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The Relation of Carbohydrates and Nitrogen to the Behavior of Apple Spurs

By

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INTRODUCTION

The investigations herein reported constitute two phases of a series of fruit spur studies being conducted by the Horticultural department. These studies are only a portion of a general problem which might be termed the nutritional changes in fruit trees as related to behavior and cultural practices.

In this work it has been considered necessary to abandon in a large measure the older type of field-plot methods in favor of a more detailed kind of laboratory study. It is no longer sufficient to divide up an experimental orchard into a number of plots, treat the trees of each differently, and then draw conclusions inferring that the treatments given hold a direct causal relation to the observed behavior. In order to arrive at more fundamental principles, much detailed knowledge must be acquired of the processes passing within the plant during the interval between application of treatment and the manifestation of the usual gross responses observed. Such is coming, fortunately, to be the attitude assumed by most investigators in horticultural science. But a study of these internal changes presents an aspect so multifarious that it is even difficult to decide what phase of the activities should receive first consideration.

The point of view of the work at this Station has been influenced strongly by the theory of the relation of carbohydrates and nitrogen recently advanced by Kraus and Kraybill[22]. The theme of this theory, that the behavior of a plant as regards growth and reproduction will depend to a considerable extent on the relative proportions of available carbohydrates and nitrogen, seemed to offer an excellent basis upon which to direct the beginning inquiries. It is perhaps unnecessary here to state that this theory of the relations of carbohydrates and nitrogen was not advanced as a panacea for plant nutritional problems, but rather to assist in stimulating, guiding, and interpreting such investigations.

In this respect it has already met with remarkable success. The importance and number of the other limiting substances and conditions to plant growth and reproduction are sufficient to prevent any horticulturist from seriously overlooking the limitations of the carbohydrate-nitrogen relations.

The experimental testing of the theory has been done only with herbaceous plants, but here with encouraging results. Kraus had obtained, however, some interesting and apparently rational inferences when he attempted to apply the theory in a deductive manner toward the interpretation of the behavior of fruit trees as reported in horticultural literature. It is largely on account of these latter considerations that the writers were influenced to attempt an experimental study of the carbohydrate and nitrogen relations in fruit trees.

Experimental work with fruit trees, however, involves many difficulties and aspects only slightly met with in the study of herbaceous plants. The latter respond more quickly, and practically as units, to various cultural and experimental treatments, while the different parts of a fruit tree behave in many respects as though they were independent individuals. Again the greater size of the tree and lesser percentage of active tissue present render slow the translocation of food materials, thus increasing the sluggishness of response. Associated with the perennial habit appears a relatively wide separation, in point of time, of the various phases of the activities of the tree as compared with the same events in annual plants. For instance, in the apple tree, the principal phases of reproduction occur at rather distinct times throughout the year; fruit-bud formation taking place in midsummer about the time that active growth ceases, blossoming occurring early the next spring, followed by fruit setting and the long period of fruit development. At any given time the tree as a whole usually represents a single phase of reproduction. Contrast this situation with that in the tomato plant where, in passing from top downward, one finds fruit-bud formation, blossoming, setting, and development of fruit taking place at the same time. These differences between typical perennials and annuals may be expressed briefly (though somewhat inadequately) by the statement that in the former there is a characteristic horizontal, and in the latter, a vertical succession of events. This might be considered as an experimental advantage in favor of the perennial plant, in that a horizontal succession permits a definite study to be made of each of the various phases concerned. The same should be possible in annuals, however, through careful selection of material from particular portions of the plant. Distinct disadvantages are encountered in other features of the perennial habit, such as the extended life cycle and the great seasonal variations in growth activities and food relations. Differences between two trees maintained under widely different cultural treatments, are not likely to be so great as the seasonal differences in a single individual. Hence it is not to be expected that the relations of carbohydrates and nitrogen will assume anything like a mathematical definiteness for the tree as a whole. The relations of these substances must vary considerably not only for different varieties under various environmental and other conditions, but also for different parts of the tree and for the individual part with the season.

In anticipation of some of the difficulties involved in the study of woody plants, the problem has been subdivided sufficiently to give rather small and specific phases for active investigation. It is the present aim in these spur studies to determine some of the inter-relations of the nutrient substances, particularly carbohydrates and nitrogen, in the spur, accompanying its usual activities; for example, growth, leaf and fruit-bud formation, blossoming, setting of fruit, and development of fruit. As means of controlling these activities of the spur, the writers are employing either common orchard practices or experimental methods closely comparable to them. For instance, defoliation has been employed in place of pruning. According to Magness'[26] results, defoliation appears to have much the same effect on the tree as a summer pruning which removes about the same leaf area.

Also in these studies, the question of food translocation to the spur has claimed considerable attention. This involves the relation of the spur to other parts of the tree, or, as often referred to, the "individuality" of this organ.

REVIEW OF LITERATURE

The literature relating to the two investigations reported in this bulletin will be discussed under three headings:

(1) Carbohydrate and nitrogen relations.
(2) Fruit-bud formation.
(3) Setting of fruit.

(1). **The Carbohydrate-nitrogen Relations.** Much of the literature significant to the recent conceptions regarding the relations of carbohydrates and nitrogen published previous to the work of Kraus and Kraybill[22] has been sufficiently reviewed by them and need not be referred to extensively here. The results of Kraus and Kraybill's work with the tomato appear to be the most important contribution to the subject in hand.

Almost simultaneously with these investigators, Fisher published a paper having an important and direct bearing on the question of the inter-relations of carbohydrates and nitrogen in plants. Studying the functions of vegetation and reproduction in relation to varying pressures of CO_2, Fisher[11] came to recognize the significance of the relative proportion of carbohydrates to nitrogen as a determining factor in these activities. When nitrogen was in abundance in respect to the carbohydrates, that is, when the value of the carbohydrate-nitrogen ratio was relatively small, vegetative activities followed, but if the value of this ratio was relatively large, reproduction took place. It is evident that these results and interpretations are closely in harmony with those of Kraus and Kraybill. Fisher's statement nevertheless is not nearly so clear cut as theirs, neither did he base his conclusions on definite chemical analyses nor make it clear that extremely high values of the ratio, due to very abundant carbohydrates and scarcity of nitrogen, arrest reproductive as well as vegetative activities.

Kraus and Kraybill have given us the most complete conception of the relations of carboydrates and nitrogen. Their studies on the tomato permitted the recognition of the following four classes into which a plant may fall as regards the proportion of its available carbohydrates and nitrogen.

Class I. Here the carbohydrate supply is small enough to be the limiting factor, but nitrogen may be very abundant. The result of such a relation of carbohydrates to nitrogen in the plant is a restriction of both vegetative and reproductive functions.

Class II. The nitrogen supply is abundant as in Class I, but the carbohydrates have increased greatly so that they are no longer the limiting factor. The plant becomes vigorously vegetative but has slight tendency to become sexually reproductive.

Class III. Carbohydrates have become very abundant and the nitrogen supply inadequate for full vegetative activity. The carbohydrates have increased, probably on account of the slightly limiting supply of nitrogen (see Hartwell[16]). Vegetative development is now restricted but the conditions are very favorable for sexual reproduction.

Class IV. Carbohydrates are very abundant, due to the nitrogen supply which is now quite the limiting factor. All activities of the plant are greatly retarded, so that both vegetation and reproduction have practically ceased. Thus the results of the conditions in Class IV are the same as those in Class I, although the relations of carbohydrates to nitrogen present the reverse extremes.

The exact limits of the foregoing classes cannot be definitely fixed on account of the nature and number of the factors involved. Axiomatically any of the essential elements; namely, moisture, probably many other specific substances, temperature, etc., could become controlling factors. But when this classification is accepted in the general sense, it seems capable of rendering valuable assistance, at least temporarily, in the interpretation of plant responses.

The work of Kraus and Kraybill has already received some substantiation from the studies of several investigators. Recently Gujar[15] announced similar results for tomato, turnip, and radish. In addition to the determination of the relative proportions of carbohydrates and nitrogen accompanying the gross responses of these plants, it was found that respiration varied approximately directly with the value of the ratio of carbohydrates to nitrogen, while photosynthesis and the chlorophyll content varied inversely with it.

Woo[38] also examined this carbohydrate-nitrogen ratio in the course of his study of the storage of nitrates by *Amaranthus retroflexus*. Large amounts of carbohydrates were found to be accompanied by low amounts of nitrogen and vice versa. He felt, however, that the actual value of the ratio is not of great significance on account of its lack of exactness.

Although, as stated before, no experimental application of the carbohydrate-nitrogen theory has apparently been made to woody plants,*

*Since preparing this manuscript, a bulletin by Hooker has come from the Missouri Station (Res. Bul. 40), presenting the results of a study of seasonal chemical changes of three classes of apple spurs: fruiting, fruit-bud forming, and barren. This work is a valuable contribution to our knowledge both of seasonal processes in the apple tree (as studied by Butler et al.), and of the detailed physiology of spurs (subject of the present report). Hooker has followed seasonal changes in apple spurs as regards: carbohydrates, nitrogen, potassium, phosphorus, and acidity. Characteristic seasonal variations in the relations of these substances in the three classes of spurs, afforded evidence for the following conclusions: that fruit-bud formation is associated with high starch and low nitrogen content; leaf-bud formation, with low starch and high nitrogen; and barrenness, with low starch and low nitrogen. Other variations of acidity, carbohydrates, phosphorus, and potassium, etc., are very instructive. Further reference will be made to this starch-nitrogen ratio, as suggested by Hooker, in the discussion on "Effect of Defoliation on Fruit-Bud Formation."

some idea of the normal seasonal variations of the relations of these substances in apple trees may be obtained from the recalculation of certain data published by Butler, Smith, and Currey.[5] These investigators give separate analyses of carbohydrates, nitrogen, and other substances for eight different portions of the apple tree at five periods of the year. The recalculations of these data have been expressed by means of graphs which show the seasonal variations of total carbohydrates, nitrogen, and the carbohydrate-nitrogen ratio for different parts of the tree. These

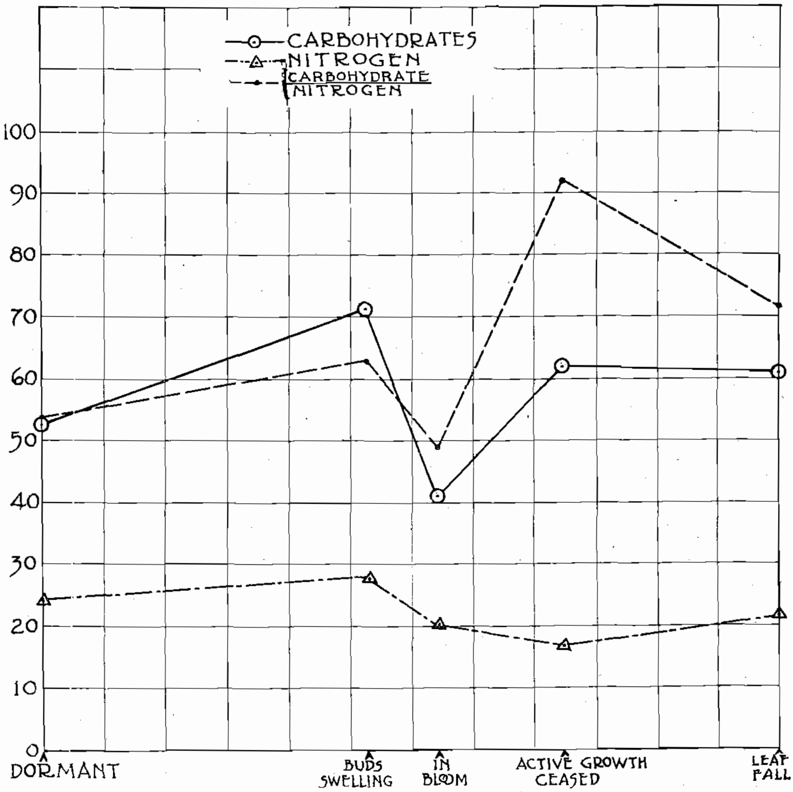

Fig. 1. Graphs* recalculated from data published by Butler et al[5]., showing average seasonal variations of total carbohydrates x 2, total nitrogen x 50, and the carbohydrate-nitrogen ratio.

graphs are of considerable interest when viewed in relation to the general seasonal activities of the apple tree. Figure 1 shows a series of such graphs which are averages of those for all parts of the tree. It will be noticed that nitrogen reaches a minimum about the time "active growth ceases," from which point it steadily increases during the summer and winter periods to the time of "buds swelling." This maximum is followed by a rapid fall during the time of blossoming and active vegetative

* The writers are indebted to Mr. F. J. Rimoldi, Assistant Pomologist, for the drawing of the graphs of this bulletin.

growth. The carbohydrate graph appears to be anomalous in having a second maximum at "buds swelling." A graph representing starch would normally show a secondary maximum at that period, but surely not for one of total carbohydrates including other hydrolyzable polysaccharides (as this one apparently does). The calculated values of the carbohydrate-nitrogen ratio show a large maximum in midsummer and a secondary maximum at "buds swelling." This latter undoubtedly is due to the anomalous carbohydrate maximum at that time and would be changed to a *minimum* for the same period if the questionable carbohydrate maximum were removed by allowing a steady falling off of total carbohydrates from midsummer to the blossoming period. Other features of these graphs will receive consideration at the close of the report on "Effects of defoliation on the setting of fruit."

