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STUDIES IN THE NUTRITION OF THE STRAWBERRY

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Nutrition As Related to Yield

V. R. Gardner

Success in the commercial production of strawberries, as of most other fruits, usually depends on yield to a greater extent than on any other single factor. Earliness or lateness of maturity, quality of berry, color, uniformity of product, shipping quality and many other characteristics of the berry or of the plant are each important, but superiority in any or all of these respects is of little avail if the yield is not at least moderate. Yield depends directly on the number and size of berries per plant or per unit of area. The number of berries depends in turn, on the number of flower clusters per plant, the number of flowers per cluster and the percentage of these flowers that set and mature fruit.

To a certain extent these features of the plant's growth are varietal characteristics. That is, some varieties produce large fruits while others under like conditions produce fruits of medium or small size. Similarly some varieties characteristically produce large and others small flower clusters. All of these characteristics, however, are supposed to be influenced to a considerable degree by the environment in which the plant is grown; chief among these environmental factors are soil or nutrient conditions and moisture. The effect of drought during the fruiting season in cutting short the crop is well known—too well known the grower would say. The influence of drought or of surplus moisture at other seasons of the year is less thoroughly understood and needs investigation. Growers find large differences in yield on different kinds of soil. Some of these variations may be due to differences in their moisture-holding capacity but presumably many of them are due to the different nutritive conditions that they produce. Growers themselves believe this to be true and and they often attempt to deal with the problem of low yields by applying fertilizers.

REVIEW OF LITERATURE

Experimental data on the question of proper nutritive conditions for the strawberry are comparatively limited and often more or less contradictory. Fertilizer recommendations often have been based principally on theoretical considerations. Sometimes their application to practice has proven profitable; often it has not. Without doubt contradictory results have been due in part to confusion incident to failure to understand clearly what may be expected from fertilizer applications.

The nutritive conditions in the soil in early spring, or at least between the time when vegetation starts and when the fruit matures have been assumed to be particularly important. A typical fertilizer recommendation reads: "The use upon the plants at blossoming time of highly nitrogenous manures, such as nitrate of soda, at the rate of about 100 pounds per acre often proves of great value. If it can be applied in solution it will give quicker results than if put on in the form of a salt. If the fertility of the soil is little more than sufficient to support the plant, when the heavy strain of fruit production comes on, the plant will only perfect the number of fruits its food supply will allow; hence the advantage of applying quickly available plant foods just at this critical time[8*]." A recent treatise on strawberry culture says: "Although the amount of plant food actually removed by the strawberry plant is small, the crop responds to liberal fertilizing. This is * * * chiefly because of the very short time between the blossom and the ripe fruit. In the north, the plants have only about four weeks in which to develop a crop that may weigh three or four times more than the plants. * * * Hence the main fertilizer requirement of the strawberry is that the plant food shall be immediately available[11]." Fletcher[12] states that "gains of 500 to 1,000 quarts an acre from a spring top dressing of nitrate of soda are not infrequent", when this is applied as the plants are coming into bloom but that there is danger of a rank growth of the leaves and of soft, poor quality berries if it is applied late in the spring. White[41] has reported an increase in yield of 31 percent from the early spring use of 200 pounds of nitrate of soda per acre on a sandy loam in New Jersey. Brown[3], in Oregon, reporting the 1916 results of a strawberry fertilizer test in which the immediate effects of spring fertilizer applications can be separated from their residual effects, shows that in 11 out of 20 instances some increase in yield followed the spring use of fertilizers. In the other cases yield either was uninfluenced or was depressed. As the decreases in yield were almost as large as the increases and as nitrogen either alone or in combination seemed as likely to reduce as to increase production it must be concluded that at least under the conditions of that experiment the immediate effects of spring applications are very uncertain. Chandler[6], working with rather infertile soils in southern

*Refers to Bibliography, page 31.

Missouri, found that spring application of nitrogen either alone or in combination invariably greatly reduced the size of the following crop, though the plants grew much more vigorously. Fletcher[12] and White [41] state that the increased yields from the spring use of nitrate of soda are due principally to the larger size of the berries and not to a greater number. The same condition may be inferred from statements made by Brown[3] regarding the increases in yield following fertilizer applications in the Hood River Valley. Chandler[6] likewise found spring treatment with nitrogen to result in greater size of berry but the accompanying reduction in their number was more than enough to compensate for it.

There is an almost equal diversity of opinion and experience regarding the effect of spring applications of fertilizers on the crop borne the second following summer and regarding the effects of application at still other times. Close[7] and some of his associates in Maryland applied commercial fertilizers to strawberry beds in late fall about the time the plants would ordinarily be mulched. Yields were reduced, some years severely. The soil was a rather heavy clay loam. Bailey[2] has reported on a series of a cooperative fertilizer experiments on soils of widely differing types in New York. In each instance the fertilizer was applied in the spring before the blossoming period, but records were taken on the crop of the second following summer. In most cases the fertilizers were applied to young plants that had not yet fruited. In all instances increased yields were obtained, but sometimes with one fertilizer, sometimes with another. In many cases the increases were large, making the use of fertilizer very profitable. Phosphoric acid and potash, in the order named, gave best results. Applications of nitrogen-carrying fertilizers yielded the poorest results. Keffer[23] in Tennessee has reported negative results from the use of muriate of potash, acid phosphate and cottonseed meal singly and in various combinations on a clay loam soil. However, no statement is made as to the time of application. Some of the increases in yield reported by Brown[3] in Oregon for his 1917 and 1918 tests are undoubtedly due to the residual effect of the fertilizers applied the second preceding spring, though the proportion assignable to such influence cannot be determined. In Missouri Chandler[6] has found that spring applications of acid phosphate usually resulted in increased yields the second following summer. Negative results were obtained from the use of potassium. He reports that "nitrogen either in the form of sodium nitrate or dried blood applied a year before the crop is harvested has given an increased yield over unfertilized plots in only one trial out of nine."

Very few data are available on the influence of summer applications of fertilizer on the subsequent growth and yield of strawberries. Fletcher[12] states: "A large number of growers in the northern and central states apply one-third of the fertilizer before the plants are set, one-third during the summer and one-third early the following spring, before the plants have started to grow. The third that is used during the growing season frequently is divided into several applications; small handfuls are dropped between the plants, at intervals of three to four weeks, and hoed in. When the plants begin to slacken in growth, they will be benefited by a fertilizer stimulant." This, however, is a statement of what has come to be accepted practice by some growers rather than a general recommendation based on experimental data. Chandler[6], in summarizing the work along this line done in Missouri, says: "Where sodium nitrate or dried blood are applied in small quantities during early summer one year before the crop is harvested, they do not cause excessive plant or weed growth the following spring. However, when dried blood is applied, say 300 or 400 pounds to the acre, even a year before the crop is harvested, it tends to cause excessive plant growth, to reduce the yield and to cause the berries to wilt worse during drought at picking time". Brown[3], in Oregon, conducted one preliminary test in which late summer fertilizer applications to an old bed (after its fifth crop) were compared with spring applications. Yield records are not given, but in summarizing his results he says: "Briefly, yields although quite small, as might be expected from old plants, consistently favor late summer applications. * * * On an average, plants receiving nitrate only gave larger berries than those receiving nitrate in combination with sulphate of potash or superphosphate. Furthermore, where combined fertilizers were used, fall applications gave somewhat larger berries than spring applications of similar fertilizers."

