}23.2 \\ 17.7 \\ \hline\end{array}$ | 16.2 6.7 |
| Dried Blood and <br> $\left.\mathrm{Fall} \mathrm{NH}_{4}\right)_{2} \mathrm{SO}_{4}:$ <br> Fall and Spring- | 420 | 662 | 675 | 400 460 | $\begin{array}{r}453 \\ 523 \\ \hline\end{array}$ | 0.123 | 1.064 | 0.191 | 0.104 | 0.112 <br> 0.18 | 4.6 5.5 | 23.2 18.1 | 16.7 <br> 12.5 |
| $\left(\mathrm{NH}_{4}\right)_{2} \mathrm{SO}_{4}:$ <br> Fall Only | 620 | 678 | 715 | 613 <br> 688 | 628 <br> 742 | 0.099 | 0.132 | 0.174 | 0.140 | 0.116 <br> 0.20 | 5.8 4.0 | 24.8 <br> 17.6 | 17.1 <br> 14.1 |
| Check Clay Soil: No Treatment.-$\left(\mathrm{NH}_{4} 2_{2} \mathrm{SO}_{4}\right.$ Sprin | 211 ---1 | 219 | 243 ---1 | 134 <br> 144 | 139 <br> 164 | 0.072 $\cdots---1$ | $\begin{array}{r}0.049 \\ -\cdots-- \\ \hline\end{array}$ | 0.045 ---- | $\underline{0.033}$ | 0.030 <br> 0.088 | 1.4 <br> 3.4 | 99.7 11.1 | 6.7 8.9 |
| Rich Loam: No Treatment. $\left(\mathrm{NH}_{4}\right)_{2} \mathrm{SO}_{4} \ldots$ | 1136 | 1195 | 1280 | 399 418 | 639 766 | 0.14 | 0.21 $-\ldots$ | 0.24 | 0.15 | 0.13 <br> 0.20 | 3.6 <br> 3.0 | 30.1 <br> 34.4 | $\begin{array}{r}18.2 \\ 18.6 \\ \hline\end{array}$ |

There was 0.118 gram (or more) nitrogen per plant on October 16 despite the considerable variation in leaf area. It may be assumed that at least 0.12 gram nitrogen per plant is desirable for the production of a maximal number of flowers of the Aroma variety. It is possible also that if that much nitrogen is not present at the time of bud differentiation, then the process of flower formation may not proceed normally until more nitrogen enters the plant. We, of course, have no histological evidence to substantiate this asumption.

Although the application of fertilizers in the spring increases the absolute amount of nitrogen in the plant, it did not affect greatly flower and fruit production. The control plants (which contained less than 0.11 gram nitrogen during the period of flower bud formation) were benefitted, however, by an additional supply of nitrogen in the spring. The number of clusters and flowers was increased as well as the number of fruits per plant.

The evidence would seem to indicate the necessity of providing favorable conditions for growth and nitrogen absorption during the period of flower bud formation. A minimum of 0.11 gram of nitrogen per plant as well as a minimum leaf area of $300-800 \mathrm{sq}$. cm. per plant seems to be essential for maximal reproduction. If this amount ( 0.11 or more) is present in the autumn, then any additional nitrogen in the spring has no marked effect on flower production. These results agree in general with those scured by Gardner ${ }^{8}$, Loree ${ }^{18}$, and others. ${ }^{33}$

## SUMMARY AND CONCLUSIONS

The strawberry plant grows rapidly during the fall if the environment is favorable. Under conditions provided in this investigation, primary adventitious roots grew to a length of $25-30$ centimeters. The leaves also develop rapidly at this time, frequently reaching an area of 1200 square centimeters or more per plant by the end of October. Leaf senescence occurred during November and December.