(2). **Fruit-Bud Formation.** The most important factor involved in fruit-bud formation is generally assumed to be the nutritive supply to the bud primordia. This point has been clearly brought out by Wiggans[37] in his review of the literature relating to this subject. While some of the older observers suggested causes for fruit-bud formation that appear quite illogical at the present time, even these men, in the main, felt that the supply of nutritive materials had the largest controlling influence on fruitfulness. In recent years more exact experimental methods having been introduced into horticultural inquiry, considerable information on the question has come to hand. The results of such investigations have firmly established the nutritive theory of fruit-bud formation, though the details of the specific nutritive effects remain largely unknown. Studying the details of flower formation in Sempervivium, Klebs[20] divided the processes into three stages, each based on light and temperature as controlling factors. These stages are: (1) production of sufficient maturity in the plant, (2) development of flower primordia, and (3) formation of the inflorescence. Light is considered the effective agent in flower formation, mainly on account of photosynthesis, and the resulting accumulation of carbohydrates. It is in the second stage only that light is assumed to be partly effective as a formative stimulus. Thus the problem of flower formation is returned largely as a nutritive one.

The more recent types of experimental investigations have been made easier through the basic studies of Goff,[12] Kraus,[21] Bradford,[4] and Magness,[26] in which they have determined with accuracy the time when fruit-bud differentiation takes place. Their results show that fruit-bud formation begins in the apple in early summer, about the time active growth in the tree ceases, but may continue throughout the summer. Bradford[4] has shown that fruit buds of the apple differentiate earlier on spurs than on other parts of the tree—for example, terminals of the current year. But fruit-bud formation may be considerably delayed on a spur which has bloomed the preceding season.

The largest amount of evidence that nutrition is the important factor in fruit-bud formation has come through the observation of blossoming and bearing responses made during the course of numerous investigations on pruning, cultivation, fertilization, and thinning of fruit, etc. The studies of Gourley[14] and Drinkard[7-8] are representative of the better type of work on some of these questions. Again much evidence comes from the results of more detailed laboratory experiments in which the food reserves in the spur have been under examination. Of this latter type of work, that of Wiggans[37] offers a good example. He found that sap of bearing spurs contained more dissolved substances than the sap of non-bearing spurs. Chemical analysis indicated that this was partly due to larger amounts of sugar and starch in the bearing spurs. Remy-Bonn,[33] on the other hand, concluded from his study of nitrogen in the leaves of bearing and non-bearing trees, that this substance is of primary significance in fruit-bud formation.

Magness[26] and Roberts[35] have contributed to the problem, in showing the dependence of fruit-bud formation upon the activities of adjacent leaves. Results similar to this had previously been recorded by Goumy[13] in France. Spurs have thus been found to possess slight ability to produce fruit buds after having been deprived of their own leaves through defoliation. These results point to the importance of carbohydrates in the process.

Careful observations of the normal habits of individual apple spurs by Bradford,[4] Wiggans,[37] Auchter,[2] Roberts,[35] and others, have shown that a very small percentage of spurs blossom in successive seasons. This fact itself strongly suggests the nutrition factor. Blossoming in alternate seasons is the general rule. Yet many spurs do bloom successively, and this ability varies greatly with the variety. Jonathan, for example, appears to possess this ability in a high degree. Successive blossoming is more likely to happen if fruit fails to set the preceding year. Auchter[2] noticed that if the spur holds this fruit only to the "June drop" the effect is about as repressive on fruit-bud formation as though the fruit had been developed to maturity.

The foregoing investigations not only indicate the importance of the nutritive factor, but they also point to a very delicate balance in the nutritive relations in the spur just previous to and accompanying the beginning stages of bud differentiation. At such time the spur would seem to be very dependent upon its own leaf system for throwing the balance in favor of fruit-bud formation. This latter involves the question of "individuality" of the spur and will be taken up later.

(3). **Setting of Fruit.** Many factors are known to prevent the setting of fruit. Of these the lack of certain nutrient substances, particularly carbohydrates, has of late received emphasis. In this respect, a certain amount of foliage, as a source of immediately available carbohydrates, either to the tree as a whole, or to the fruiting spurs, has been found to be of the greatest consequence. Under certain circumstances, however, an increased supply of nitrates to the tree shortly before the time of blossoming has produced very favorable results.

Much information on the relation of nutrition to reproductive functions of horticultural plants may be extracted from older horticultural literature, particularly French and English. Most of it is, however, of an empirical nature. Quantitative investigations of the effects of nutrition on the setting of fruit may be said to have begun with Klebs[20] and Muller-Thurgau.[28] The former has considered the more theoretical side of the subject, while the latter has investigated its application to horticultural practice. As early as 1897 Muller-Thurgau[28] demonstrated that nutrition is one of the main factors in the setting of fruit of the grape. When the vines were ringed 10 to 14 days before blossoming, fruit setting was enhanced above the point of ringing. Very few blossoms set below this point, and such as did were incomparably smaller in size, contained less sugar and more acid. It may be remembered here that the effect of ringing of fruit trees has since then been carefully recorded by Howe,[19] Drinkard,[7,8] Hibino,[18] and others.

Muller-Thurgau[28] believes that setting of fruit follows the growth of the pollen tube into the pistil, fertilization not being absolutely necessary, wherefore many seedless fruits. But for the development and growth of the pollen tube into the pistil a certain amount of carbohydrates is absolutely indispensable. Weather conditions may often prevent the transformation (hydrolysis) of carbohydrates, thus creating a shortage at the time of fertilization. Moreover, in the constant struggle for nutrients the weaker blossoms will not be able to obtain enough nourishment, or, because of lack of carbohydrates, growth of the pollen tube will be prevented. Hence the loss of blossoms. In the case of a diminishing food supply this drop may be very extensive. The presence of seeds in the fruit is of tremendous assistance in this struggle. This emphasizes the value of fertilization. Data from defoliation experiments indicate that setting is dependent upon the supply of carbohydrates to the blossoms.

What was true with the grape was found by Muller-Thurgau[28] to be true also with other fruits. Blossoms will not set if sufficient organic substances are not available. And as most of these come from the leaves, any external or internal factors influencing the size or condition of leaves will determine the production of fruit.

In agreement with the results of Muller-Thurgau,[28] Ewert [9-10] points out that more blossoms are always formed by the tree than can possibly be nourished and that dropping of flowers is due largely to lack of food supply. But because of the possibility of parthenocarpic development of fruit, which was proved to take place in many varieties of pears and apples, the abscission of blossoms is not due to lack of pollination or fertilization, but is the direct result of poor nourishment. In the competition for food supply, fertilized blossoms have, however, a superior advantage over unfertilized.

To determine the relation of fertilization to dropping, Osterwalder[29,30] conducted a series of microscopical and histological studies with blossoms of several varieties of pears and apples. No causal relation was found to exist between fertilization and falling of blossoms. He, too, believes that fruitfulness is dependent upon the condition of nutrition of the tree, the stored nutritive substances available for the developing blossoms, or the ability to translocate such substances. The author, however, does not state or define what he means by condition of nutrition (Ernahrungszustand).

Manaresi and Tonegutti,[27] analyzing twigs of the pear, apple, plum, and cherry, found that fruit-bearing wood was much higher in organic substances than wood that carried only foliage. A few years previous Loew[25] analyzed the bark of cherry trees for seven consecutive seasons before and after blossoming of the trees and showed that as a result of the setting of flowers, protein had diminished 37.16 percent, fat 30.35 percent, and starch 40.59 percent.

In the meanwhile, working with the grape, Reviere and Bailhache[34] came to the conclusion that a strict relation exists between leaves next above a cluster of grapes and their sugar content. When 0 to 5 leaves were left above a cluster, sugar decreased in proportion to the number of leaves left, up to 5, after which the amount of sugar remained stationary, while acidity decreased in the same proportion. The same authors found that in the case of pears, the weight of the fruit, its sugar content, and acidity are dependent upon the leaves of the spur.

The more recent studies of Coit[6] show quite opposite results. Various amounts of defoliation of twigs with terminal fruit (orange) had but a slight influence upon the average weight and total solids of the fruit as tested at maturity.

Comparing measurements of the fruit and foliage of nine hundred seedling strawberry plants, Pickett,[32] however, obtained positive proof that a strict correlation exists between the total production of fruit and the total amount of foliage per plant. A close relation was also found to exist between the number of leaves and berries.

Similarly Auchter[2] observed that when rust had caused the dropping of all leaves on certain apple trees, fruit remained small—the size of walnuts—throughout the season. Considering individual fruits, he found that the number and weight of seeds seemed to be correlated with the weight of the fruit. If, however, the tree produces a large crop, the seeds will not be able to overcome the general shortage of food supply—the fruit, though showing considerable individual variation, will be small.

The rather detailed experiments of Heinicke[17] have brought out a number of interesting points on this subject. Among other things, he says that spurs set fruit in direct proportion to the size of leaves on them. If the growth of a spur during the preceding season is more than one centimeter, it has a greater tendency to set fruit. Defoliation of spurs before the opening of flower buds will restrict fruitfulness. If, however, only two leaves are left per spur, the set will be almost normal. The diameter of the conducting vessels and the water supply to the spur have a direct bearing upon setting. Heinicke[17] concludes *(loc. cit.* p. 111*)* that judging from the observations and experiments conducted by him, unfavorable conditions of nutrition and water supply are two of the basic factors causing the normal drop of flowers and partly developed fruits of the apple. Pollination, weather, cultivation, and any other factors that have a direct or indirect bearing on nutrition and water supply to the flowers and the fruits are naturally of importance.

It will be observed that all of the foregoing evidence points to carbohydrates as the possible nutritive substances affecting or determining fruitfulness. But in view of the recent considerations of the relation of carbohydrate and nitrogen—as discussed elsewhere in this bulletin—it is but natural to expect that not only carbohydrates, but the absolute or relative amount of nitrates or nitrogen may frequently be the limiting factors in setting of fruit. Kraus and Kraybill[22] have demonstrated this to be the case with the tomato, although, because (we assume) of the nature of the material used, they do not make a clear-cut distinction between the effects of relative amounts of carbohydrates and nitrates on fruit-bud formation and on setting of fruit.

In this respect the nitrate fertilizer experiments of Lewis and Allen[23] and Lewis and Brown,[24] are of particular significance. Nitrate of soda, applied either as crystals or sprayed on the ground, had a profound influence upon devitalized apple tees. Fruit setting was increased at once to a remarkable degree, in many instances sevenfold. Moreover, the fruit was larger and of better color, and the vegetative growth, both of twigs and leaves, was enhanced in a most striking manner. The fertilizer was applied in March, or about a month before the flowers opened. Very little benefit was derived from fertilization in May. No mention is made of the effects of the treatment on fruit-bud formation, but it is stated that the trees have always borne an abundance of blossoms. No chemical analyses of any part of the trees were made either before or after fertilization. From the foregoing results it appears that while other nutritive substances may have been quite adequate for fruit-bud formation, the lack of nitrogen at the time of setting of fruit acted as a limiting factor.

Petri[31] obtained similar evidence in his studies on the olive. A relative abundance of carbohydrates over nitrogen may create desirable conditions for fruit-bud formation, but a further reduction of the nitrogen supply will prevent the setting of fruit. This may express itself in sterility of the flowers due to incomplete development of the ovary. Chemical analysis showed that fertile branches contained approximately three times as much nitrogen as those not setting fruit.

The comparatively recent observations and investigations of Wiggans[37] and Roberts[35] are of particular value here. They bring forward new facts and throw additional light on this subject.

Wiggans[37] points out the great demand on food substances at the time of blossoming and fruit setting. Tests taken of Jonathan spurs, bearing and non-bearing the same year and bearing and non-bearing the previous year, showed that sap from spurs bearing fruit during the current year is slightly more concentrated than from non-bearing spurs. No seasonal variations were noted at the time of setting of fruit, but there is a great drop in sap concentration during the period of fruit-bud differentiation (June to July). Chemical determinations of total sugars and starch did not reveal any striking differences as to accumulation of these substances in bearing and non-bearing spurs, although in the former they were in slightly higher amounts. Sap taken from spurs bearing three, two, and one fruit, respectively, showed upon testing that the number of fruits on a spur affects the concentration of neither spur nor leaf sap. Measurements of leaves of several varieties of apples indicated that in all cases the number of leaves and average leaf area is greater in non-bearing than bearing spurs. The average size of the individual leaf was found, however, to be approximately the same, the increase in area coming from the increase in number of leaves per spur.