THE PROBLEM STATED

In all of the field investigations cited the only specific method mentioned by which fertilizers effected an increase in yield is through increasing the size of the berries. No mention is made of the methods by which yields were decreased by certain fertilizer applications, except the statement by Chandler that fewer berries were produced. This reduction in number must have been considerable in some of Chandler's experiments for he states that the size of the berries was often increased by the use of certain of the fertilizers. Yield, however, depends on the number of flower clusters per plant, the number of flowers per cluster, the percentage of these flowers to set and mature fruit, as well as on the size of the berries.

The principal objects of this particular investigation have been to determine the influence of the general nutritive conditions (1) in the soil and (2) within the plant itself, at different seasons. on these features of the plant's growth. Especially was an effort made to differentiate between the effects of influences that might be operative just before and during the period of fruit bud differentiation and those that might be operative after that period and during fruit development. Factors other than those associated directly with nutrition were eliminated so far as possible.

MATERIALS AND METHODS

In July, 1921, when runners were starting on a newly planted bed of Senator Dunlap strawberries, 3-inch pots were plunged in the soil beside established plants and the runners were pegged down so that they could become rooted in the soil of the pots. Half of the pots had been filled with pure quartz sand, the other half with a fine, moderately productive sandy loam like that in which the mother plants were growing. The runners struck root readily in both sand and soil. During the course of the season a little soil was washed into the pots containing sand, but the amount was negligible. On September 1 the pots were lifted and the plants shifted to 5-inch pots, care being taken to disturb as little as possible the masses of soil in which the roots had been growing. Those that had been growing in sand were repotted in sand—river-bottom sand with a very small amount of silt. A compost, such as is commonly used in potting greenhouse plants and consisting of sifted soil, rotted sod, a little sand, to which some bone meal was added, was employed for the plants that had been growing in soil. The plants that had been growing in sand appeared but little different from those growing in soil, at the time of repotting. Data presented later, however, show that there was a distinct difference in size and composition.

The use of the soil and sand as media in which to grow the plants was designed to provide two series, one having as nearly as possible optimum and the other very poor nutrient conditions.

Associated with these extremes of soil, it was expected that there would be materially different nutritive conditions within the plants themselves, an expectation verified by analyses given later. To produce still greater extremes, or at least more diverse conditions of food supply within the plants, half of the plants of each series were repeatedly defoliated during September and October. The defoliation forced the plants to put out new leaves, thus curtailing the manufacture of food materials and utilizing a part of those already stored. By the time of fruit bud formation[15] the defoliated soil-grown plants should present a condition of semi-starvation, while the sand-grown defoliated plants should present a condition of extreme starvation. That this condition was obtained in the last mentioned group was evidenced by the fact that some died, their reserve supplies evidently having been completely exhausted and their recuperative ability destroyed.

Suitable records were made from time to time of the number of leaves on the plants in the various groups, and on October 31, a time assumed to represent fairly the period of fruit bud formation, representative plants were taken for the purpose of making determinations of fresh weight, dry weight, total carbohydrate, starch and nitrogen.

When severe freezing weather came on in December the plants were covered with a thin layer of straw, thus imitating conditions in the field. February 1 all the plants were taken into a greenhouse and the pots were plunged in a bed of soil. Within a few days new leaves were being pushed up from the crowns, except in several of the soil-grown defoliated lot. Though they had been alive in the fall their reserves apparently had been so exhausted that recuperation was impossible. Each of the four lots was then sub-divided into two parts and one of each pair of these subdivisions was watered each week with a weak liquid manure solution. This was obtained by making a water extract of well rotted barnyard compost, such as is often used by the florist in greenhouse practice. Ordinary tap water was used for all other watering. The effect of this treatment was to provide one series of plants, part of which had been starved in the fall previous to their period of fruit bud differentiation, with an abundance of nutrients, while the other series, part of which had been similarly starved, could obtain only such nutrients as were available in the soil or sand in which they were growing. The pots were lifted frequently to prevent any roots from penetrating the soil into which they had been plunged.

Watering was frequent enough so that at no time did the plants suffer because of its lack.

In addition to the work with the Senator Dunlap plants grown in pots a series of records were taken on some Gandy plants grown in the open. These were vigorous and productive. They were growing in a moderately fertile clay loam that was well watered by frequent rains, especially during the ripening season of 1922 when the records were taken. Soil moisture therefore was at no time a limiting factor in the development of their berries.

PRESENTATION OF DATA

Influence of Soil Conditions During Summer and Fall on Vegetative Characters of the Plant.—At the time the rooted runners were lifted, September 1, little difference was evident between those rooted in soil and those rooted in sand. As all of these plants were still connected with the strong mother plants they presumably were receiving both nutrients and elaborated foods from them. Determinations were made September 22, of the fresh weight, dry weight, total carbohydrate and starch content of average plants of each lot. These data, given in Table 1, show that the soil-grown plants were actually considerably heavier and relatively richer in starch and total carbohydrates than those grown in sand. Possibly, however, these differences had developed during the first three weeks of September, following the repotting.

The records show that during the last two weeks of September and the month of October the undefoliated soil-grown plants increased in fresh and dry weight while those in sand remained practically constant in these respects. The effects of the repeated defoliation of both sand-grown and soil-grown plants was a decrease in both fresh and dry weight, especially in dry weight. This decrease was very marked in the sand-grown plants, the loss amounting to almost 50 percent. Toward the end of this period it was noted that the sand-grown defoliated plants were rapidly losing their recuperative ability. The leaves of each successive lot were distinctly smaller than those of the preceding lot. It was plain that the plants were becoming exhausted. The same tendency was evident in the soil-grown defoliated plants, but it was not so pronounced. All four groups of plants showed somewhat higher total carbohydrate percentages October 31 than six weeks earlier, the differences between the defoliated and the undefoliated lots being greater however than those between corresponding lots grown in

TABLE 1.—EFFECTS OF SOIL AND DEFOLIATION ON FALL GROWTH AND NUTRITIVE CONDITIONS IN THE STRAWBERRY PLANT.

Date	Soil	Treatment	Fresh wt. gr.	Dry wt. gr.	Dry wt. per cent	Total carbohydrate per cent dry wt.	Starch per cent dry wt.	Nitrogen per cent dry wt.
Sept. 22	Sand	....	26.800	7.050	26.3	18.64	1.62	....
	Soil[1]	....	36.251	9.525	26.3	20.07	1.96	2.102
Oct. 31	Sand	Defoliated	13.294	2.9595	22.2	23.73	1.37	....
	Sand	Undefoliated	25.063	7.2880	29.1	27.39	1.69	2.016
	Soil[1]	Defoliated	23.079	4.9725	21.6	24.88	2.43	2.005
	Soil[1]	Undefoliated	38.764	10.4385	26.9	29.31	2.54	2.038

[1]Knox silt loam.

