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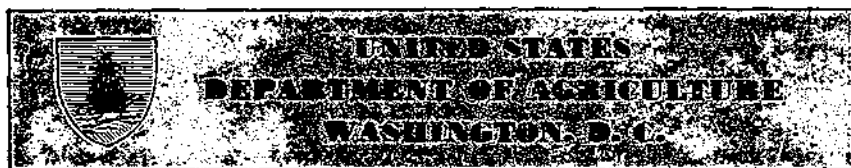
Investigations on the Cause and Control of Biennial Bearing of Apple Trees [1]

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INTRODUCTION [2]

Since the beginning of horticulture, fruit growers and investigators have studied the factors that appear to be associated with blossom-bud formation. The apple has probably been the object of more study of this type than all other fruit trees combined. The literature covering investigations on factors associated with fruitfulness in the apple is exceedingly voluminous.

Two problems in apple production have greatly stimulated interest in the study of blossom-bud formation. The first and most important of these is the tendency of many apple varieties to bear heavy crops one year and little or no fruit the year following. This alternate- or biennial-bearing tendency is recorded in the earliest horticultural writings, and the condition can be found today to a greater or less degree in practically every orchard. All varieties may become biennial in bearing habit under certain conditions, and once the habit becomes firmly established in a tree it has usually been extremely difficult to correct. There is, however, a great difference in the tendency of varieties to become biennial in bearing habit. The second

[1] Submitted for publication May 1941.
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problem that stimulated study is the relatively long time that is required with many apple varieties before they begin to bloom and bear fruit. Both of these problems are intimately associated with the basic conditions within the tree and within the individual buds which are associated with the formation of flower parts.

For many years attempts to maintain trees in annual bearing or to restore them to the annual-bearing condition dealt mainly with modifying such practices as pruning, cultivation, and the application of fertilizers. During more recent years the problem has been approached through chemical and physiological studies of tree tissues, particularly the specialized reproductive portions or fruit spurs, to try to determine the nutritional conditions within these organs associated with the formation of flower buds.

The investigations reported in this bulletin include (1) an intensive and accurate study of the changes in nutritive materials in buds associated with their differentiation into either flower buds or leaf buds; (2) studies through adjustment of leaf areas and ringing to modify the performance of buds; and (3) studies to determine the practicability of fruit thinning as a means of modifying the biennial-bearing habit.

This work has been conducted in the irrigated orchards in the vicinity of Wenatchee, Wash., and in orchards in the Potomac Valley, representative of those in the eastern United States. Not only vigor of trees but also light intensity, injury to foliage from sprays, and other factors differ in the eastern and western areas. While the fundamental factors that influence bud differentiation are undoubtedly similar in different sections of the United States, the practical results that may be expected from orchard treatments may vary greatly. The detailed biochemical and physiological studies herein reported were made at Wenatchee, Wash., where material of very uniform behavior was available for study. Extensive tests to determine the practicability of fruit thinning as a means of controlling biennial bearing were made both in the Wenatchee district and in eastern orchards, where the practical problem of biennial bearing is more acute than in western orchards.

Because some variability in results from practical orchard thinning tests is to be expected and was found, the results from the work in the two areas are presented and discussed separately.

INVESTIGATIONS IN THE PACIFIC NORTHWEST [3]

SUITABILITY OF THE AREA FOR STUDIES

The commercial apple-growing sections of the Pacific Northwest offer many advantages for studies of this kind as the physical characteristics tend to reduce to a minimum certain disturbing influences found in many other fruit-growing sections. Some of these advantages are control of soil moisture, practical freedom from spring frosts, absence of certain fungus diseases and sprays for their control that may cause injury to foliage, maximum quantity of sunshine during the growing

season, and availability of a wide selection of trees best suited for the study.

Three general types of investigations have been conducted for a period of 7 seasons at Wenatchee, Wash. They included chemical analyses of bearing (on-year) and nonbearing (off-year) tissues, physiological studies of effects of leaf-fruit ratios and ringing on bearing, and commercial fruit thinning.

BIOCHEMICAL STUDIES

The classical work of Kraus and Kraybill (27),[4] in which they found fruitfulness in the tomato to be associated with a relatively high proportion of carbohydrates to nitrogen, prompted many other investigators to discover a similar relationship in other plants. Hooker (24) was the first to make a systematic chemical analysis of nonfruiting and fruiting apple spurs. He concluded that the ratio of starch to nitrogen was a better index of fruitfulness than was the total carbohydrate-nitrogen ratio of Kraus and Kraybill. A high percentage of starch and a low percentage of nitrogen in the spur at the time of differentiation were considered essential for blossom-bud formation, and a relatively low concentration of starch was considered essential for leaf-bud development.