Though not touching directly upon the question of fruit setting, the investigations of spur growth and off-year bearing habit of the apple by Roberts[35] are very significant. Emphasizing the individuality of the spur, he shows that it is dependent upon local nutrition or the adjacent leaves. Close correlation was found to exist between the length of the spur and fruitfulness. On the average, medium long spurs, from ½ to 1¼ cm., bear most frequently. There is a great variation in length, however, of spurs blossoming or fruiting in successive years. The production of blossoms has a decided effect upon the amount of secondary growth of the spurs. This, he believes, explains at least in part the biennial bearing habit of the tree. The leaf area produced by secondary growth of a spur that was permitted to develop its fruit either to the "dropping stage" or to maturity was only half of that on spurs from which blossoms were removed.

Since Roberts shows that correlation exists between the length of the spur and fruitfulness and also between length of spur and leaf area, and knowing the importance of the adjacent leaf area as a source of food supply to the developing fruit, we can assume that a correlation exists between the leaf area on the spur and fruitfulness.

I. EFFECT OF SPUR DEFOLIATION ON THE FORMATION OF FRUIT BUDS

By

E. M. HARVEY

The specific aim of this study was to determine to what extent the leaves of the individual apple spur control its metabolism, as reflected in the relations of carbohydrates and nitrogen and the formation of fruit buds.

MATERIAL

Spurs utilized in this study were of the varieties Wagner, Grimes, and Jonathan. The trees furnishing them were seven years old and apparently in good condition.

In planning the experiment the spurs were separated according to their performance, into three general groups: (1) non-blossoming, (2) blossoming without setting fruit, and (3) blossoming and setting fruit. The first group would appear as the most fitting for a study of fruit-bud formation, but it was soon found that the heavy bloom of 1919 left too few spurs of this class for a satisfactory chemical examination. In fact for this purpose, sufficient material would not be available unless groups (2) and (3) could be combined. It was finally decided that these groups might be so combined if the fruit were removed from group (3). Accordingly the fruit was removed, the work being performed about the beginning or middle of the "June drop." It should be noted in this connection, however, that results of other investigations indicate that the fruit was probably removed too late to bring about a complete merging of groups (2) and (3). The condition of the spurs used is shown in Fig. 2.

A total of about 7,000 spurs were taken for analysis, and these were procured from ten trees of each variety, and proportioned among the varieties as follows: 1500 Grimes, 2500 Wagener, and 3000 Jonathan. Each tree furnished 150 to 300 spurs, depending upon the variety. One half of the total number of spurs were defoliated and de-fruited, and the other half de-fruited as checks. The date of defoliation and de-fruiting was June 12-16, 1919. To avoid mechanical injury to the spur, the two operations were performed with scissors, the petioles and pedicels being cut at a little distance away from the spur. Later the petiole and pedicel bases were cast off naturally by the formation of abscission layers.

Collection and Preservation of Material. Three general collections of spurs were made: the first, at the time of defoliation, June 16 and 17; the second, two weeks later, July 1 to 5; and the third, about five weeks after defoliation, July 23 to 26.

For the chemical samples all spurs were divided, at the time of collection, into two portions; the growth made in 1919, and growth made in previous seasons. The first were called "new growth," the second "old growth." Of course "new growth" samples also included the buds.

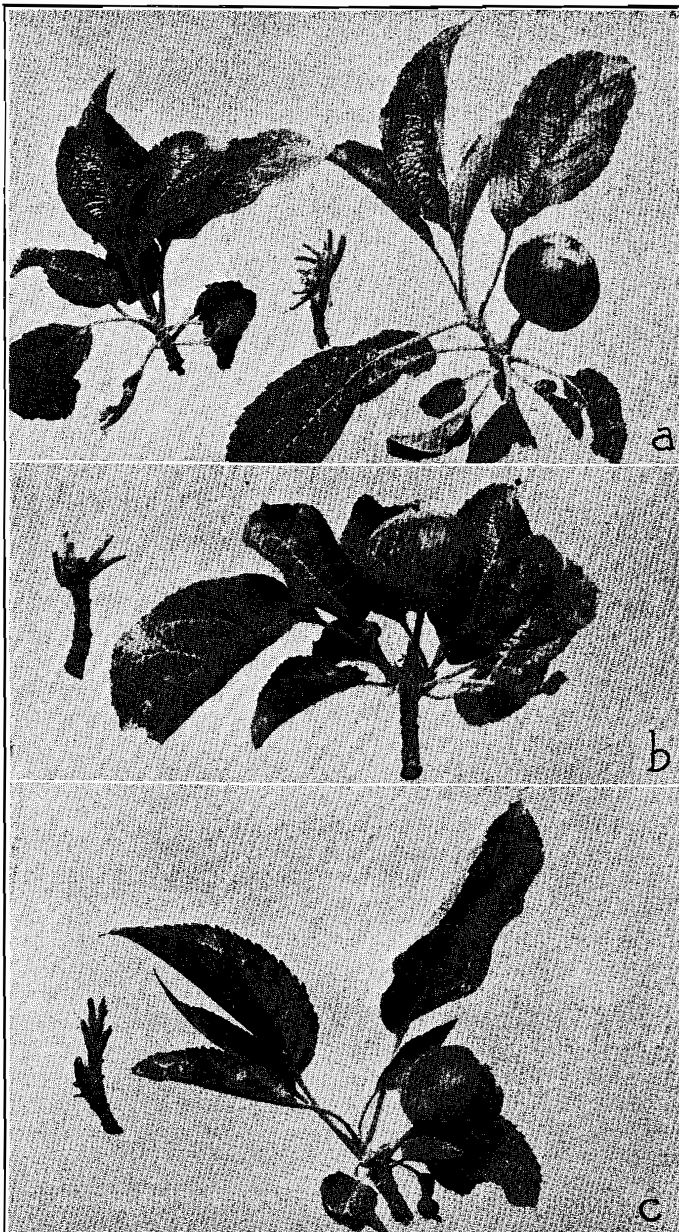

Fig. 2. Spurs, showing the seasonal development of leaves and fruit at the time defoliation and defruiting were performed. (a) Jonathan, also one spur as immediately after defoliation; (b) Wagener; and (c) Grimes.

First collection samples of each variety consisted simply of "new" and "old" growths while those of the second and third were made up of defoliated—"new" and "old," and check- "new" and "old." Duplicate samples were taken throughout for Jonathan and Wagener.

Collection procedures were always carried through as rapidly and systematically as possible. Spurs were cut from trees, the leaves removed from checks (also defoliated spurs had sometimes developed a few small leaves); the spurs themselves were then cut into "new" and "old" portions, and placed in separate wide-mouth bottles, which were kept tightly stoppered between additions of material. The samples were afterwards brought to the laboratory, where the fresh weight was determined. The samples were immediately covered with enough 94-percent alcohol (redistilled) to make the final concentration about 80 to 85 percent, allowing for the water in the tissue; to each was added one gram of calcium carbonate, and the whole placed in a water bath at 70° C. for one hour. Wet weights of "new" and "old" samples varied from 60 to 120 grams and 96 to 154 grams respectively. The rather large size of samples was considered desirable in order to make them thoroughly representative, and on account of the difficulties previously experienced by the writer in the determination of nitrate nitrogen in apple tissue.

METHODS OF ANALYSIS

Anatomical

Microscopic examinations to determine the amount of flower-bud differentiation were made upon the "new" growth chemical samples of the third collection. A representative number of spur parts carrying buds were removed singly from the alcohol; placed upon a lantern-slide cover-glass on the stage of a binocular microscope and there dissected. This lantern-slide cover-glass had a ridge of paraffin built around its margin to prevent an overflow of the preserving alcohol which would of course have many substances in solution. As soon as the presence or abscence of flower parts had been recorded, the dissected material was transferred quantitatively back to the bottle. Dissections were made under a magnification of either 57 or 88 diameters, usually the latter.

Chemical

The chemical analyses reported here have been made very painstakingly; partly on account of the fact that the results of previous workers on the analysis of woody tissues of the apple tree gave little reason to hope for very large variations in such a case as the present. In fact, many things pointed to the improbability of determining, by the chemical means at hand, the small metabolic changes as could likely be induced in spurs by defoliation. The results in the present case, however, have been gratifying in several respects.

Extraction. All samples were separated into hot-alcohol soluble and insoluble fractions before proceeding with the detailed analyses.

The entire preserved sample was transferred to a large filter funnel and the liquid allowed to filter through. The solid tissue was then washed on the filter several times with fresh alcohol and placed in an oven at about 80° C. After 6 to 10 hours this material was ground to powder in a mill and transferred quantitatively to a special large-size extraction apparatus capable of handling 250 c.c. of dry powder. The extraction was of the continuous type and carried on in two periods: the first, for three hours with about 300 c.c. of alcohol, and the second for twenty-three hours with about 400 c.c. of alcohol. Total extraction time, therefore, was twenty-six hours. The two extractive lots were added to the original preserving filtrate; this after being made up to 1000 c.c., constituted the hot-alcohol soluble fraction. The insoluble fraction was the residue remaining in the extraction thimble.

Dry Weight. Dry weights were determined on the soluble and insoluble fractions separately. An aliquot part dried in vacuo gave dry weight of the former, while that of the latter was determined on a representative sample of the air-dry material. A dry-weight factor was then used to correct all air-dry weighing for other determinations. The total dry weight was obtained by adding the dry weights of the two fractions.

Nitrates. Nitrate nitrogen was determined on 350-c.c. portions (made alcohol-free) of the soluble fraction, using the Allen-Metscherlich-Devarda reduction method. This method was found to be far superior to any modification of the Tiemann method because the nitrate nitrogen is present in such small amounts, and associated with so much organic matter. The Allen[1] method was followed practically as published, though a number of details had to be modified for best results; for instance, total reduction of nitrates could not be obtained where known amounts of nitrates had been added to strong solutions of apple tissue unless three to four times Allen's recommended quantity of Devarda Alloy was used. Again, a partial precipitation of tannins, etc., with a little basic lead acetate was found necessary to prevent too great frothing even with the addition of paraffin. At first a substitution of ordinary glass tubing for Allen's quartz distilling tube was attempted, but the results not being satisfactory a heavy-walled quartz tube of the Folin type was procured. It should be noted that the 350-c.c. portions used for nitrates were taken in duplicate and each was equivalent to 35 to 55 grams of fresh material.

Total Nitrogen. Total nitrogen determinations were made separately for the two fractions by the Kjeldahl method as modified by Gunnin-Arnold. Total nitrogen analyses of the soluble fraction were made upon the same portions as used for nitrates. For the insoluble fraction 1.5 grams of the air-dry powder were used.

Carbohydrates. (1) *Reducing sugars.* Fifty-c.c. portions of the soluble fraction were freed from alcohol and used for determination of reducing sugars. The official procedure was followed throughout, except that the copper was determined by the provisional Bertrand permanganate titration method, which the writer has employed for several years. The n/20 potassium permanganate solution was standardized against a standard sugar sample from the United States Bureau of Standards. All sugars were calculated as invert sugar.

(2) *Total sugars.* Fifty-c.c. portions of the soluble fraction were freed from alcohol and hydrolized by the official hydrochloric-acid method for ten minutes at 69° C. Sugars were then determined as for reducing sugars.

(3) *Total polysaccharides.* Starch and other hydrolizable polysaccharides were determined on one-gram portions of the insoluble fraction. These samples were placed in 2-litre, round-bottom, short ring-neck flasks and to them were added 200 c.c. distilled water and 20 c.c. hydrochloric acid (sp. gr. 1.125). The solutions were boiled under a reflex condenser for exactly three hours. The resulting red solution was then cooled, neutralized, filtered into a 300-c.c. volumetric flask, the residue washed on the filter and made up to volume. Fifty-c.c. portions were used directly for the determination of total hydrolizable polysaccharides calculated as invert sugar.

PRESENTATION OF RESULTS

Fruit-bud Formation

Comparative microscopical examinations of defoliated and check spurs clearly show that defoliation during June hindered the formation of fruit buds for the ensuing year. Table I gives the relative percentage of fruit buds differentiated on the two types of spurs at the end of July. Comparing the record of performance of check and defoliated spurs it is clear that the formation of flower parts has been greatly retarded in the latter. These results are in agreement with the previous findings of Magness,[26] but are a little more convincing, perhaps, on account of the much larger number of spurs under observation in the present experiment.

TABLE I. EFFECT OF DEFOLIATION ON THE FORMATION OF FRUIT BUDS

Variety	Treatment	Percentage of fruit buds	Performance of defoliated spurs (checks as 100%)	Number of buds examined
Jonathan	check	16.0	......	116
	defoliated	6.2	38.7	110
Grimes	check	13.0	......	99
	defoliated	7.1	54.6	129
Wagener	check	18.1	......	118
	defoliated	10.6	58.6	137

It will be noted that the three varieties differ in sensitiveness to the defoliation effect. Jonathan spurs after defoliation were able to produce only 28.7 percent as many fruit buds as those having their own leaf system. The defoliated Wagener and Grimes spurs were more nearly able to approach the performance of their checks. Their records were 58.6 and 54.6 percent respectively. The Jonathan spur may therefore be considered as more dependent upon its own leaf system for fruit-bud differentiation than either of the other two varieties, yet the others show a distinct "individuality," the Grimes being somewhat more "individual" than the Wagener. A better expresson of this individuality of the spur in respect to fruit-bud formation may be had by subtracting from 100 the percentage values given above. The three varieties are thus shown to be dependent upon their own leaf systems to the following degrees: Jonathan 61.3 percent; Grimes 45.4 percent, and Wagener 41.4 percent.