TABLE 2.—YIELD RECORDS OF STRAWBERRY PLANTS AS INFLUENCED BY SOIL TYPE AND DEFOLIATION THE PRECEDING SEASON.

Date	Sand-grown, undefoliated		Sand-grown, defoliated		Soil-grown, undefoliated		Soil-grown, defoliated	
	No. berries	Wt. gr.	No. berries	Wt. gr.	No. berries	Wt. gr.	No. berries	Wt. gr.
April 4	2	8.0	1	4.0	1	7.5	3	15.0
April 7	5	7.4	1	2.1	2	8.0	7	27.8
April 11	14	15.8	2	3.5	7	27.1	26	98.1
April 15	11	20.0	7	14.0	13	54.0	25	69.0
April 17	31	40.0	4	3.9	15	40.8	26	56.3
April 20	27	31.2	5	7.4	28	65.7	48	95.7
April 22	10	8.1	6	5.4	28	38.6	22	36.0
April 26	27	37.0	6	6.2	48	99.0	28	41.8
April 29	13	10.3	2	1.4	58	117.0	31	48.0
May 4	11	12.9	7	7.3	104	172.1	34	50.8
May 8	9	15.0	2	0.8	29	67.2	18	30.0
May 11	4	4.8	....	....	14	14.7	13	15.1
May 15	1	0.8	....	....	19	29.4	6	8.3
Total	175	211.3	43	56.0	366	741.1	287	601.9
Average per plant	5.8	7.0	3.1	4.0	14.1	28.5	13.0	27.3
Average number aborted flowers per plant	5.2	....	3.6	....	11.9	....	11.6	....
Average number of flower clusters per plant	2.5	....	1.2	....	4.2	....	4.0	....
Average size of berry, grams	....	1.2	....	1.3	....	2.0	....	2.1

the sand and soil. Differences in starch content were still more pronounced. Here, moreover, the contrast between soil-grown and sand-grown plants was greater than between corresponding lots of defoliated and undefoliated plants. It is interesting that neither soil treatment nor defoliation seemed to have much effect on nitrogent content.

Briefly, the effect of the poor soil during the summer and fall months was to check the increase in size of the plants, slightly reduce their total carbohydrate content and greatly reduce their starch content. The effect of the defoliation was to reduce total fresh and dry weight, slow down starch and total carbohydrate accumulation and in the sand-grown plants reduce the percentage of starch. The soil and defoliation treatments therefore resulted in producing a series of plants representing a considerable range in fresh and dry weight, total carbohydrate content and starch content at and during the period of fruit bud differentiation.

The Influence of Nutritive Conditions in the Fall on Vegetative Growth the Following Spring.—When the plants were taken into the greenhouse February 1 they all started to grow promptly. In ten days they presented a smoothly graded series. Those of the undefoliated soil-grown lot were by far the largest and most vigorous; then came the defoliated, soil-grown lot, followed very closely by the undefoliated, sand-grown lot. The defoliated sand-grown plants were very small and weak, with few leaves having short petioles and small leaflets. By May 8, toward the close of the fruiting season, these four lots still held the same relative positions except that less difference was evident between the defoliated and undefoliated soil-grown plants. Neither of the sand-grown lots showed signs of runner formation; a few runners developed on both defoliated and undefoliated soil-grown plants.

The Influence of Nutritive Conditions in the Fall on Flowering and Fruiting the Following Spring.—Table 2 summarizes data on the flowering, fruit setting and fruiting of the plants in the different lots.

It is clear that soil exerted a marked influence on the number of flower clusters and the number of flowers per plant. With good nutrient conditions in the soil and within the plant itself previous to and during the period of fruit bud differentiation more fruit buds were formed and the resulting clusters averaged a larger number of flowers than under conditions approaching starvation. Twice as many flowers were produced by the undefoliated soil-grown plants as by the undefoliated sand-grown plants. In both lots, however, a considerable portion of these flowers, the later ones to develop in the individual flower cluster, were sterile. That is, they appeared to be perfect, but they were in effect pseudo-hermaphrodites and unable to set fruit. Valleau[39] has shown that this is a characteristic of most strawberry varieties and attributes it to a general evolutionary tendency in this species. The interesting point in this connection is that this flower abortion is not greatly influenced—though there is some influence—by extremes of nutritive conditions in the soil and in plants at the time of fruit bud formation.

Berries on the soil-grown plants averaged nearly twice as large as those on the sand-grown plants. Data presented in Table 8 are of particular interest in this connection. The favorable fall growing conditions resulted in a slight increase in the number of pistils per flower, a factor that has been shown to be associated with size of berry[39]; but, more important, these favorable nutritive conditions have been followed by a better "setting" of these individual pistils and consequently by the maturing of larger numbers of akenes per berry. More attention will be devoted to this aspect a little later.

The effects of the poorer nutritive conditions within the plant at the time of fruit bud differentiation and brought about by defoliation have in some respects been similar to those accompanying similar changes brought about by soil conditions. In other respects they have differed. Defoliation reduced the average number of flower clusters per plant, especially in the sand-grown plants, and the average number of flowers per plant. It increased slightly the percentage of sterile flowers in the sand-grown plants but not in those grown in soil. It had very little influence on size of berry. Kind of soil had no influence on season of maturity of the berries. On the other hand the early pickings from the defoliated plants were much heavier than those from the undefoliated plants, though the reverse was true of the later pickings. This is particularly interesting because the beginning and end of the picking season was identical under the two treatments. This is brought out by the data presented in Table 2.

Influence of Nutritive Conditions in the Soil in the Spring on Growth and Fruiting of the Strawberry.—As has been indicated a series of plants after being brought into the greenhouse February 1 was watered each week with liquid manure. The effect of this treatment was soon evident in the larger leaflets and longer petioles of the new leaves. Especially was this true with the two lots of sand-grown plants. However, the influence of the fertilizer was temporary rather than permanent, for by the time the plants were maturing their fruit the differences were much less pronounced. The fertilizer applications had very little influence on the number of the new leaves or on runner formation.

Table 3 summarizes flowering and fruiting records of the various lots receiving spring fertilizer applications. Comparison of these data with those presented in Table 2 shows that the treatments resulted in an increase in the number of flower clusters and of flowers in the sand-grown plants. Yields were similarly increased. On the other hand there was an equally marked decrease in number of flower clusters, flowers and yield in the soil-grown lots. These findings are in line with the results of field tests reported by Chandler[6]. The data indicate that in the sand-grown fertilized plants either some flower bud formation took place after growth started in the spring or that in the nearly starved sand-grown unfertilized plants the food reserves and nutrients were insufficient to permit the development of those already differentiated. Observation of the time the flower clusters appeared in the various lots leads to the acceptance of the latter view. The decrease in average number of flower clusters, flowers and yield of fruit accompanying the fertilizer applications to the soil-grown lots appears to be due largely to the suppression of already formed flower buds. A number of these spring-fertilized plants developed no flower clusters. Though there were a few barren plants in the other lots, they were much less common. Spring fertilizing had practically no influence on the percentage of flowers that aborted after flowering. The figures, taken as a whole, do not indicate any significant influence on size of berry.