Many workers have since found evidence to support in general this starch-nitrogen relationship, although others have obtained what appear to be contradictory results. Explanations for this lack of unity are varied, but two principal reasons have been advanced: First, difficulty in the interpretations of the data, and second, materials selected for analysis by different individuals were not physiologically the same and hence the variations in results. Methods of chemical analysis have also been subjected to their share of criticism.

Regardless of the seeming confusion attending chemical analyses, the preponderance of data, gathered from both microchemical and macrochemical studies of many species of plants, tends to show relatively high concentrations of starch in tissues giving rise to flower primordia. Neither the total carbohydrate-nitrogen ratio nor the starch-nitrogen ratio, however, has been generally accepted as the key to the fundamentals underlying the initiation of blossom buds, and the specific factor or factors responsible for this phenomenon remain unidentified. The hoped-for solution to the problem by chemical analysis has, therefore, been somewhat disappointing, but consideration must be given to the fact that much of the later and perhaps more productive physiological work is based to a measurable degree on the results of these biochemical investigations.

DESCRIPTION OF TREES SAMPLED IN 1935

During the growing season of 1935 a chemical study was made of certain carbohydrate and nitrogen fractions in fruit spurs, bark, and wood tissues of biennial-bearing Yellow Newtown apple trees. A group of trees was located from which samples for analysis could be taken with more confidence as to their physiological character than from any trees that have heretofore been observed. They were large and vigorous, about 28 years of age, and growing in a deep, well-drained soil, classified as Wenatchee loam (26). The biennial bearing exhibited by these trees was of the "individual main leader" type, that

is, some main branches bore a heavy crop and the remaining bore practically none in the same year.

It was found (*19*) that these individual main scaffold limbs or main leaders of the trees functioned independently of the remaining aboveground portions of the tree and that one or more main leaders may be definitely in an off- or on-year condition, regardless of the fruiting habit of the other leaders. A careful study of the spurs of these leaders has shown this variation in performance to have been maintained over a period of several years.

Thus it was possible to obtain from a single tree samples of fruit spurs of extreme physiological contrast without the introduction of such variables as tree vigor, fertilizer treatments, and soil types, which are difficult to eliminate if different trees are used. That fertilizers, especially those containing nitrogen, may affect the chemical composition of apple spurs has been pointed out by Lagasse (*28*).

ANALYTICAL PROCEDURE AND METHODS

COLLECTION AND PRESERVATION OF SAMPLES

Chemical samples were taken from four trees. Spur-performance history of the main leaders of these trees is shown in table 1.

TABLE 1.- *Spurs blossoming on main leaders of Yellow Newtown trees sampled for chemical analysis at Wenatchee, Wash., 1935*

Tree No.	Leaders	Spurs blossoming		Tree No.	Leaders	Spurs blossoming	
		1935	1936			1935	1936
	Number	*Percent*	*Percent*		*Number*	*Percent*	*Percent*
1	3	0	95.70	3	3	0.15	95.10
	3	88.10	.24		3	94.50	0
2	2	.20	93.30	4	4	0	96.70
	3	95.20	.18		2	94.20	.32

Two classes of spurs were collected for analysis: Those taken from off-year leaders making vegetative growths only and differentiating blossom buds for the next year are designated here as nonbearing spurs; and those from on-year leaders, each bearing a fruit and having secondary growths that were forming leaf buds, are called bearing spurs. The spur as taken from the tree comprised growths made in both 1934 and 1935. Not only was the new growth separated from the old but also morphological components of both the old and new growths were preserved and analyzed separately. The samples consisted of the following components:

(1) Bearing spurs:
    1934 vegetative growths.
    1935 cluster bases.
    1935 secondary growths.
(2) Nonbearing spurs:
    1934 cluster bases.
    1934 secondary growths.
    1935 vegetative growths.
(3) Bark tissue from 2- to 4-year-old nonbearing branches.
(4) Wood tissue from 2- to 4-year-old nonbearing branches.
(5) Bark tissue from 2- to 4-year-old bearing branches.
(6) Wood tissue from 2- to 4-year-old bearing branches.