One of the showings of Table I may at first sight seem a little surprising. This is the rather large percentage of fruit buds developing on the spurs as a whole, since it will be recalled that all these spurs under observation had bloomed the current season and many had set fruit (although the fruit was later removed). The explanation probably lies partly in the fact that all three of these varieties are rather annual bearers in this region. In this connection it is interesting to note a coincidence of figures for the observed performance of Jonathan check spurs with those reported for the same variety by Wiggans[37] who observed in Missouri that 15.8 percent of the spurs bloomed in 1914 after having bloomed in 1913.

Chemical Analysis

In connection with the presentation of data from the chemical analyses the writer wishes to state again that every available precaution was taken throughout all procedures. The spurs also were carefully selected in the orchard and equal numbers of check and defoliated spurs were removed from each tree. Large samples were taken not only in order to furnish sufficient material for analysis but also to reduce, in so far as possible, the fluctuations due to unknown factors. All numbers

TABLE II. PERCENTAGES OF MOISTURE AND SOLIDS IN APPLE SPURS

(On basis of fresh weight)

Portion analyzed		"Old Growth"			"New Growth"		
Treatment	Date	Moisture	Substances soluble in hot alcohol	Substances insoluble in hot alcohol	Moisture	Substances soluble in hot alcohol	Substances insoluble in hot alcohol
			Jonathan				
Check	June 16	52.9	9.74	37.39	55.6	8.90	25.50
	July 5	50.3	10.13	39.57	60.3	9.81	28.89
	July 25	49.9	9.52	40.58	58.9	9.13	31.92
Defoliated	....	......	......	......	......	......	......
	July 5	52.1	9.74	38.16	63.3	9.21	27.49
	July 25	51.2	9.42	39.40	61.3	9.07	29.54
			Grimes				
Check	June 16	52.1	9.36	38.54	55.7	9.32	24.93
	July 5	49.9	9.73	40.37	58.3	10.27	30.90
	July 25	48.5	9.48	42.08	55.7	9.36	34.87
Defoliated	....	......	......	......	......	......	......
	July 5	52.3	8.80	38.90	62.5	9.24	28.26
	July 25	49.5	9.23	41.09	58.6	8.94	32.46
			Wagener				
Check	June 17	53.7	8.68	37.62	55.3	9.57	25.11
	July 3	53.1	9.04	37.86	63.3	10.13	26.57
	July 26	50.9	8.88	40.20	57.7	10.02	32.24
Defoliated	....	......	......	......	......	......	......
	July 3	53.7	8.85	37.45	63.6	9.75	26.65
	July 26	52.7	8.73	38.57	59.7	8.72	31.58

presented in the tables are the averages of at least two determinations and sometimes four. In Table VI, in which are combined the results of the second and third collections, the averages (with the exception of those for nitrates) represent eight to sixteen determinations. The percentage differences between check and defoliated spurs of the same collection are not usually great, yet the results of the individual determinations have shown a consistency which leads to the belief that the directions indicated by the averages are, in the main, real.

Moisture and Soluble and Insoluble Solids. The amount of moisture, and hot-alcohol soluble and insoluble substances are presented in Table II.

The moisture content of both check and defoliated spurs diminishes steadily through the experimental period, June 16 to July 25. But the defoliated spurs show a higher moisture content than the checks. Of course only collections of corresponding dates should be compared. The same moisture relations hold for all varieties and both "old" and "new" portions of the spur. Differences between varieties are not large, though Wagener spurs appear to have slightly the greatest moisture content in both lots.

The soluble substances, in both check and defoliated spurs, show maxima on July 5 in all varieties. This falling off of soluble substances

TABLE III. PERCENTAGES OF NITROGEN IN APPLE SPURS

(On basis of total dry weight)

Portion analyzed		"Old Growth"				"New Growth"			
Treatment	Date	Nitrate nitrogen	Soluble nitrogen minus NO_3-N	Insoluble nitrogen	Total nitrogen	Nitrate nitrogen	Soluble nitrogen minus NO_3-N	Insoluble nitrogen	Total nitrogen
				Jonathan					
Check	June 16	....	0.089	0.694	0.783	....	0.384	1.418	1.802
	July 5	0.000	0.037	0.675	0.712	0.072	0.226	1.229	1.455
	July 25	....	0.056	0.614	0.670	....	0.150	0.984	1.134
	....	....	....	....	....	....	....	....	....
Defoliated	July 5	0.024	0.089	0.703	0.792	0.156	0.504	1.292	1.796
	July 25	....	0.063	0.671	0.734	....	0.281	1.228	1.509
				Grimes					
Check	June 16	....	0.076	0.630	0.706	....	0.281	1.136	1.417
	July 5	0.014	0.047	0.548	0.595	0.038	0.144	0.827	0.971
	July 25	....	0.061	0.614	0.675	....	0.099	0.843	0.942
	....	....	....	....	....	....	....	....	....
Defoliated	July 5	0.022	0.069	0.522	0.591	0.121	0.325	1.113	1.438
	July 25	....	0.067	0.557	0.625	....	0.252	0.997	1.249
				Wagener					
Check	June 17	....	0.113	0.736	0.849	....	0.287	1.345	1.632
	July 3	0.038	0.076	0.651	0.728	0.094	0.223	1.168	1.391
	July 26	....	0.090	0.650	0.740	....	0.177	1.005	1.182
	....	....	....	....	....	....	....	....	....
Defoliated	July 3	0.041	0.089	0.692	0.781	0.126	0.325	1.277	1.602
	July 26	....	0.093	0.636	0.729	....	0.240	1.104	1.344

perhaps corresponds to the summer lowering of sap concentrations in spurs as noted by Wiggans.[37] A comparison of amounts of soluble substances in check and defoliated spurs reveals considerable fluctuation. A cursory inspection of Table II leads one to feel that defoliation has brought about a decrease of these in the spur, but total averages of figures of all varieties and spur parts show practically no difference between the two kinds of spurs.

Substances insoluble in hot alcohol show a steady accumulation from June 16 to July 25 in all spurs and in both "old" and "new" growths. Both portions of defoliated spurs contain less of these insoluble materials than the check spurs of corresponding dates.

Nitrogen. Table III gives the distribution of nitrogen in the different spur lots.

Nitrate determinations were made only on samples of the July 5 collection. The procedure was so time-consuming, that their determination was abandoned in the other collections. The results obtained strongly indicate a greater amount of nitrate nitrogen in the defoliated spurs, this being especially true for the "new" growths. These figures, however, are perhaps not above criticism by reason of the very high concentration of organic matter in the mixtures when reduction of nitrates was

TABLE IV. PERCENTAGES OF CARBOHYDRATES IN APPLE SPURS

(Total dry weight basis)

Portion analyzed		"Old Growth"					"New Growth"				
Treatment	Date	Direct reducing sugars	Sucrose	Total sugars	Polysaccharides	Total carbohydrates	Direct reducing sugars	Sucrose	Total sugars	Polysaccharides	Total carbohydrates
		Jonathan									
Check	July 16	2.32	0.76	3.08	23.48	26.35	2.64	0.65	3.29	24.66	27.95
	July 5	2.00	1.12	3.12	28.23	31.35	2.00	1.07	3.07	24.70	27.77
	July 25	1.80	0.77	2.57	27.18	29.75	2.15	0.68	2.83	27.00	29.83
Defoliated	July 5	2.45	1.03	3.48	26.52	30.00	2.58	0.78	3.36	21.88	25.24
	July 25	2.22	1.18	3.40	26.43	29.83	2.24	0.91	3.15	25.52	28.67
		Grimes									
Check	June 16	2.43	1.09	3.52	25.36	28.88	2.75	0.75	3.50	25.16	28.66
	July 5	2.28	1.11	3.39	29.86	33.25	2.30	1.26	3.56	25.63	29.19
	July 25	2.11	0.94	3.05	28.87	31.92	2.10	0.59	3.28	25.25	28.53
Defoliated	July 5	2.35	0.84	3.19	29.07	32.26	2.71	1.13	3.84	25.49	29.33
	July 25	2.44	0.99	3.43	25.18	28.61	2.58	1.41	3.99	22.52	26.51
		Wagener									
Check	June 17	2.29	0.41	2.70	24.45	27.15	2.95	0.86	3.81	23.20	27.01
	July 3	2.00	1.07	2.07	29.16	31.23	2.29	1.56	3.85	24.78	28.63
	July 26	2.05	0.69	2.74	26.55	29.29	2.53	0.64	3.17	23.66	26.83
Defoliated	July 3	2.34	0.96	3.30	28.50	31.80	2.78	1.42	4.20	22.44	26.64
	July 26	2.23	0.88	3.11	25.82	28.93	3.23	0.62	3.85	23.44	27.29

made. A considerable degree of reliability might be assumed from the fact that very small amounts of nitrate added to similar mixtures of apple tissue could be quantitatively recovered by the methods employed.

Soluble nitrogen (minus nitrate nitrogen) in the "new" growths of all spurs decreased throughout the experimental period. In the "old" growth it fluctuated considerably. But both "old" and "new" portions of defoliated spurs contained more soluble nitrogen than the checks.

The insoluble (protein) nitrogen exhibited practically the same situation in respect to its distribution in check and defoliated spurs, the latter containing the greater amounts.

Total nitrogen was also more abundant in defoliated spurs of all varieties.

Carbohydrates. The data pertaining to carbohydrate determinations are summarized in Table IV.

Directly reducing sugars diminish steadily in all spurs from June 16 to July 25. The "new" growths contained the larger percentages. On corresponding dates the defoliated spurs contained more reducing sugars than the checks.

Sucrose showed considerable variation but appeared to have slight significance in indicating the effects of the experimental treatment employed.

Total sugars were found to vary approximately the same as noted above for reducing sugars. The direction of the variations is not so clearly indicated, however, on account of the disturbing irregularities of the sucrose values.

The hydrolyzable polysaccharides (starch, hemi-celluloses, and higher pentosans, etc.), unlike the total insoluble substances, do not increase throughout the experimental period, but present maxima near July 5. This is true mainly of the check spurs. Apparently the defoliated spurs were retarded in their normal processes to the extent that the maximum accumulation of hydrolyzable polysaccharides had not yet been reached by July 5, and a determination of a maximum was not possible on July 25. The general decrease in these polysaccharides was probably due to both translocation from the spur and to utilization in building permanent spur structures. The latter is indicated by the data for solids in Table II. Both parts of the defoliated spurs contained less hydrolyzable polysaccharides than the checks.

The total carbohydrates determined show practically the same situation as the polysaccharides in being less abundant in defoliated spurs.

As bearing on the question of the kind of carbohydrates determined in these analyses, it is unfortunate that the lower pentose sugars and pentosans have not been specifically examined. There can be slight doubt that these are present in sufficient quantities in apple tissue to be of considerable importance, and their role in woody perennials should be established as early as possible. The probable general vital function of the monosaccharide pentoses in metabolism and Spoehr's[36] recent remarkable contribution on the relation of pentosans to the water-holding power of plant cells will likely make the pentose group appear significant to most horticultural investigators.

Summary of Chemical Data. A brief summarization of chemical data is given in Table V. The figures for check and defoliated spurs of each variety were obtained by averaging all the corresponding results of analyses of "old" and "new" growths of the second and third collections.

TABLE V. SUMMARY OF CHEMICAL ANALYSIS OF APPLE SPURS

	—Jonathan—		—Grimes—		—Wagener—		
Treatment	Check	Defoliated	Check	Defoliated	Check	Defoliated	Remarks
	%	%	%	%	%	%	
Water	54.8	57.0	53.1	55.7	56.2	57.4	Of these substances the defoliated spurs contain **more** than the checks. Sucrose (?!) Total sugars (?)
Reducing sugars	1.99	2.35	2.20	2.52	2.22	2.64	
Sucrose	0.92	0.97	0.97	1.09	0.99	0.97	
Total sugars	2.89	3.32	3.17	3.61	3.21	3.61	
Nitrate nitrogen	0.036	0.090	0.026	0.071	0.066	0.083	
Soluble nitrogen	0.135	0.304	0.101	0.214	0.175	0.227	
Insoluble nitrogen	0.875	0.974	0.708	0.797	0.868	0.928	
Total nitrogen	1.010	1.278	0.809	1.011	1.043	1.155	
Soluble solids	9.65	9.36	9.72	9.05	9.52	9.01	Of these substances the defoliated spurs contain **less** than the checks.
Insoluble solids	35.24	33.65	37.05	35.18	34.22	33.56	
Total solids	45.2	43.0	46.9	44.3	43.8	42.6	
Polysaccharides	26.78	25.09	27.35	25.56	26.04	25.05	
Total carbohydrates	29.61	28.41	30.52	29.17	29.25	28.66	
Total carbohydrates / Total nitrogen	29.3	22.2	37.7	28.8	28.1	25.7	c/n ratio less in defoliated spurs.