FACTORS INFLUENCING SIZE OF BERRY

Relation of Pistil Number to Berry Size.—Without doubt many factors may influence the size of the berries; some of them external, others internal. Among the internal factors the number of pistils has long been recognized as important. Recently Valleau[39] has pointed out a relationship between number of flower parts and position of flower in the flower cluster. The primary, secondary, tertiary and quaternary flowers are characterized by progressively fewer flower parts. Table 4 summarizes data along this line obtained from ten large vigorous Gandy plants growing in the field.

TABLE 3.—YIELD RECORDS OF STRAWBERRY PLANTS AS INFLUENCED BY SPRING TREATMENT.

Date	Sand-grown, undefoliated spring fertilized		Sand-grown, defoliated spring fertilized		Soil-grown, undefoliated spring fertilized		Soil-grown, defoliated spring fertilized	
	No. berries	Wt. gr.	No. berries	Wt. gr.	No. berries	Wt. gr.	No. berries	Wt. gr.
April 4	1	3.5	1	3.5	1	7.5	1	6.0
April 7	7	17.2	12	18.8	2	12.5	10	28.6
April 11	24	50.2	29	31.5	9	28.3	18	41.5
April 15	16	33.0	22	31.0	16	52.0	24	60.0
April 17	35	39.4	25	24.3	19	37.2	17	26.0
April 20	12	10.4	15	23.0	17	31.5	17	27.6
April 22	9	7.0	6	6.2	21	27.0	11	15.0
April 26	17	12.6	11	8.2	15	21.8	12	13.4
April 29	5	4.6	10	8.1	45	78.0	5	11.0
May 4	13	17.0	4	4.2	39	71.9	10	14.9
May 8	2	0.5	1	0.4	6	15.0	4	4.2
May 11	....	....	2	2.0	3	3.9	3	3.0
May 15	....	....	....	....	5	6.5	....	....
Total	141	196.4	138	161.2	198	393.1	132	251.2
Average per plant	7.8	10.9	5.5	6.4	11.0	21.8	7.4	13.4
Average number aborted flowers per plant	7.8	....	4.4	....	9.7	....	7.7	....
Average number flower clusters per plant	2.5	....	2.5	....	4.2	....	3.5	....
Average size of berry, grams	....	1.9	....	1.2	....	2.2	....	1.7

TABLE 4.—SIZE OF BERRY AS INFLUENCED BY NUMBER OF PISTILS.
(Averages for ten flower clusters)

Number of berry to ripen	1	2	3	4	5	6	7	8	9	10	11	12	13
Av. ripening date	5/26	5/28	5/31	5/31	6/1	6/2	6/2	6/11	6/12	6/12	6/12	6/13	6/13
Percent of pistils aborting	6.6	7.9	5.2	14.9	11.5	11.5	14.2	15.5	28.5	28.2	32.0	22.8	14.4
Av. number pistils	518	352	309	294	242	242	232	194	224	195	150	192	83
Av. weight of berry, grams	10.7	7.1	4.9	3.9	3.7	3.4	2.8	2.4	1.9	1.9	1.4	1.5	0.2
Av. number aborted pistils	34	28	16	44	28	28	33	30	64	55	48	44	12
Av. number akenes	484	324	283	250	214	214	199	164	160	140	102	148	71

At no time during the fruiting season was soil moisture a limiting factor, rains being frequent and heavy. Each plant bore only one cluster, but the clusters were large, 20 to 25 flowers being not uncommon. However, the average number of fruits was about 8; two clusters matured 13 fruits apiece. It will be noted that there was a steady decrease in the size of the berries as the season advanced and this was accompanied by a corresponding decrease in number of akenes per berry. There was, on the contrary, an increase in the total number of aborted pistils as the season advanced, due to a very marked increase in the percentage aborting. This would indicate either an increasing percentage of defective pistils in the later flowers, an abortion due to exhaustion of food reserves occasioned by the development of the earlier berries, or perhaps the appearance of some other limiting factor, e. g., high temperature.

Further data on the relation of pistil number to fruit size are furnished in Table 5, giving individual berry weights of a single large vigorous Gandy plant that bore three fruit clusters. The primary cluster matured 11, the second 4 and the third 3 berries. These three clusters ripened their fruit at successive intervals, though there was some overlapping of the first and second clusters. When the first cluster was maturing the last of its berries, which were small and had less than 200 pistils to the flower, the second cluster started to ripen fruits twice or three times as large and having from 240 to 370 pistils apiece. However, the number of pistils per flower in the blossoms of the third cluster was below the averages for the first and second clusters and the size of berry was correspondingly reduced. These data would indicate that, assuming an adequate moisture and nutrient supply in the spring, size of berry is determined principally by the number of pistils per flower. This in turn depends on varietal characteristics and on nutritive conditions during the period of fruit bud differentiation in the fall.

That nutritive conditions within the plant itself in the spring are of considerable importance in influencing both setting of the fruit and size of berry is shown, however, by data presented in Table 6. These records were obtained from seven vigorous Gandy plants in the field. The soil was a good clay loam and at no time did they suffer from lack of moisture. Each plant bore a single large inflorescence, the number of flowers per cluster ranging between 20 and 25. When these flower clusters were well developed, but before any of the blossoms had fully opened, the eight largest

TABLE 5.—SIZE OF BERRIES ON SUCCESSIVE FLOWER CLUSTERS FROM THE SAME CROWN.

Ripening date	Number of berry to ripen	Weight gr.	Akenes	Aborted pistils	Number of berry to ripen	Weight gr.	Akenes	Aborted pistils	Number of berry to ripen	Weight gr.	Akenes	Aborted pistil
May 24	1	12.0	368	6	....	....	....	....	....	....	....	....
May 24	2	8.5	333	8	....	....	....	....	....	....	....	....
May 26	3	6.4	290	7	....	....	....	....	....	....	....	....
May 26	4	6.9	250	16	....	....	....	....	....	....	....	....
May 26	5	4.6	221	23	....	....	....	....	....	....	....	....
May 27	6	5.5	263	14	....	....	....	....	....	....	....	....
May 27	7	4.7	207	9	....	....	....	....	....	....	....	....
May 29	8	2.6	170	19	....	....	....	....	....	....	....	....
May 29	9	2.3	140	51	1	5.5	334	36	....	....	....	....
June 1	10	2.4	119	78	....	....	....	....	....	....	....	....
June 3	11	1.8	98	21	....	....	....	....	....	....	....	....
June 7	....	....	....	....	2	5.2	260	10	....	....	....	....
June 7	....	....	....	....	3	4.4	215	117	....	....	....	....
June 7	....	....	....	....	4	3.4	210	29	....	....	....	....
June 11	....	....	....	....	....	....	....	....	1	2.6	158	26
June 11	....	....	....	....	....	....	....	....	2	1.7	204	20
June 11	....	....	....	....	....	....	....	....	3	1.5	145	40

TABLE 6.—FRUIT SETTING AND BERRY SIZE AS INFLUENCED BY FLOWER REMOVAL.
(The first eight blossoms on each cluster were removed before opening. Averages of seven clusters)