In some of the earlier investigations no distinction was made between the current and previous seasons' growths, which were preserved and analyzed together. It was found (15), however, that the chemical composition of older spur tissues differed considerably from that of the new or current season's growth, and that the new growth alone probably gave a more accurate index of the relationship of chemical content and blossom-bud formation. Any inclusion of old growth in the samples, therefore, might tend to mask this relationship.

Samples were taken on the following dates during the growing season of 1935: April 15, May 1 and 17, June 4 and 18, July 8, and August 13. In terms of days from full bloom these dates represent 18 days before, 2 days before, and 14, 32, 46, 66, and 102 days after full bloom, respectively. All collections were made in the morning hours, usually between 8 and 11 a. m. The spurs were carefully selected for anatomical uniformity with special attention to length and thickness of the new growth portions. To insure further uniformity in samples a like number of spurs of each type were taken from each of the four trees. Leaves and fruits were removed when the spurs were cut from the tree.

After collection, samples were immediately taken to the laboratory where the spurs were quickly divided into their 3 types of growth, weighed, and killed with boiling redistilled 95 percent ethyl alcohol. The tissues were preserved in 80 percent alcohol, and the flask stoppers were covered with paraffin. The number of spurs comprising a sample averaged about 65. A greater number was required in the earlier samples to insure a sufficient quantity of new growth tissue for analysis. It was felt that because of the physiological uniformity of the material a greater number of spurs per sample was neither necessary nor desirable. Bark and wood tissues were preserved in the same manner as the spurs, and each sample comprised 40 to 60 gm. of fresh tissue. All samples were analyzed within 6 months of the dates of collection. Since some deviations from the usual analytical methods appear in this work a rather detailed description of certain steps in the procedure will be made.

PREPARATION OF MATERIAL

The alcoholic preserving extract was separated from the solid portion of the samples by filtration into volumetric flasks. After several washings with 80 percent alcohol the residue from the containers and filter papers was transferred to a vacuum oven and dried at a temperature of 80° C. for 48 hours and weighed. An aliquot of the liquid fraction was evaporated to dryness and then dried to constant weight at 80° in vacuo. Total dry weight of the tissue was obtained from the combined weights of the two dried fractions.

The dried tissue was ground to a fine powder in a ball mill, and the entire sample was passed through a 100-mesh screen and dried again for 48 hours at 80° C. in vacuo.

EXTRACTION

The method herein described for the extraction of soluble carbohydrates and soluble nitrogen has been found to be more rapid, simple, and complete than the standard Soxhlet method.

Aliquots of from 2.5 to 5 gm. of the dry powder for carbohydrate analysis and of 1 to 2 gm. for nitrogen analysis were transferred to

filter funnels containing a fine qualitative filter paper, and each sample was extracted 20 times with 5-ml. portions of cold 50 percent alcohol. Qualitative tests for carbohydrates and nitrogen on the filtrate of the last extractions were always negative with this type of woody tissue, and it was found that both carbohydrate and nitrogen fractions were much more soluble in 50 percent alcohol than in higher concentrations of this solvent employed in Soxhlet extraction. Also, the number of samples that could be extracted at one time was not limited by the number of Soxhlet extractors on hand, and the use of ordinary folded filter paper lent itself to an easier and a more complete removal of extracted residue than did the Soxhlet thimbles.

The following substances were determined in the combined fractions of material soluble in 50 and in 80 percent alcohol: Free reducing substances, sucrose (soluble carbohydrates hydrolyzed with cold 2.5 percent hydrochloric acid), and nitrogen. The insoluble residue was analyzed for starch and nitrogen.

DETERMINATION OF REDUCING POWER

In all carbohydrate determinations the reduction procedure was essentially that of Quisumbing and Thomas (37). In the estimation of the cuprous oxide a modification of the Shaffer and Hartmann (41) iodometric method was used. This modification consisted of collecting the cuprous oxide precipitate on an asbestos mat in a Gooch crucible and washing it with hot distilled water before it was dissolved for titration. It was discovered that certain materials, other than reducing substances, were present in the tissue extracts and interfered with the iodine-oxidation procedure. Subsequent titrations were therefore variable and inaccurate. Gardner (10) found this same deviation from the Shaffer and Hartmann method necessary when analyzing pear shoots. Since the Fehling solution was discarded in the filtration, a smaller quantity of 5 N sulfuric acid was required to dissolve the copper precipitate. In this work 10 ml. was sufficient.