The defoliated spurs are shown to contain MORE *water, reducing sugars, total sugars (?), nitrate nitrogen, soluble nitrogen,* and *total nitrogen,* but LESS *soluble solids (?), insoluble solids, total solids* and *hydrolyzable polysaccharides,* than spurs supplied with their own leaf systems.

The average total carbohydrate-nitrogen ratios have been calculated for all varieties and placed in the table for inspection. Although a rigid mathematical interpretation of the ratios does not seem desirable, nevertheless the figures show a smaller value of the ratio for all defoliated spurs. In respect to the carbohydrate-nitrogen ratio and the above listed substances, the difference between check and defoliated spurs was almost always greater for Jonathan and Grimes than for Wagener, thus indicating that the spurs of the former varieties are more influenced by defoliation than those of the latter. While the responses to defoliation of Jonathan and Grimes are similar in degree, in several respects the chemical response is somewhat greater in the former.

For a more complete view of the fluctuations of the ratio of carbohydrates to nitrogen throughout the samples, Table VI has been prepared. It gives the separate total carbohydrate-nitrogen ratio for "old" and "new" growths at different collection dates. The interrelations of carbohydrates, nitrogen, and carbohydrate-nitrogen ratios are graphically shown in Figs. 3, 4, and 5.

Table VI shows that defoliation has resulted in smaller ratios throughout, but the "new" growths are usually more responsive to the treatment than the "old" portions of the spurs. The ratios generally show maxima about July 5. The observed decrease in sugars and polysaccharides after July 5 would largely account for lowering of the ratios. The carbohydrate-nitrogen graph calculated from Butler's data (see Fig. 1) shows a corresponding decrease near this period.

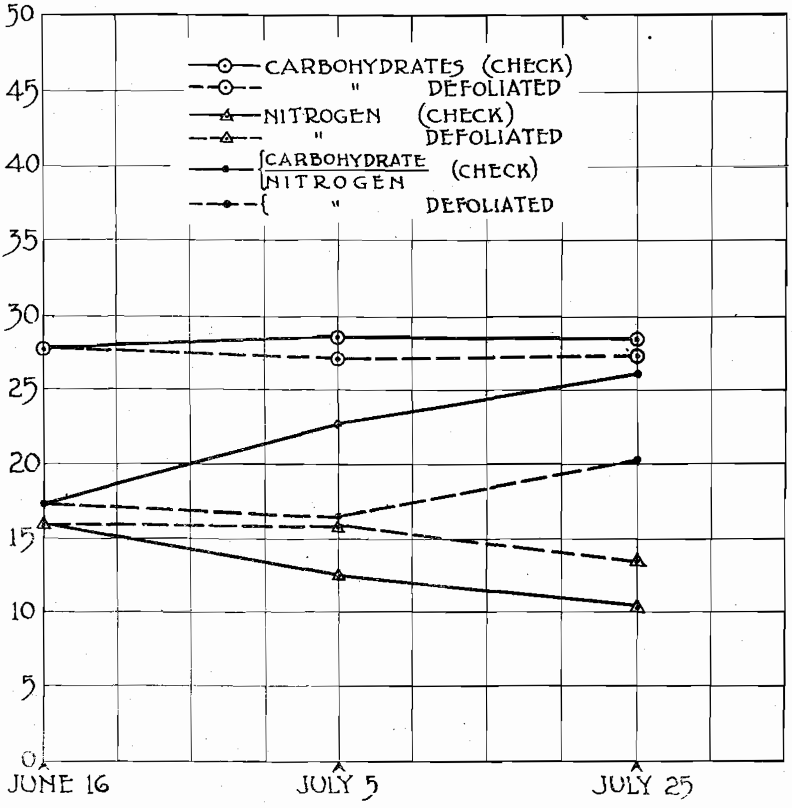

Fig. 3. Graphs showing effects of defoliation on chemical composition of "new" portions of the spur. Average of all varieties. Nitrogen percentages are multiplied by 10.

DISCUSSION

Fruit-Bud Formation. Defoliation of spurs seriously restricted the differentiation of fruit buds. On the basis of the carbohydrate-nitrogen theory, this response of spurs to defoliation would most readily be interpreted by assuming that carbohydrates were made the limiting factor to fruit-bud differentiation. Decreasing carbohydrates without disturbing the nitrogen supply would be assumed to have altered relations in favor of nitrogen to a point where the resulting conditions no longer allowed fruit-bud formation to take place. If this is the correct explanation, it can be further assumed that through defoliation, spurs were partially changed from the reproductive class III to the vegetative class II. In the same way it should be theoretically possible to select a group of spurs which are representative of the unproductive class IV and by defoliation, cause a greater production of fruit buds through this limitation of their carbohydrate supply, thus changing them to class III.

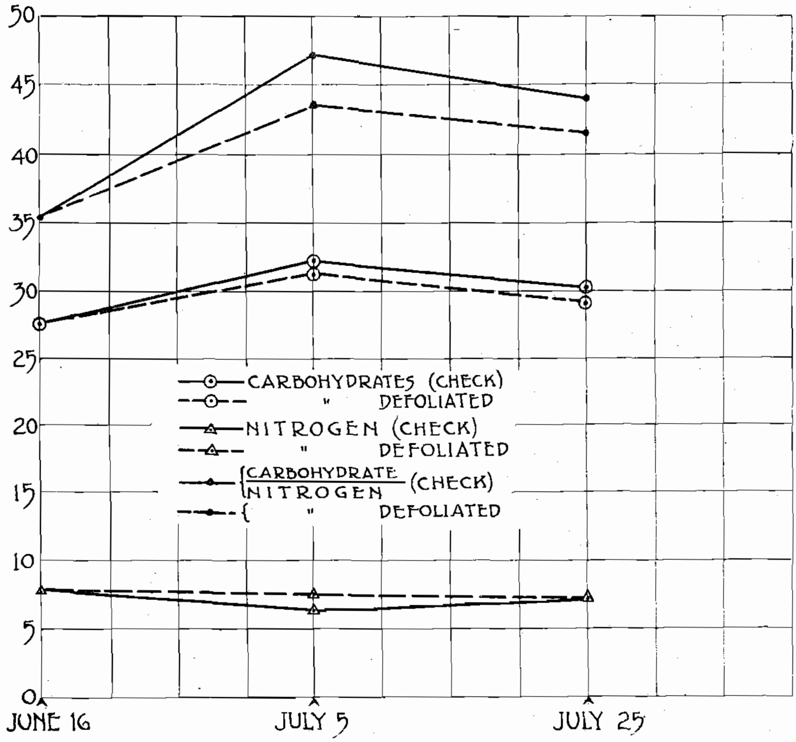

Fig. 4. Same as Fig. 3 except graphs show the chemical variations in the "old" portions of the spur.

Such a result would seem highly probable in consideration of the large number of instances on record where applications of nitrogen to the soil have increased fruit-bud differentiation as well as fruit yield. The studies of Remy-Bonn[33] in which he found the greatest fruit-bud formation accompanied by the highest nitrogen content of leaves, may represent a situation where a certain amount of defoliation would have increased flower production.

Whether or not the foregoing suppositions can be accepted as the correct explanation of the observed response to defoliation, will depend largely on the degree of confidence held in the importance and applicability of the carbohydrate-nitrogen theory. Some evidence that the defoliated spurs became more vegetative came from their frequent, and rather disturbing, habit of putting out shoots and fresh leaves. The defoliated

Grimes spurs showed a distinct tendency to vegetate in this manner. More important evidence bearing on this point comes from the chemical examination of modifications in food materials in the spur. These analyses have at least shown that defoliation causes a relative increase of reducing sugars and soluble nitrogen, and a decrease of hydrolyzable polysaccharides and perhaps some other insoluble substances. Such changes as these are commonly associated with increased vegetative activity of plant tissue. Finally the modifications produced by defoliation were in the proper direction to lower the value of the carbohydrate-nitrogen ratio, a circumstance of eminent interest in this investigation.

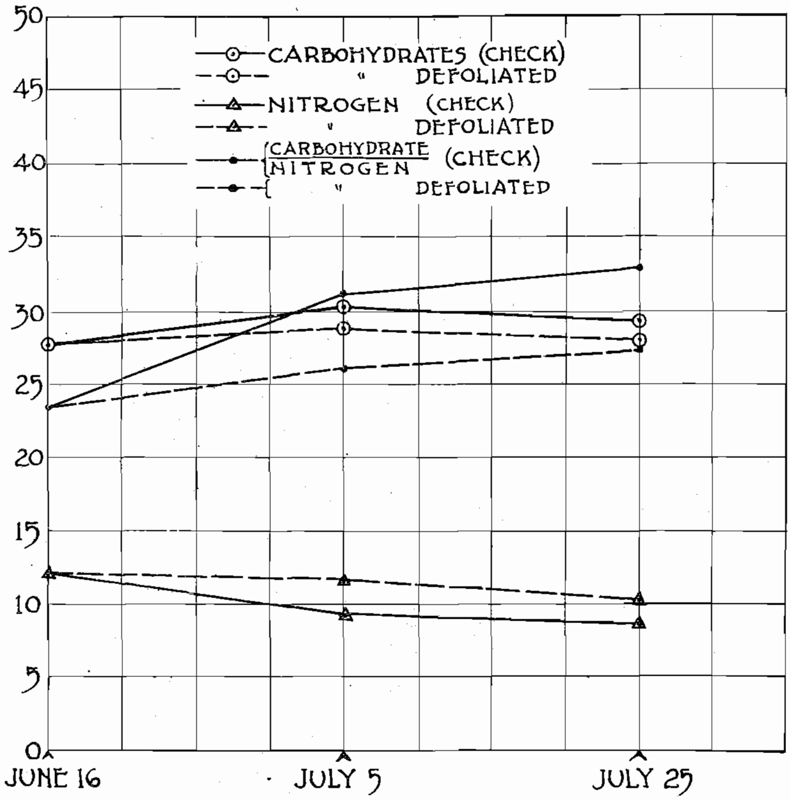

Fig. 5. Same as Fig. 3, except graphs show the chemical variation in the entire spur.

It must be admitted, however, that this change in value of the ratio was not strikingly large, at any rate not so large as the recorded effect of the same treatment on fruit-bud formation. The latter was hindered in the three varieties to the extent of about 40, 45, and 60 percent, while the ratio was lowered 6, 22, and 25 percent respectively.

A very delicate balance probably exists in spurs during the period of late June and early July, between factors favoring and opposing fruit-bud formation. In determining and studying the factors involved in this and other activities of the fruit tree, it will likely often occur that small variations in relationship or quantity of a substance will cause a response which is apparently disproportional to the recorded variation of the factor. Certainly it is impossible from the evidence at hand, to determine the significance of a given modification of this ratio* in fruit-bud formation.

TABLE VI. RATIOS OF TOTAL CARBOHYDRATES OVER NITROGEN

Portion analyzed	Date	"Old" c/n ratio	"New" c/n ratio
	Jonathan		
Check	June 16	33.9	15.5
	July 5	43.9	19.1
	July 25	44.4	26.3
Defoliated	....	......	......
	July 5	37.9	14.0
	July 25	40.6	19.0
	Grimes		
Check	June 16	40.9	20.2
	July 5	55.9	30.0
	July 25	47.3	30.3
Defoliated	....	......	......
	July 5	54.6	20.4
	July 25	45.9	21.2
	Wagener		
Check	June 17	32.0	16.5
	July 3	42.9	20.6
	July 27	39.6	22.7
Defoliated	....	......	......
	July 3	40.7	16.6
	July 27	39.4	20.3

Although the results of this investigation do not indicate an exact operation between a total carbohydrate-nitrogen ratio of the spurs and the formation of the fruit buds, it should be noted that the variations in the production of the latter were accompanied by somewhat accordant variations in the former. It may be stated, too, that these changes in relations of carbohydrates and nitrogen induced by defoliation appear to be in agreement with the general theory advanced by Kraus and Kraybill. Other relations than total carbohydrates and nitrogen have been considered from the chemical data and examined as to their consistency with the actual performance of the spurs. Ratios of total sugars over soluble nitrogen, polysaccharides over insoluble nitrogen, polysaccharides over total nitrogen and others, all exhibit variations

*Hooker considers the relations of starch and nitrogen of more significance than those of total hydrolyzable carbohydrates and nitrogen in fruit-bud differentiation. His data do show greater variations in the former relations through the three types of spurs near the bud formation period. But starch and total carbohydrates both vary in the same direction, and it does not seem that the larger variations in quantity of starch necessarily have the greater significance. Nevertheless, it is very important that attention has been called specifically to the starch situation. The same also is certainly to be said in respect to the attention this investigator has given to other possible factors in fruit-bud formation, particularly acidity and potassium.

similar in kind to those of total carbohydrates over nitrogen, but no consistent advantage was found in any of them.

The writer believes that no rigid interpretation of a carbohydrate-nitrogen ratio in fruit trees is justifiable at the present time. Yet it looks as though the general theory of the relations of these substances will be found about as applicable to these as to herbaceous plants. Therefore, while no conclusion is now drawn as to the existence of a definite causal relation between a carbohydrate-nitrogen ratio and performance of a plant organ, it is believed that the relations as indicated by this term should be given an important place, for the present at least, among that group of large controlling factors, such as light, temperature, and essential elements and substances, etc.