Number of berry to ripen	1	2	3	4	5	6	7	8	9	10	11
Average ripening date	5/29	6/1	6/2	6/3	6/5	6/6	6/7	6/8	6/8	6/9	6/10
Average weight of berry, grams	4.8	3.3	3.3	2.7	2.4	1.8	1.4	1.5	1.1	1.1	0.9
Average number pistils	238	203	201	187	183	165	139	148	125	130	123
Average number akenes	216	185	168	164	159	133	115	119	102	103	85
Average number aborted pistils	22	18	33	23	24	32	24	29	23	27	38
Per cent of pistils aborting	9.2	8.8	16.4	12.3	13.1	19.5	17.3	19.6	18.4	20.8	30.8

flower buds on each cluster were removed. As was to be expected, this removal of the early blossoms delayed somewhat the date of ripening of the crops, the ripening season covering the period May 29 to June 11, inclusive, as compared with May 26 to June 13 for plants of the same variety that had no flowers removed. That their ripening season should close earlier is rather surprising and perhaps accidental. Particularly interesting is the fact that these "thinned" or "defloresced" flower clusters matured as many berries as those not receiving such treatment. Table 4 shows that in no instance did untreated plants mature more than 13 berries per cluster; in fact, the average number was 8.8, the flowers to open later aborting without setting fruit. Yet when the first eight flowers on every cluster of these seven plants were removed an average of 9.1 younger flowers set and matured fruit. Here is clear evidence that nutritive conditions within the strawberry plant at the time of fruit setting are of considerable importance in influencing the setting of the flowers. The average yield of the untreated plants was 41.12 grams; that of the treated plants was only 22.5 grams. The plants that had their early flowers removed yielded less because their berries were of smaller size, due to their smaller number of pistils per flower. Nutritive conditions within the plant at the time of fruit setting, therefore, influenced yield principally through their influence on fruit setting.

Relation of Percentage of Pistils Developing Into Akenes to Size of Berry.—Counts were made of the numbers of fully developed akenes and of aborted pistils in 447 Senator Dunlap berries gathered at random from the different lots fruited in the greenhouse and collected in such a way as to be representative of the entire crop. The data obtained are summarized in Table 7. The weights

TABLE 7.—RELATION OF PISTIL ABORTION TO SIZE OF BERRY.

Percentage of pistils developing into akenes	No. of berries averaged	Average berry weight (grams)	Average total no. of pistils	Average no. of pistils developing into akenes
0-10	40	1.08	206	15.3
11-20	64	1.18	186	29.6
21-30	53	1.95	229	57.8
31-40	40	1.53	181	63.9
41-50	51	1.95	198	90.2
51-60	48	2.29	210	115.3
61-70	51	2.75	225	147.4
71-80	50	2.50	194	142.8
81-90	41	2.23	169	144.2
91-100	9	1.82	143	134.2

given in the third column are not strictly comparable as measures of the influence of individual pistil setting on fruit size, for there is considerable variation between the different groups in the number of pistils per flower. When due allowance is made for the influence of pistil number on size of berry it is clear that there is a very important relation between the setting of the individual pistils and the size of the resultant berry. Thus berries averaging 180 to 195 pistils weighed on the average only 1.18 grams when 11 to 20 percent of their pistils set, 1.53 grams when 31 to 40 percent of their pistils set, and 2.50 grams when 71 to 80 percent of their pistils set. Flowers averaging only 169 pistils apiece matured fruits averaging 2.23 grams in weight when 81 to 90 percent of their pistils set, while flowers averaging over 200 pistils apiece produced berries less than half that weight when less than 10 percent of their pistils set. Individual pistil abortion thus explains in part the progressive decrease in size of fruit with the successive appearance of primary, secondary, tertiary and quaternary flowers on the cluster. This relationship is of special interest also in emphasizing the importance of the influence on size of berry of nutritive conditions within the plant at the time of fruit bud differentiation. (See Table 8.)

TABLE 8.—RELATION OF NUTRITIVE CONDITIONS IN THE FALL TO ABORTION OF INDIVIDUAL PISTILS THE FOLLOWING SPRING.

Treatment	No. berries averaged	Average wt. grams	Average total no. pistils	Percentage of pistils developing into akenes
Not fertilized in the spring				
Sand-grown, undefoliated	41	1.2	173	24
Sand-grown, defoliated	17	1.3	160	43
Soil-grown, undefoliated	74	2.0	188	47
Soil-grown, defoliated	96	2.3	214	58
Fertilized in the spring				
Sand-grown, undefoliated	54	1.9	224	29
Sand-grown, defoliated	52	1.2	186	24
Soil-grown, undefoliated	66	2.2	191	54
Soil-grown, defoliated	51	1.7	215	58

DISCUSSION

The data that have been presented should not be taken to mean that yield, size of berry, date of maturity or other characteristics of the fruit or the plant are entirely uninfluenced by nutritive conditions in the spring before harvesting. As a mater of fact they indicate that soil conditions in the spring exert some influence, especially on size of berry and it is conceivable that soil treatments other than those discussed might have an even greater influence. However, the data point clearly to the fact that soil and other conditions surrounding the plant during and previous to the period of fruit bud differentiation are relatively of much greater importance. This is a time of the year to which little attention generally is given. Runners that form early are often removed. Late runner formation is often tolerated or even encouraged. A partial defoliation by fungi or insects late in the season is not generally regarded as a serious matter; tillage is discontinued and weeds come in. Nutritive conditions within the soil at this time of the year are not thought of as being particularly important. Yet this is the period that very largely determines not only how many flower clusters shall develop and how many flowers each will have but it is likewise important in determining the percentage of berries that will have to be classed as culls the following season because of small size. The exact fertilizer and cultural treatments that are best for the plant at this season of the year remain to be determined. They will probably vary considerably with variety, soil and other environmental conditions. It is clear, however, that the nutrition question, as it relates to strawberries, is a late summer and fall question to a much greater extent than has been generally suspected, and that investigators and growers can well afford to give it consideration from this point of view.

Nutritive Conditions and Change of Sex

REVIEW OF LITERATURE

In General.—Numerous theories have been formulated to account for the determination of sex in plants. The earlier view, still held by many, is that sex is determined at or before fertilization, each gamete being supposed to carry either the factors for both sexes or those for a single sex. The particular combination brought together at the time of fertilization would consequently determine the sex of the resultant individual according to the laws of chance. Strasburger[37] expresses the opinion that only male gametes bear the tendency to produce male offspring, while only female gametes bear the tendency to produce female offspring. Should the one tendency dominate over the other the resulting individual would be unisexual; should there be no dominance the individual would be hermaphroditic. In either case the sex of a gamete is regarded as definitely determined at the time of the chromosome diversion preceding its formation and the sex of the resultant individual as likewise being definitely determined at the time of fertilization (though perhaps Strasburger's conception might admit the possibility of sex development being materially modified at a later stage).

Acceptance of this theory, however, leads to difficulty in explaining unusual sex ratios in different or unusual conditions. Wilson[42] would meet this difficulty by suggesting that "sex is determined by certain metabolic processes which are spread over a considerable number of cell generations, and which, as a rule, are unaffected by external conditions." Goldschmidt[16] would explain the appearance of intersexual forms (in moths) by assuming that the same sex factors in different combinations are present in different quantities and that the degree and kind of sexual development attained by the individual is a result of a kind of mass action of these sex factors. From these conceptions it is but a step to the view that sex determination is incident to the development of the somatic tissue and is a particular response to environmental conditions. This concept is well expressed by Schaffner[31].