As was to be expected, the dry weight of strawberry plants increases rapidly in autumn and reaches a maximum at approximately the time of the greatest leaf development. Decrease in dry weight begins in the dormant season and continues through the periods of spring growth of leaves (March-April), flowering and fruiting (April-June) and runner production (July-August). In this respect the strawberry plant behaves as other perennials do in that it increases in dry weight and stores organic food reserves in the summer and autumn and decreases in dry weight or depletes its food reserves during the remainder of the year.

Chemical analyses show that the nitrogen content of strawberry plants varies with the seasons. The leaves contain in autumn 2.0 to 2.4 per cent nitrogen and at their greatest development 70 per cent of this element may be in the foliage. The nitrogen content of leaves decreases rapidly during their senescence with a simultaneous increase in the roots and stems. Roots usually store during the winter $30-40$ per cent of the total amount of nitrogen of the plant.

Young strawberry leaves are high in nitrogen. Consequently a great demand is made during their growth upon the storage reserves in the roots and stems. Stored nitrogen is utilized in considerable quantities also for the development of flowers and fruits and for runner plant production. Therefore the roots and stems are almost completely depleted by midsummer of this essential element. During the later part of summer and throughout the fall nitrogen accumulates again. There is little fluctuation in nitrogen content in any part of the strawberry plant during the dormant season.

There is a rapid flow of soluble carbohydrates during the summer and autumn, but especially at time of leaf senescence, to the stems and roots. Sugars reach a very high concentration in these permanent organs of the plant during the dormant season when the temperatures are lowest. At the same time there is a decrease in starch and hemicellulose, indicating a reciprocal relationship between sugars and the insoluble carbohydrates.

Two seasonal maxima (February and November) and three minima (April, October and January) of starch concentration seem to occur each year in the strawberry plant. Starch and hemicellulose serve as storage forms of carbohydrates and are utilized not only during the winter but drawn upon most rapidly in the spring for growth of leaves and development of flowers and fruits. Consequently the carbohydrate content of the roots and stems decreases rapidly in March and April.

Though fluctuating in amount, the sugar content of leaves is quite high ( $7 \%$ or more). When the foliage has reached its greatest development, $50-75 \%$ of the total sugar content of the plant may be in the leaves.

In general then, as regards carbohydrate and nitrogen metabolism too, the strawberry behaves very much like a perennial plant storing organic foods during the later part of the growing season and depleting them in the spring of the next year in the production of leaves, flowers, fruits and runners.

Organic nitrogen fertilizers (dried blood) and inorganic form of nitrogen (sulphate of ammonia), or a combination of the two, did not alter markedly in these plants the seasonal variation in nitrogen and
carbohydrate content over a year's duration. The unfertilized plants, of course, were lower in dry weight with consequently smaller content of nitrogen and carbohydrates.

Nitrogen fertilizers of all forms used in this experiment increased the number of flowers formed.

The addition of fertilizers in the spring to plants growing in pots produced a larger leaf area and a higher nitrogen concentration in all parts, but did not affect fruit production in any appreciable way. However, if the fall supply of nitrogen was deficient, then a spring application of nitrogen may cause more flowers to develop into fruits.

In order to realize the best results from the use of nitrogen fertilizers, it would seem desirable to know the relative amounts of organic food reserves present in the autumn. A minimum quantity of .12 grams of nitrogen per plant in October would seem to be necessary for the production of a maximum number of flowers of the Aroma variety. Any amount above this quantity does not seem to improve flower formation. When one-half of this quantity of nitrogen is present, only about onethird of the number of flowers are formed. With ample nitrogen reserves present in the fall, additional nitrogen given in the spring had no effect on flower and fruit development. Emphasis should be placed on the desirability of getting nitrogen into the strawberry plants in autumn.

A minimum leaf area of 300 square centimeters per plant would appear to be desirable for the production of the largest number of flowers by the Aroma variety. Areas that are in excess of this size do not seem to contribute much to the increase in number of flowers, but a plant which has a smaller leaf area will develop fewer flowers.

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[^1]:    *Numerical references are to "Literature Cited," Page 51.