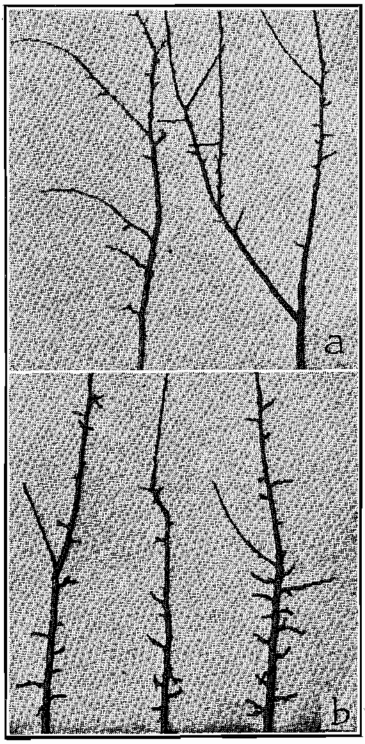

Fig. 6. Showing characteristic branching and spur formation of Jonathan (a) and Wagener (b).

Individuality of the Apple Spur. That apple spurs possess a high degree of individuality has been demonstrated by a number of previous workers. The general changes recorded during the present study offer additional evidence as to the individuality of apple spurs; since defoliation: (1) retarded fruit-bud formation; (2) increased moisture; (3) diminished carbohydrates and increased nitrogen (i. e., nitrogen was relatively increased over that in checks); and (4) decreased the carbohydrate-nitrogen ratio.

Most horticulturists have accepted as fact that the spur is greatly dependent on its own leaf system for its activities. Recently Barker and Lees[3] extended this conception to all parts of the tree by saying, "At first sight it might appear that a fruit tree, such as an apple or pear, is one single organism, but a far clearer picture of the processes involved may be obtained by treating each as a colony of competing units." Undoubtedly this is the most effective way of looking at the situation, but with the rapidly accumulating evidence pointing to the individuality of the various parts of the tree, there may be a slight tendency to carry the idea of the independence of such organs too far. When the results of the present study are viewed from another angle, as of the unity of the spur with the rest of the tree, they show that a spur which has been deprived of its own leaves can draw sufficient nutrients from the rest of the tree to carry on considerable activity. It might be said that in general, an apple spur, defoliated early in the season, is probably able to take from the rest of the tree, one-half or more of the effective carbohydrate supply which would normally have come from its own leaf system. This ability, which on the basis of one hundred, could be considered as the complement of "individuality," varies with conditions and variety. The data presented show that these varieties responded in different degrees to defoliation. In the order of decreasing response (or dependence of the spurs on their own leaves), they stood: Jonathan, Grimes, and Wagener. This order was the same for practically every effect recorded. An explanation, based on relative characteristics of spur and branch systems, is here offered for these consistent varietal differences. (Fig. 6.) The Jonathan tree is widely and repeatedly branched, the branches are small and slender and the spurs borne upon them are also slender. Thus there is a tendency to distribute widely the available food supply and to decrease transportation facilities, rendering it more difficult for the spur to draw from the general supply. On the other hand, the Wagener tree branches less, the branches are larger and sturdier, and the spurs are also thicker. Here the conditions favor better available food storage and transportation to the spur in case of necessity. The Grimes tree more nearly resembles the Jonathan in the foregoing characteristics; and the experimental results place it nearer the Jonathan in respect to individuality.

II. EFFECTS OF SPUR DEFOLIATION ON THE SETTING OF FRUIT

By

A. E. MURNEEK

The immediate object of the present study was to ascertain to what extent, if any, unfolding leaves of the individual spur of the apple influence the setting and development of fruit on the spur. Both statistical data on the number and size of fruit developed and chemical evidence of internal changes, as expressed by the relative amounts of carbohydrates and nitrogen, have been taken into account.

MATERIAL

Ten trees each of Jonathan, Wagener, and Grimes varieties were used as material for this investigation. The trees were seven years old and growing in a block of mixed varieties. Excepting the poor drainage conditions of one corner of the lot, the soil was quite uniform throughout. Only such trees as showed a good bloom and a fair amount of growth were selected for the work. Moreover, only good average spurs not more than three inches in length were considered.

The spurs were treated as follows:

(1) All leaves were removed from spurs.
(2) All leaves but one were removed.
(3) All leaves but two removed.
(4) No leaf removed—check.
(5) Deflorated.

By completely defoliating spurs, material was secured showing the effect of a total absence of leaves from a spur on its behavior in respect to setting of fruit and on its chemical composition. Heinicke[17] found that spurs on which only two leaves were left usually produced a normal set, thus indicating that a comparatively limited amount of foliage apparently furnished the necessary substances to the developing blossoms and insured a normal function of the spur. In order to learn whether this would be true with the varieties under consideration, spurs in lot 3 were permitted to grow only two leaves. To test still further the effects of a restricted leaf area on the composition and performance of the spur, only one leaf was permitted to remain on spurs in lot 2. Defloration was performed with the object in view of learning what effect it would have on the total leaf area of the spur and the relative amounts of carbohydrates and nitrogen.

The spurs were defoliated on April 23 to 28. The work was accomplished by means of pinching off with fingers not only the opened but also the embryonic leaves. Most of the blossom buds were pink at this time and many were about to open. Only in very rare instances a cluster showing an open (usually central) blossom was included (Fig. 7). During the season occasional new leaves developed on the defoliated spurs; these were removed at the time the fruit had set or after the first collection of spurs, May 20 and 21. It should be noted here that spurs collected on the various dates were, with some exceptions, in the original condition of treatment. Defloration was performed on May 2 and 3, at which time most of the trees were in full bloom. The blossoms were pinched off close to the base of the pedicels.

Altogether 3200 spurs of each of the three varieties were involved, or a total of 9600 spurs. They were distributed equally over all trees, averaging about 320 spurs per tree. Each tree furnished its proportional share of spurs of the various treatments.

The weather conditions were very favorable throughout the period of blossoming, pollination, and fertilization. The trees set an unusually heavy crop. Fruit on all trees that furnished material for the study was left as set; i. e., unthinned.

Collection and Preservation of Material. Each separate lot of preserved material contained approximately 200 spurs. The first lot of 200 spurs of each of the varieties was collected for chemical analysis at the time of defoliation. The spurs were cut as close to the branch as possible. As soon as a part of the collection was secured, the leaves, together with any new growth, were removed and the spurs placed in stoppered bottles. Immediately after the completion of the collection, the samples were taken to the laboratory, were weighed, and the spurs counted. The lots varied in weight from 65 grams to slightly over 100 grams. The material was then covered with redistilled alcohol, 94 percent. To neutralize acidity of the tissues, about one gram of calcium carbonate was added to each sample. It was then heated for one hour in a water bath at 70° C.

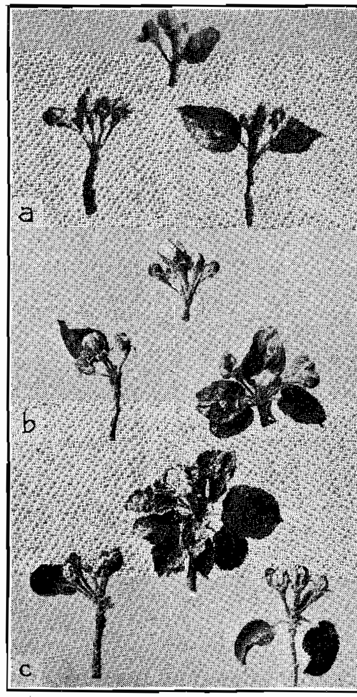

Fig. 7. Spurs, showing development of leaves and blossoms at time of defoliation. (a) *Grimes*—total defoliation, one leaf, two leaves; (b) Wagener—one leaf, total defoliation, check; (c), Jonathan—one leaf, check, two leaves.

The first collection, consisting of 200 spurs of each variety and each treatment, was made on May 20 and 21, or about 25 days after defoliation. These data coincided closely with the latter part of the "early drop." The exact set of fruit, as will be shown later, could not be ascertained at this time. It was considered of interest, however, to obtain evidence of the approximate relation of leaf area to performance of the spur but particularly so on its chemical composition. The material was placed in paper bags and brought immediately to the laboratory where statistical data were taken. The spurs were then preserved for chemical investigation in a manner previously described. All work, from collecting to preserving, was performed on the same day.

The second collection of spurs, similar in scope to that secured on May 20 and 21, was made on June 14 and 15. The "June drop" was practically over on this date. As the effects of defoliation were now clearly evident, careful statistical records of the performance of the collected spurs were secured. All samples were then preserved for chemical analyses.

Very favorable weather conditions prevailed during the summer. The trees showed on the average very good growth and were apparently in a healthy condition. The yield of Grimes was about medium, while both Wagener and Jonathan had a heavy set of fruit.

The last collection of material was cut on September 25, at the time of harvesting of the crop. Records of fruit were taken in the field. The spurs were immediately brought to the laboratory and preserved for further chemical investigation.

METHODS OF ANALYSIS

Statistical. Statistical data were taken from all three collections. Those gathered on May 20 and 21 were recorded in respect to the number of fruits set, percentage of spurs bearing, and average leaf area per spur. This last was obtained by taking representative fractions of each lot. Such fractions contained 20 to 25 spurs. The leaves were removed and the average area measured by means of a planimeter. Calculations were made to determine the number and average leaf area per spur, as expressed in percentage of check.

Similar statistical information was secured from the second collection, June 14 and 15. As the effects of the various treatments were more clearly conspicuous at this time, the greatest care was exercised in gathering of all data.

At the time of the last collection, September 25, when most of the fruit was ready to be picked, it was thought to be of interest to learn to what extent the gross effects of defoliation may be measured by the number and size of fruit present on the treated spurs. Hence information was secured of the number of fruits set, percentage of spurs bearing, and the average weight of fruit. This was done in the field at the time the crop was harvested.

Chemical. Of the four lots of samples of spurs collected and preserved, only one, including four samples of each of the respective varieties, has been analyzed so far. The method employed and detailed procedure in all steps of the chemical work were identical to those described on pp. 18-20. *All analyses were performed in duplicate.

PRESENTATION OF RESULTS

Statistical. Considering all statistical data it is clearly apparent that a correlation exists between the leaf area of the individual spur and

* The methods and procedure used in the chemical analyses were worked out in detail by the senior author.

its performance in respect to setting of fruit. All types of defoliation markedly lowered the amount of fruit set. The effects of the various treatments were conspicuous even before the "first drop" was over.

TABLE VII. EFFECT OF SPUR DEFOLIATION ON SETTING OF FRUIT MAY 20 AND 21

	Grimes			Wagener			Jonathan		
Treatment	Leaf area sq. in	Area % of check	No. of fruits per spur	Leaf area sq. in	Area % of check	No. of fruits per spur	Leaf area sq. in.	Area % of check	No. of fruits per spur
Defoliated	9.25	93.3	....	12.03	80.6	....	13.14	110.1	....
Check	9.91	....	2.50	14.93	....	2.72	11.93	....	5.00
Two leaves	1.71	1.72	2.88	6.96	46.6	2.43	2.78	2.34	5.35
One leaf	1.45	1.46	3.27	2.72	18.1	2.61	1.78	1.49	4.91
No leaf	.07	.07	2.39	.82	.55	1.00	.30	.25	3.79

Table VII gives the results of observations and measurements of leaf area at the time of the first collection, May 20 and 21. While partial defoliation shows but a slight effect upon the number of fruits per spur at this time, spurs from which all leaves had been removed had a much smaller set as compared with checks. The Wagener and Jonathan varieties are particularly conspicuous in this respect. That the final set could not be even estimated thus early in the season can be seen from the abnormally large number of fruits present. Untreated spurs of Jonathan, for instance, still held on the average five fruits per spur, while Grimes and Wagener had 2.50 and 2.72 fruits respectively.

After the second or "June drop" the gross effects of defoliation were very distinct. (Table VIII). The number of fruits per spur varied in direct proportion to the amount of foliage or leaf area present. (Figs. 8, 9, 10). Totally defoliated spurs of Grimes produced .28 fruit per spur as compared with .77 on checks. In Wagener and Jonathan the removal of all leaves caused a still greater decrease in setting: Wagener —checks .79 fruit per spur; no leaf .12. Jonathan—check 1.04; no leaf .17. When only two leaves were left on the spur or, according to measurements of leaf area at time of defoliation, approximately one-third of the normal area of foliage was present, the number of fruits per spur diminished to half of that on the check spurs. The set was correspondingly and proportionally lowered when one or no leaf was left. This slightly disagrees with the results obtained by Heinicke,[17] who found that when two leaves were left per spur, their behavior was approximately similar to those left untreated. Possibly varieties differ somewhat in this respect. Another point illustrated in Table VIII is the effect of defloration on the leaf area. The latter was increased in the three varieties on the average by 9.2 percent, 33.5 percent, and 39.6 percent, respectively.