"In its simplest form sexuality is a physiological difference expressed only in the developing sexual cells * * * in at least the vast majority of cases, and probably in all, the sexual condition is simply a state of the living substance which may continue for a greater or less length of time before a neutral state or the opposite sex condition is set up. * * *

"Sex appears in some way to be associated with physiological and chemical states of the living protoplasm. It is perhaps most reasonable to assume, at present, that a certain organization or complexity of the cell is necessary before sexual states originate. But it is not true on the other hand that these states are necessarily set up at any stage of the life history even in organisms that have the essential complexity. * * *

"In the higher plants the reduction of chromosomes has nothing to do with the maleness or femaleness of the gametophyte. The determination of the sex takes place in the vegetative tissues of the sporophyte. Whatever it is that determines that the given tissue shall develop as a megasporophyll or a microsporophyll also determines absolutely the sex of the following generation of gametophytes."

Observations and experimental evidence that have long been accumulating lead unmistakably to the conclusion reached by Schaffner. The real question at issue is the exact nature of the environmental and internal conditions associated with, or responsible for, the determination of the sexual state. Following is a brief review of some of the more important literature bearing on the subject.

Nutritive Conditions and the Sex Ratio.—Observations of Hoffman[40] indicate that the ratio of males to females in the dioecious genera *Lychnis, Spinacia* and *Rumex* varies according to the distance apart the plants are growing. When crowded together and more or less stunted, males predominate; with wider spacing and better growing conditions there are relatively more females. Schaffner[33] has found that in *Arisaema* there are often three times as many pistillate plants in a rich, wet soil as in a soil that is poor and dry. Burbidge[4] and Geddes and Thompson[14] record similar observations with other dioecious plants. Meehan[27] records the fact that in England where they are wont to make a moderate growth plant of a certain species of *Rumex* are characteristically hermaphrodite. Near Philadelphia, however, in the same species, only those plants of average vigor are hermaphrodite, the stronger being almost entirely pistillate.

Evidence that nutritive conditions are associated with variations in the sex ratio is not limited to the flowering plants. Nagai[29], working with various species of *Asplenium* and *Osmunda,* found that the sex ratio among the prothallia varied with the concentration of the nutrient solution in which they were grown. With a decreasing concentration, to a certain point, there was an increase in the percentage of archegonia; beyond that point, that is, in a very weak nutrient solution, there was an increasing tendency for the prothallia to remain sterile, vegetative. His work with these and other genera shows that male organs often develop under comparatively unfavorable growth conditions but the development of the female organs requires better growth conditions. In *Osmunda* he found antheridia forming freely in prothallia that were very much dwarfed because of their growth conditions and that had accumulated an abundance of starch. Similar observations have been made by other botanists[14].

Sex Reversal With the Season.—Still more significant are instances of changes in sex, or sex reversal, during the life of the individual and of the occasional appearance of hermaphrodite flowers on plants usually unisexual. Organs of mixed sex have been found in plants of the supposedly dioecious moss, *Mnium hornum*[42]. Martins[28] records a "male" plant of *Chamaerops humilis* that bore only male flowers from 1851 to 1861, but in 1861 it bore a few, and in 1862, many female flowers. Maples have frequently been observed to bear only hermaphrodite flowers one year and staminate flowers the next[35] or pistillate flowers for a series of years and then staminate flowers[25]. In these cases the general tendency has been from the female to the male, pistillate flower production being associated more frequently with the vigor of young trees. Willow branches have been observed to bear male catkins one year and the following year female catkins. Apparently in certain willows[5], long immersion in water tends to promote the development of male catkins only. A high water table has been known to disturb the ordinary sex ratio in *Pistacia terebinthus*[5]. Young vigorous Japanese persimmon trees of certain varieties bear pistillate flowers only. As they become older they bear staminate flowers as well, though occasionally they may return temporarily to the pure pistillate condition. Such varieties have been called "staminate sporadics"[22]. Plants of the bog myrtle (*Myrica gale*) may be male one season, female the next, hemaphrodite the third and female again the fourth season; or they may present any other conceivable series of sex changes[9]. The water soldier (*Stratiotes aloides*) is said[14] to bear only female flowers north of 52°lat. and only male flowers south of 50°.

Mutilation and Change of Sex.—Mutilation is frequently followed by a change of sex. The male papaya (*Carica papaya*) has been known to bear hermaphrodite flowers and to set and mature fruit following severe mechanical injury[21]. Removal of flowers and flower buds from female hemp plants often induces them to produce both staminate and pistillate flowers and occasionally the production of pistillate flowers has followed the similar treatment of male plants[30]. By heavy pruning of *Pinus densiflora* Fujii has stimulated the production of female flowers in positions usually occupied by the staminate inflorescences[13]. He attributes the sex change to a local increase in nourishment.

Nutritive Conditions and Sex Reversal.—The Hope grape, a Muscadine variety bearing hermaphroditic flowers under good cultural conditions, gradually changes to a non-fruiting staminate pseudohermaphrodite under neglect[10]. By varying atmospheric humidity and light intensity Tournois[38] was able to change a male hop vine to the monoecious and even to the female condition. Meehan[26] observed that in *Pinus* and *Thuja* "a high stage of vitality, or vigor, is favorable to the production of female flowers; and a low stage, or comparative weakness, to the production of male ones." He called attention to the fact that "the cones of these trees are always on the strong vigorous branches towards the top of the tree, or on the ends of the strong laterals. * * * The male flowers are never on these strong branches, seldom near the ends of the main shoots, but down amongst the lowermost and weakest branches, and in the more interior parts of the trees." The observations of Guinier[17] on *Pinus montana* and *P. sylvestris* to the effect that the young vigorous trees of these normally monoecious species are often unisexual accord with Meehan's conclusions.

Atkinson[1] succeeded in changing male plants of *Arisaema triphyllum* to female plants in one year by potting them in a rich soil. Large neuter plants were similarly changed to females. By cutting the bulbs before the period of flower bud formation so as to leave only a small amount of stored food he succeeded in changing large vigorous plants to males. Schaffner[33], working with the same species, has been able to change practically all the plants to males by growing them in a rather dry soil and under unfavorable conditions. Then by fertilizing them heavily and watering them liberally he was able to change them back into females. He states: "Sex reversal is complete in the individual in either direction from time to time, the male to the female or *vice versa,* or the reversal may be partial, from a pure male or female state. * * * Apparently in *Arisaema triphyllum* the sexual state depends mainly on the water supply, or on the nutrition, or on both combined."

Instances of change of sex in the strawberry apparently are not uncommon. Hibberd[20] records an instance of the Hautbois changing from a male to a female, though the growth conditions accompanying the change are not mentioned. Valleau[39] lists a number of standard varieties that often produce "pistillate primary flowers early in the flowering season, while those produced later are all perfect." Meehan[27] observed that varieties of *F. vesca* grown in Europe were for the most part hermaphroditic, grown in Pennsylvania they were chiefly unisexual. He was able to make some of these hermaphroditic varieties become pistillate "by growing them on the shelves along the back wall of a lean-to hothouse, and manuring with as strong manure-water as they would bear."