TABLE VIII. EFFECT OF SPUR DEFOLIATION ON SETTING OF FRUIT JUNE 14 AND 15

	Grimes				Wagener				Jonathan			
Treatment	Leaf area sq. in.	Area % of check	No. of fruits per spur	Ratio: Area over no. of fruits	Leaf area sq. in.	Area % of check	No. of fruits per spur	Ratio: Area over no. of fruits	Leaf area sq. in.	No. of fruits per spur	Area % of check	Ratio: Area over no. of fruits
Deflorated	12.95	109.2	....	......	21.00	133.5	....	......	19.74	139.6	....	......
Check	11.87	....	.77	.065	15.74	....	.79	.052	14.14	....	1.04	.073
Two leaves	5.24	44.1	.38	.072	4.08	25.9	.31	.076	5.29	37.4	.43	.081
One leaf	2.49	10.9	.35	.140	4.14	26.3	.24	.058	3.38	23.9	.28	.083
No leaf	0.88	7.3	.28	.318	3.78	24.0	.12	.032	1.20	8.5	.17	.141

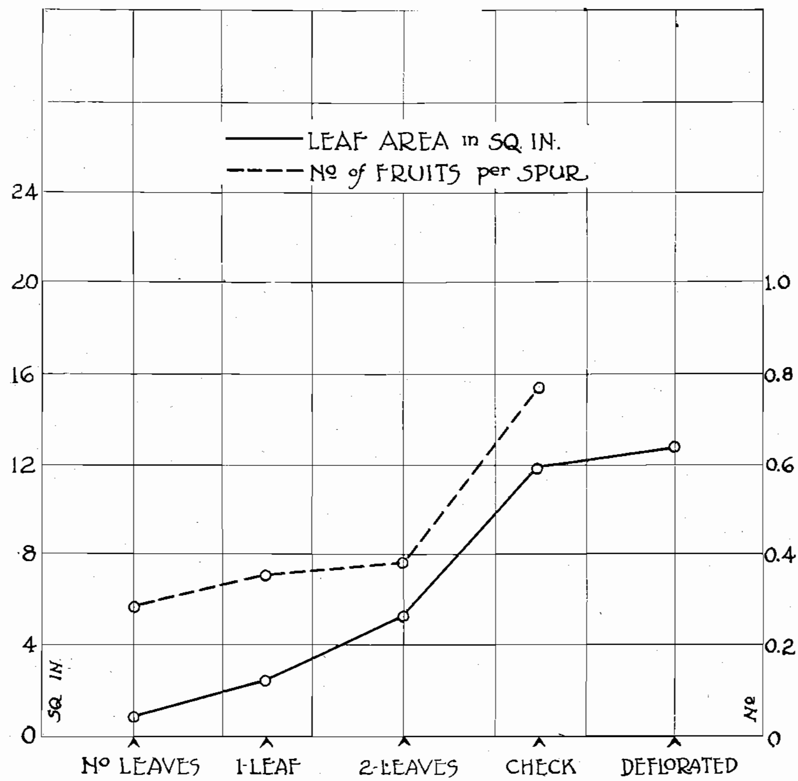

Fig. 8. Graphs showing effect of defoliation on leaf area and number of fruits per spur. June 14-15. Variety Grimes.

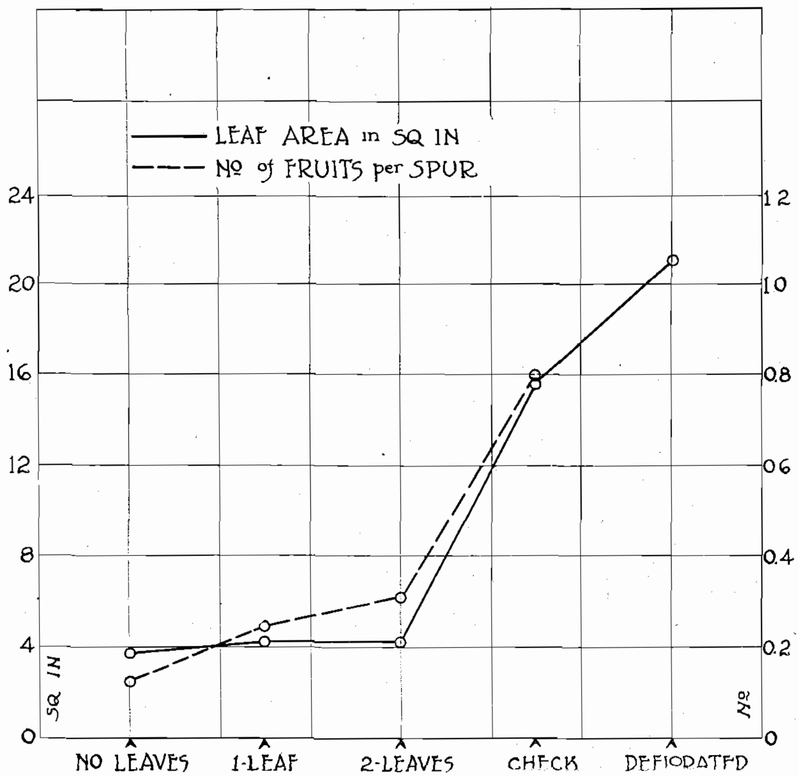

Fig. 9. Graphs showing effect of defoliation on leaf area and number of fruits per spur. June 14-15. Variety Wagener.

TABLE IX. EFFECT OF SPUR DEFOLIATION ON SETTING AND SIZE OF FRUIT SEPTEMBER 25

Treatment	Grimes: No. of spurs considered	Grimes: No. of fruit set	Grimes: Spurs bearing	Grimes: Ave. wt. of fruit	Wagener: No. of spurs considered	Wagener: No. of fruit set	Wagener: Spurs bearing	Wagener: Ave. wt. of fruit	Jonathan: No. of spurs considered	Jonathan: No. of fruit set	Jonathan: Spurs bearing	Jonathan: Ave. wt. of fruit
			%	oz.			%	oz.			%	oz.
Check	184	121	65.8	4.49	178	115	64.6	5.17	164	131	81.0	3.79
Two leaves	151	52	34.5	3.74	146	43	29.4	3.58	119	38	32.5	3.58
One leaf	174	62	35.6	3.39	171	37	21.6	3.68	150	26	17.3	4.00
No leaf	148	47	31.7	2.93	145	25	17.2	4.00	133	24	18.0	3.42

Table IX illustrates that a decreased leaf area exerted a continuous influence throughout the growing season as shown by data taken at the time of maturity of fruit. With but few exceptions, both the percentage of spurs bearing and the number of fruits set varied directly with the amount of foliage present and remained more or less constant throughout the season when once established after the "June drop." Moreover, data on weight of Grimes at least would indicate that the amount of foliage present on the spur determined also the average weight of fruit on that spur. (Fig. 11). It should be pointed out here, however, that

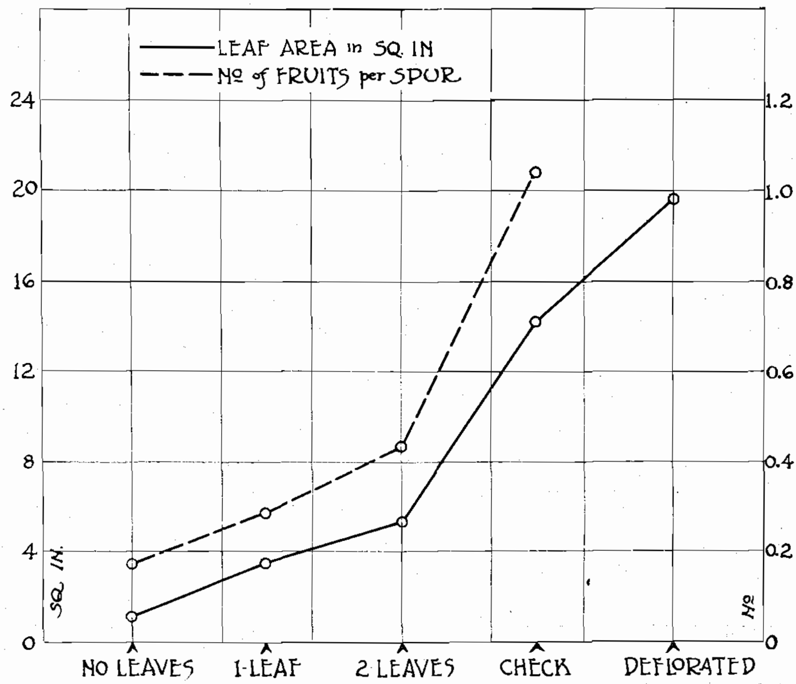

Fig. 10. Graphs showing effect of defoliation on leaf area and number of fruits per spur. June 14-15. Variety Jonathan.

TABLE X. EFFECT OF DEFOLIATION ON THE CHEMICAL COMPOSITION OF APPLE SPURS—MAY 20 AND 21

Variety—Grimes				
Treatment	No leaf	One leaf	Two leaves	Check
Water	55.32	54.86	55.69	53.82
Solids	44.68	45.14	44.31	46.18
Reducing sugars	1.71	1.53	1.63	1.85
Sucrose	2.014	.675	.903	.827
Total soluble sugars	3.724	2.205	2.533	2.677
Starch, etc.	25.11	25.75	24.83	24.81
Total carbohydrates	28.83	27.95	27.36	27.49
Total nitrogen	.705	.646	.715	.777
$c/n \frac{\text{Total nitrogen}}{\text{Total carbohydrates}}$	40.9	43.2	38.6	35.4

no measurements were taken of the area of foliage on the various groups of spurs on September 25. Undoubtedly a few new leaves developed on a number of treated spurs during the latter part of the season, which may have thrown them from a group they were intended to be in to one next adjoining it. Hence the greater variation of results on this date.

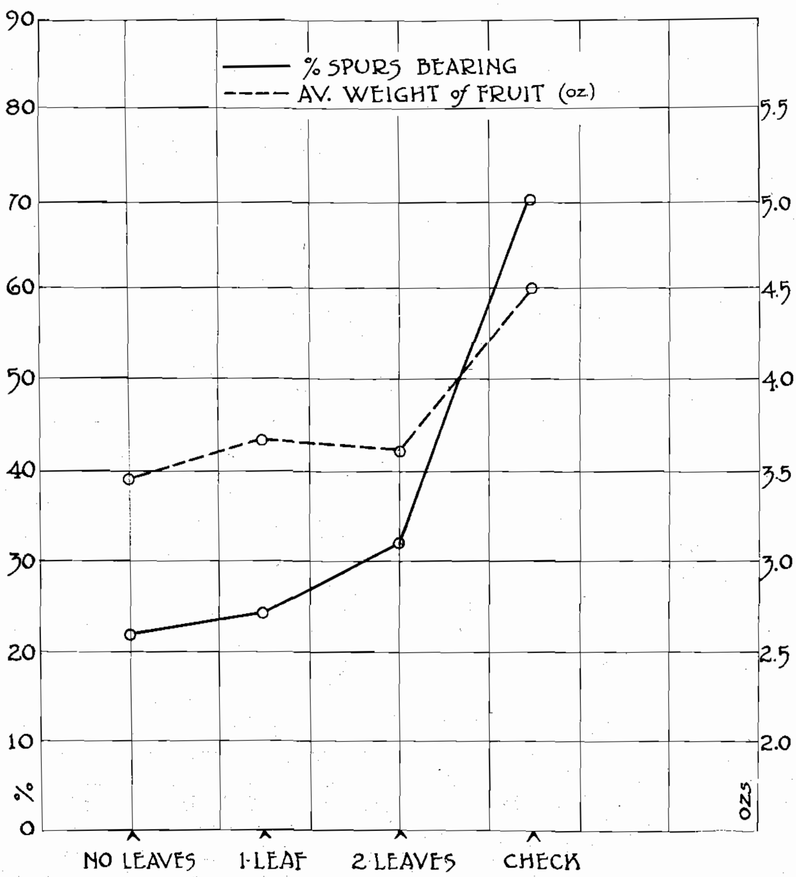

Fig. 11. Graphs showing percentage of spurs bearing and average weight of fruit. September 25. Ave. of all three varieties.

Chemical. In the accompanying tables are presented the results of analyses of twelve samples of the first collection of spurs of all three varieties. It is thought that the physiological influence of defoliation must have become established at the time of the May collection, twenty-five days after the treatment, though the gross results, as previously stated, were much more evident by the middle of June. The figures are given in percentages of dry weight.

In general the removal of leaves decreased the total solids in spurs of all three varieties. The amounts, however, do not seem to vary with the area of foliage present. The loss in solids appears to be greater in Jonathan and Grimes than in Wagener.

No consistent differences may be observed either in the amount of reducing sugars or sucrose. Great variability is exhibited by all samples.