Instances of abnormal sex ratios found under somewhat unusual environmental or cultural conditions and of changes of sex during the life of the individual might be multiplied. Enough, however, have been cited to show that environment often has an important influence, either direct or indirect, on the development of the sexual states and the sexual organs. Instances where sex ratios of dioecious species have not been changed when put to experimental tests, like those of Haberlandt[18] and Heyer[19] with hemp and of Sprecher[34] with *Rumex*, simply mean that these investigators did not provide the conditions necessary for sex change or that they were working with material more fixed in respect to this character. They do not warrant negative conclusions, even in regard to these species, for other investigators have obtained positive results with them.

Table 9 brings together a number of typical instances that have been cited in this paper in which a change of the sex ratio or sex reversal in the individual plant has accompanied some change in the plant's environment.

Sometimes season, sometimes location, sometimes moisture supply, temperature, or light is mentioned as the principal contributing factor. In many instances a combination of several factors is associated with the change. Foremost among the factors, however, is nutrition. Femaleness is associated with rich soils, abundant moisture, liberal spacing, the vigor of youth, favorable growing conditions. Maleness on the other hand, is associated with somewhat less favorable growing conditions.

EXPERIMENTAL DATA AND DISCUSSION

In the light of these general conclusions it was thought that possibly the extreme nutritive conditions produced in the strawberry plants used in these experiments might lead to certain sex changes. So it proved. Senator Dunlap is normally a perfect-flowered variety. As the appearance of pistillate flowers in this variety has apparently not been recorded it may be regarded as having its hermaphroditism pretty firmly fixed. Yet only two of the 93 plants grown in pure sand produced perfect flowers, while all of those grown in soil were hermaphroditic. The remainder pro-

TABLE 9.—TYPICAL INSTANCES OF SEX CHANGE ACCOMPANYING CHANGED ENVIRONMENT CHANGES IN SEX RATIO.

Plant	Investigator	Direction of change	Accompanying conditions
Lychnis Spinacia Rumex	Hoffman[16]	Male to female	Wide spacing
Rumex	Meehan[27]	Hermaphrodite to female	Vigorous growth
Arisaema	Schaffner[17]	Male to female	Rich, wet soil
Asplenium	Nagai[23]	Hermaphrodite to female	Weak concentration of nutrients
Osmunda	Nagai[23]	Female to sterile (vegetative)	Very weak concentration of nutrients
Sex Reversal in the Individual Plant.			
Willow	———[28]	Male to female	Long immersion in water
Bog myrtle	———[30]	All directions	Season to season
Chamaerops	Martins[24]	Male to female	Season to season
Stratiotes	———[19]	Male to female	More northern latitude
Catrica papaya	Higgins[31]	Male to female	(Mechanical injury (Higher altitude
Fragaria vesca	Meehan[27]	Hermaphrodite to female	Heavy manuring
Pinus densiflora	Fujii[33]	Male to female	Heavy pruning
Arisaema	Atkinson[37]	Neuter to female	Rich soil
Arisaema	Schaffner[17]	Male to female	Wet, rich soil
Arisaema	Schaffner[17]	Female to male	Dry, poor soil
Hope grape	———[34]	Hermaphrodite to male	Poor cultural treatment
Pinus and Thuja	Meehan[36]	Female to male	Decreasing vigor
Maple	Meehan[25]	Female to male	Increasing age
Pinus montana	Guinier[38]	Female to hermaphrodite	Increasing age
Japanese persimmon	Hume[29]	Female to hermaphrodite	Increasing age
Hemp	Pritchard[32]	Female to hermaphrodite	Flower removal

duced pistillate flowers only. Furthermore, liberal spring fertilization had no influence on the sex of the flowers. Sex was determined absolutely at the time of fruit bud differentiation in late fall and through the winter months.

Reference to Table 1 shows that the sand-grown starved plants were relatively low in total carbohydrates and very low in starch at the time of fruit bud formation. The soil-grown plants were comparatively rich in these materials. High carbohydrate and high starch content was therefore associated with the production of hermaphroditic flowers; low carbohydrate and low starch content was associated with the pure female condition. These pistillate plants, it will be recalled, were weakly vegetative, as compared with the perfect-flowered soil-grown specimens.

These circumstances would seem at first to contradict the evidence presented in the review of literature bearing on this question, for in most cases (including the greenhouse-grown strawberries with which Meehan[27] worked) femaleness was associated with vigorous growth and good growing conditions generally while maleness or hemaphroditism was associated with less rapid growth and more unfavorable growing conditions. The contradiction, however, is apparent rather than real. It must be remembered that vigorous vegetative growth is made at the expense of stored carbohydrates or of carbohydrates that are being manufactured. Growth utilizes carbohydrates and consequently vigorously growing tissues are relatively low in these materials. When growth and consequently carbohydrate utilization is checked, opportunity is afforded for carbohydrate accumulation. As accumulation continues conditions favorable for the development of male organs appear and the plant becomes hermaphroditic or male. Let manufacture of carbohydrates be stopped or reduced, through the influence of some limiting factor (soil nutrients, leaf area, etc., in this experiment) and the ultimate exhaustion of carbohydrates through respiration and a limited amount of new tissue formation will again produce a condition which inhibits the production of male organs and automatically brings about the nutritive conditions essential for pure femaleness. Femaleness is thus to be conceived as a response to a fairly definite nutritive condition—a condition, however, which may be produced by either one of two extreme types of culture and cultural conditions.

The major aspects of the whole situation, as it is conceived, are illustrated in Fig. 1. The lines, **a**, **b**, **c**, and **m** represent the varying relationships existing between the vegetative and reproductive states and carbohydrate content, as pointed out by Kraus and Kraybill[24]. That is, when plants are relatively low in carbohydrates they are vegetative; when carbohydrates accumulate in sufficient amounts they become reproductive. As a rule the young plant is vigorously vegetative and unproductive, this condition being asso-