TABLE XI. EFFECT OF DEFOLIATION ON THE CHEMICAL COMPOSITION OF APPLE SPURS—MAY 20 AND 21

Variety Wagener				
Treatment	No leaf	One leaf	Two leaves	Check
Water	55.48	57.03	56.52	54.76
Solids	44.52	42.97	43.48	45.24
Reducing sugars	1.43	1.66	1.71	1.37
Sucrose	.75	2.306	2.270	2.254
Total soluble sugars	2.18	.646	.560	.884
Starch, etc.	23.35	24.71	23.20	22.50
Total carbohydrates	25.53	27.02	25.47	24.75
Total nitrogen	.745	.853	.818	.901
c/n $\frac{\text{Total nitrogen}}{\text{Total carbohydrates}}$	34.3	31.7	30.9	27.5

TABLE XII. EFFECT OF DEFOLIATION ON THE CHEMICAL COMPOSITION OF APPLE SPURS—MAY 20 AND 21

Variety Jonathan				
Treatment	No leaf	One leaf	Two leaves	Check
Water	56.06	57.09	57.34	54.36
Solids	43.94	42.91	42.66	45.74
Reducing sugars	2.07	1.98	1.89	2.07
Sucrose	.74	1.21	.66	.75
Total soluble sugars	2.81	3.19	2.55	2.82
Starch, etc.	24.34	22.93	22.83	21.70
Total carbohydrates	27.15	26.12	25.38	24.52
Total nitrogen	.832	.797	.883	.795
c/n $\frac{\text{Total nitrogen}}{\text{Total carbohydrates}}$	32.6	32.8	28.7	30.9

Unlike the soluble carbohydrates, the hydrolyzable polysaccharides, consisting of starch, hemicelluloses, pentosans, etc., appear to have been influenced by defoliation. A corresponding increase of these substances is noted as a result of decrease of leaf area. This is exhibited quite consistently by all three varieties. It must be remembered here, however, that the number of fruits per spur varied directly with the amount of foliage present on the spurs. Those receiving the greatest amount of defoliation had to support the least number of fruits. To what extent the developing fruit absorbed and utilized the carbohydrates, particularly starch, supplied by the leaves can only be conjectured. The writer is at present conducting a separate series of studies of this question.

No separate determinations of nitrate nitrogen were made. The difficulties involved and the small amounts present (as found in several lots of Jonathan spurs) did not justify this labor. The amount of total nitrogen shows quite striking differences. A strict correlation is indicated between the total amount of nitrogen and leaf area. This is particularly significant in view of the fact that the fruit undoubtedly required considerable quantities of nitrogenous substances for the formation and development of seeds.

The carbohydrate-nitrogen ratio may be used as a ready index of the relative amounts of total carbohydrates and total nitrogen. It is seen that the ratio decreases with the increase of foliage, although one would expect quite the contrary effect; that is, an increase of the ratio because of the relative increase of the carbohydrate-producing leaf

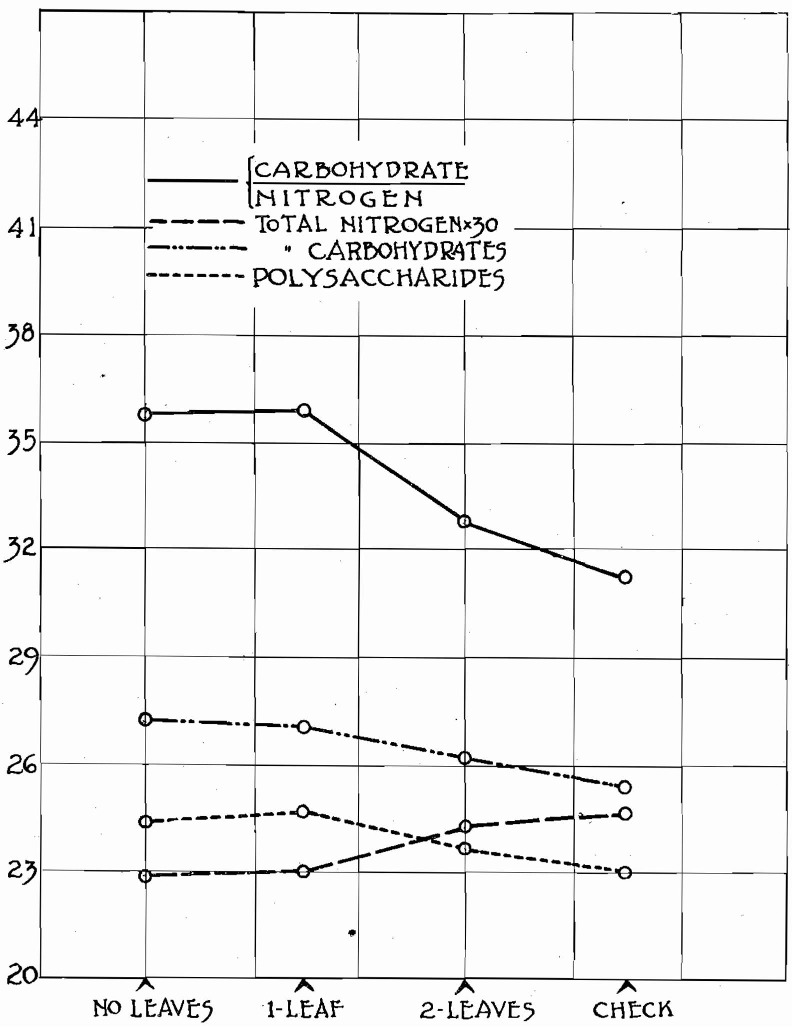

Fig. 12. Graphs showing the effect of defoliation on polysaccharides, total carbohydrates, total nitrogen and the carbohydrate-nitrogen ratio. May 20-21. Ave. of all three varieties.

area. These results are due to both a relative increase of the total carbohydrates, with the lowering of leaf area, and a corresponding decrease in total nitrogen.

The graph presented as Fig. 12 shows the changes in polysaccharides (starch, etc.), total carbohydrates, total nitrogen, and the carbohydrate-nitrogen ratio, as influenced by the various treatments. The results are given in averages of all three varieties.

DISCUSSION

The results of this investigation emphasize forcibly the fact that the setting of fruit in the apple is determined to a large measure by the amount of foliage present on the spur. In general this substantiates the conclusions reached by other investigators. Various amounts of defoliation decreased correspondingly the percentage of fruit set.

These records may also be considered as additional evidence of the high degree of " individuality " of the apple spur. A considerable number of fruits set, however, even when all the leaves were removed. This shows that the spur, though being markedly individual in respect to supply of nutrients, still obtained a large amount of the necessary food material from the tree as a whole. In this respect a marked variation was observed between the different varieties. Grimes spurs were able to set a much larger number of fruits, under these circumstances than those of either Wagener or Jonathan.

The removal of leaves undoubtedly lowered the carbohydrate supply of the spur. The analytical data, however, do not indicate any conspicuous differences in the amount of either soluble or insoluble carbohydrates. But as the presence of leaves was strictly correlated with the number and amount of fruit per spur, it is difficult to ascertain to what degree the actual amounts of carbohydrates found in the spur are indicative of the source of supply. Considering the opinions of other investigators, it is but natural to assume, however, that the developing fruit drew in the first place upon the local carbohydrate supply. Hence it is probable that very few carbohydrates of any kind were stored in the spur at this time.

A fact of the greatest significance is the strict relation of the leaf area, the number of fruits per spur, and the amount of total nitrogen. This relation is particularly important in view of the fact that one would naturally expect a much greater demand for nitrogen by the developing fruit, particularly the seeds. The investigations of Petri[31] and Loew[25] throw some interesting light upon this question. Their results show that the setting and developing fruit utilize large quantities of nitrogen. This helps to explain the striking response obtained by Lewis and Allen[23] and Lewis and Brown[24] by application of nitrates about one month before blossoming of the trees. That relatively high amounts of nitrogen are associated with parts of the plant closest to the setting fruit are indicated by Kraus and Kraybill.[22] The upper stem and leaves of the tomato were found to be generally higher in total nitrogen than the basal portions.

The analytical data of Butler *et al.*[5] tend to indicate also (Fig. 1) a relatively high nitrogen content in the apple trees as a whole at the time of blooming. No spurs were analyzed. May it not be assumed, however, that, because of the localization of function in the bearing spurs, these differences would have been still more conspicuous? Another point of interest noted by Butler is the low minimum of carbohydrates at the time of fruit setting.*

If the relative amounts of carbohydrates and nitrogen are considered and expressed by a carbohydrate-nitrogen ratio, it is evident that at the time of setting of fruit, the ratio for the spur is very low. This is readily seen when a comparison of results is made between the ratios of check spurs at the time of fruit-bud formation (Table VI) and those at the time of setting of fruit. (Tables X, XI, and XII.) If the theory of the carbohydrate-nitrogen ratio were accepted, then from the data at hand it must be assumed that a relatively low value of the ratio is correlated with setting. The various amounts of defoliation seem to have increased the carbohydrate-nitrogen ratio largely by decreasing the amount of nitrogen.

Attention should be called here to the considerable seasonal changes in the relative amounts of total carbohydrates and nitrogen as found by Butler *et al.*, in all parts of the plant. These variations, as shown by the present investigations, are particularly great in spurs and are coincident with the periodic succession of the various phases of reproductive functions.† The differences are most evident between the time of " bud swelling " and " active growth ceased." This fact necessitates exercising great care in collecting material for analysis and in expressing the capacity of a tree, or of its parts, for vegetative or reproductive activities by a carbohydrate-nitrogen ratio. The condition in the spurs appears to vary most rapidly at this period. An herbaceous plant, like the tomato, for instance, because of a vertical sequence of events, or the practically continuous succession of reproductive activities, from the formation of fruit buds to blossoming, setting, and maturing of fruit, would lend itself much more readily to such an interpretation. Kraus and Kraybill have taken into account this fact by stating that " the condition for initiation of floral primordia and even blooming are probably different from those accompanying fruit setting ".[22] Moreover their analyses show that in the tomato, considering the stem from the top to the bottom, there is a descending gradient of total nitrogen and an ascending gradient of total carbohydrates. Is it permissible to correlate these changes with the vertical sequence of reproductive activities of the plant? It is possible that in the various stages of its activities the particular condition of the apple spur may be expressed by a more or less definite relation of carbohydrates to nitrogen.

*Recently Hooker has added valuable information on this question. He shows that bearing apple spurs contained the largest maximum of nitrogen at the time of fruit setting. That this was correlated closely with the blossoming of the spurs is seen from other graphs, which show no maxima of nitrogen in non-bearing spurs at this time of year. The least minima of total carbohydrates coincide with the period of setting of fruit.

†Loc. cit. Hooker.

GENERAL SUMMARY

Effects of defoliation on fruit-bud formation and chemical composition of apple spurs.

(1) Defoliation strongly hindered fruit-bud formation as shown by the fact that Jonathan, Grimes, and Wagener spurs were able to produce only 38.7 percent, 54.6 percent, and 58.6 percent, respectively, as many fruit buds as the untreated spurs.

(2) Defoliation tended to make the spurs, especially the Grimes, more vegetative as evidenced by the frequent putting out of shoot growth and new leaves.

(3) Defoliation modified the chemical composition of spurs so that they contained, as compared with the checks:

(a) *More* water and *less* of soluble solids (?), insoluble solids, and total solids.

(b) *More* nitrate nitrogen, total soluble nitrogen, and insoluble nitrogen.

(c) *More* reducing sugars, total sugars (?), and less of hydrolyzable polysaccharides and total carbohydrates.

(d) *Smaller* values of the carbohydrate-nitrogen ratio.

(4) The carbohydrate-nitrogen ratio, if given a general interpretation, might be classified along with other important controlling factors of plant development, but a strict mathematical interpretation is not justified from the present study.

(5) The effects of defoliation on spurs suggest a high degree of "individuality," or dependence of the spur on its own leaves for normal activity.

(6) In respect to the degree of "individuality" shown, the three varieties assume the following decreasing order: Jonathan, Grimes, and Wagener. A general explanation for this relative behavior is suggested.

(7) It is pointed out that the idea of the "individuality" of spurs might possibly be over-emphasized, since defoliated spurs were able to carry on about 50 percent or more of their normal fruit-bud formation.

Effect of defoliation on setting of fruit and chemical composition of apple spurs.

(1) Defoliation had a direct effect upon the setting of fruit. The number of fruits per spur varied with the area of foliage of the spur.

(2) The influence of a restricted leaf area extended more or less throughout the growing season. This was evidenced by a close relation existing between the number of leaves at the beginning of the season and the percentage of spurs bearing and average weight of fruit at time of maturity.

(3) A marked "individuality" was exhibited by apple spurs. Those totally defoliated, however, were able to set and mature a considerable number of fruits. In this respect the different varieties showed wide variations.

(4) In every case defloration increased the leaf area of the spur.

(5) As a result of defoliation, the chemical composition of spurs was altered in the following ways:

(a) Total solids decreased, though evidently not in the exact proportion to the amount of treatment.

(b) No apparent effect was noted in total amounts of soluble sugars, including both reducing sugars and sucrose.

(c) Hydrolyzable polysaccharides increased with reduction of leaf area.

(d) Total nitrogen decreased in proportion to defoliation. A fair correlation was established between leaf area and total nitrogen.

(6) A rather consistent increase in the carbohydrate-nitrogen ratio was effected by defoliation. The possible cause and value of this change in the ratio is discussed.

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