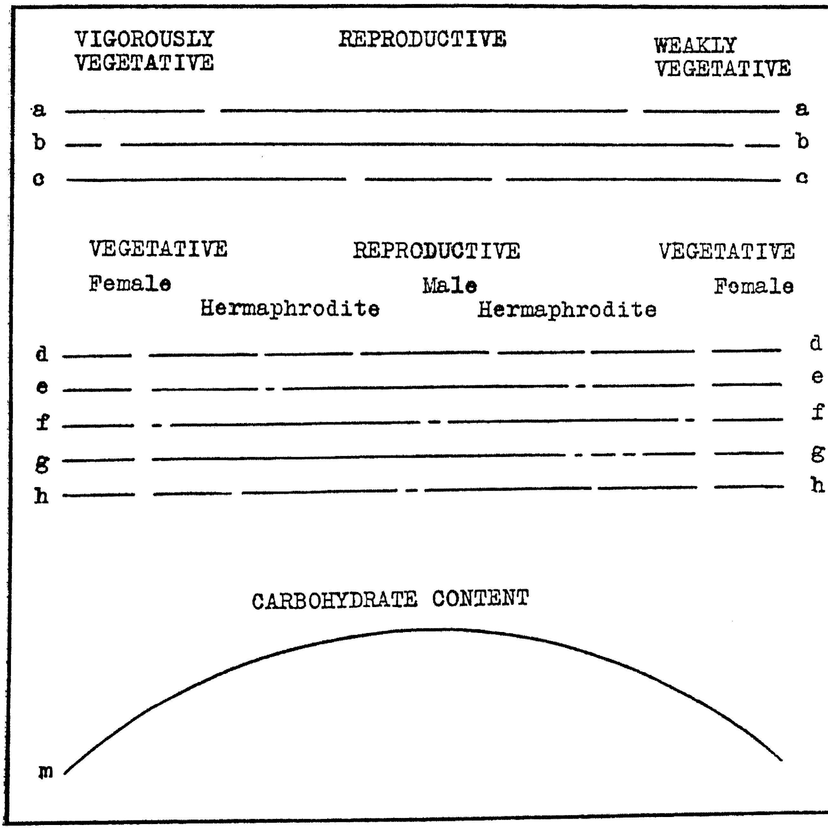

Figure 1.—Diagram illustrating the relation of nutritive conditions within the plant to vegetative and reproductive tendencies and to the development of the sexes.

ciated with or occasioned by the rapid utilization of carbohydrates in tissue building. In the presence of some factor or factors limiting new tissue building (i. e. growth) carbohydrates accumulate and the reproductive condition develops. Presumably this condition will continue as long as environmental conditions are favorable for carbohydrate manufacture that keeps pace with their utilization. Should utilization overtake manufacture, however, and the supply be seriously depleted the plant again becomes vegetative but this time weekly vegetative because of factors limiting both growth and carbohydrate manufacture. This is the condition so often found in old rapidly declining fruit trees. The varying length of the different parts of the lines, **a**, **b**, and **c** serves to bring out the point that some plants are reproductive within comparatively wide limits; for others there is apparently a comparatively narrow nutritive range within which they are fruitful.

Line **d** illustrates how still narrower fluctuations within the carbohydrate range accompanying the reproductive condition is associated with the development of the different sexes. With carbohydrate accumulation just above the point necessary to make the plant reproductive femaleness is developed. With greater accumulations maleness appears and the plant (or part of a plant) becomes hermaphrodite. With still greater accumulations femaleness is suppressed and maleness alone develops. When carbohydrate reserves decrease a similar series of sex changes takes place, but in reverse order. Line **d** represents the type of sex distribution often found in such species as *Diospyros kaki.* Line **e** will serve to represent the condition of a species such as the Muscadine grape that is classed as strictly dioecious but in which hermaphrodite individuals occasionally are found. Line **f** represents a typical hermaphroditic species in which pure pistillate or pure staminate forms are seldom or never found. Lines **g** and **h** together with **d**, **e** and **f** illustrate some of the many conditions found in those species which are more or less erratic in their sex development.

That varying nutritive conditions, particularly carbohydrate content often find expression in still other modifications of sexual development and interrelationships is probable. The production of cleistogamous instead of normal flowers in the violet during a part of the year may be a case of this kind. The frequent abortion of the first or the last flowers before they open and variations in self-compatibility as the season progresses, as found by Stout[36] in certain species of *Brassica*, are conceivably reactions to various nutritive conditions.

It is not to be presumed that carbohydrate accumulation alone is responsible for changes from the vegetative to the reproductive condition, or for the change from the unisexual to the bisexual form, or for instances of sex reversal. Probably other constituents and other factors are important. In many cases they may be the determining factors.

Furthermore, it is not to be assumed that a particular carbohydrate content, which in one plant is associated with maleness will necessarily be associated with maleness in another. In the second plant it may be associated with the hermaphroditic or female, or even the vegetative condition. As pointed out by Schaffner[32], there are some species in which changes in sex ratios or sex reversals are difficult if not almost impossible to bring about. May this not mean simply that, say, in a given species, the range in carbohydrate content within which the differentiation of male organs will take place is practically the same as that for the differentiation of female organs, or that the limits within which maleness alone will develop are so narrow that only rarely do we find a unisexual individual? Relative carbohydrate content, however, seems to be very important as an index of the direction of the plant's activities and the kind or kinds of structures it shall build. Particularly does it seem to be important in determining whether the plant shall be vegetative or reproductive and, if reproductive, whether the flowers shall be female, hermaphroditic or male. Fundamentally the initiation of the reproductive condition in the higher plants is nothing more nor less than the differentiation of sexual states from tissues in a neuter state. It is not surprising, therefore, that not only those general nutritive conditions, but that those particular compounds as well, that are associated with the differentiation of fruit buds are likewise associated with the determination of sex.

To what extent knowledge of the exact nutritive conditions that are associated with maleness or femaleness or hermaphroditism in those species in which sex changes are comparatively frequent, would be of value to the cultivator it is impossible to say. That it would be of considerable scientific interest is certain. That accurate information along this line might be put to good use in the culture of the various cucurbit crops and the Japanese persimmon is possible. It is also possible that it might furnish information that could be put to good use in dealing with the sterility question in many fruit varieties which experience shows are very variable in this respect.

SUMMARY

1. The results that have been reported on fertilizer investigations with the strawberry are more or less contradictory. This is due largely to a failure to differentiate between the effects of spring applications on the first following and on the second following crops.

2. The investigations here reported show that when moisture and temperature are not limiting factors, number of flower clusters, number of flowers and size of berries are dependent on nutritive conditions within the plant the preceding fall and winter and they are practically independent of soil fertility conditions during the spring and at the time of fruiting. Treatment that would increase production through modifying fertility, therefore, should be given during the summer and fall months.

3. Maximum production of flower clusters, flowers and berries was associated with those summer and fall treatments that led to the greatest accumulation of starch and total carbohydrates at the time of fruit bud differentiation.

4. Favorable nutritive conditions within the plant at the time of fruit bud differentiation, as influenced by soil the season before, led to somewhat better setting of the individual pistils of the flower and to the slightly better setting of the flowers. Fertilizer applications in the spring before blossoming had no clear-cut influence on these processes.

5. Size of berry is closely correlated with number of pistils per flower and the setting of these pistils. Both are influenced by soil condition the preceding fall and but little by fertilizer treatments shortly before fruiting.

6. There is a progressive decrease in number of pistils per flower, from the earliest to the latest flowers to open on the inflorescence. Apparently this decrease is uninfluenced by soil or fertilizer treatments, but the mean number of the pistils per flower may be increased.

7. Early removal of the primary, secondary and tertiary flowers of the cluster leads to the setting of later blossoms that otherwise would not set, but the resultant berries are small and yield is correspondingly reduced, because of the smaller number of pistils per flower.

8. Low carbohydrate and low starch content at the time of fruit bud differentiation led to the production of female flowers in a variety that normally is hermaphroditic.

9. It is suggested that variations in the relative carbohydrate content are responsible for changes in sex development, low carbohydrate content being associated with the female condition, high carbohydrate content with the male condition and an intermediate carbohydrate content with hermaphroditism.

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