Sugar equivalents of the copper values were obtained from the tables of Quisumbing and Thomas (37) for dextrose (glucose). This expression was applied to all carbohydrate determinations. According to Quisumbing and Thomas (37), for dextrose, the mean error in their reducing method is ±0.08 mg. of copper, or ±0.12 percent. Although they recommend the use of 50 to 150 mg. of dextrose per reduction, presumably this error applies within the limits of their table, namely, 5 to 250 mg. of dextrose per reduction. Data obtained from analysis of varying amounts of pure dextrose, however, indicated a larger and a seriously increasing error with decreasing amounts of dextrose, below a 9 to 10 mg. content per reduction. Recovery of dextrose in low concentrations is shown in table 2. A factor curve was therefore constructed and applied to all reductions when there was less than 10 mg. of reducing substances in the aliquot.

TABLE 2.—*Reducing value of low amounts of pure dextrose*

Sample No.	Dextrose present	0.1 N sodium thio-sulfate	Dextrose recovered	Sample No.	Dextrose present	0.1 N sodium thio-sulfate	Dextrose recovered
	Milligram	*Milliliter*	*Percent*		*Milligram*	*Milliliter*	*Percent*
1	10.5	3.5	100.0	5	4.6	1.5	90.5
2	9.0	3.0	99.8	6	3.1	1.0	81.1
3	7.6	2.5	97.8	7	1.5	.5	64.3
4	6.1	2.0	95.7				

DETERMINATION OF FREE REDUCING SUBSTANCES

The 50 percent alcoholic extract together with its corresponding aliquot from the original 80 percent preserving alcohol was dealcoholized on a water bath in a current of air. A volume of about 100 ml. was maintained during the evaporation by frequent additions of distilled water. The water extract was cleared with neutral lead acetate and made to volume, filtered, deleaded with anhydrous sodium oxalate, and again filtered. Suitable aliquots of this cleared extract were taken for reduction.

DETERMINATION OF SUCROSE

An aliquot of the cleared extract was hydrolyzed with 2.5 percent hydrochloric acid for 24 hours at laboratory temperature. After hydrolysis the solution was brought almost to the neutral point with sodium hydroxide, made to volume, and the reducing power was determined. The difference between the free reducing values and those after hydrolysis was considered as sucrose.

DETERMINATION OF STARCH

Since considerable importance has been assigned to the association of the starch content of spurs with blossom-bud initiation, a careful study was made to develop a method for the estimation of starch in these tissues. While these studies were under way some chemical methods for starch determination appeared in the literature (*9, 36, 42*). None of these methods was adopted, although later it was found that the procedure herein described gave values in good agreement with the method of Sullivan (*42*). The present method involves the digestion of starch in the ground sugar-free tissues with a commercially prepared purified pancreatic amylase. This preparation was capable of digesting not less than 75 times its own weight of starch to soluble carbohydrates, and gave no blank reduction with Fehling solution even in relatively large amounts. The use of this starch-digesting enzyme of the pancreas overcame practically all of the difficulties found in other enzyme methods, especially those involving the use of enzymes of plant origin. Saliva was found to be generally satisfactory, although the digesting power was at times variable, and it was inconvenient to obtain a supply sufficient for a large number of determinations.

The powdered residue, from which soluble sugars had been removed with 50 percent alcohol, was transferred to 500–ml. Erlenmeyer flasks by washing through the punctured filter paper with about 50 ml. of hot distilled water. The flasks were then placed on a hot plate and

the contents boiled for 1 hour. After cooling to 35° to 40° C., 5 ml. of a 0.25-percent suspension of the pancreatic amylase was added to each flask and the mixture incubated at 40° C. for 1 hour. This gelatinization and enzyme treatment was repeated, and incubation was continued until the tissue was free of starch as determined by the iodine test. Following the second digestion the mixture in the flasks was brought to the boiling point to inactivate the enzyme, cooled, cleared with neutral lead acetate, filtered, and deleaded with dry sodium oxalate. The reducing power was determined directly on 50-ml. aliquots of this cleared solution by the modification of the Shaffer and Hartman (41) and the Quisumbing and Thomas (37) methods as described above.

Values for starch were obtained directly from the reducing power of the cleared enzyme hydrolysate by the use of a factor instead of by the usual acid hydrolysis. This factor was computed from data obtained by digesting known amounts of purified potato starch with the pancreatic amylase under the same conditions as those given the tissue samples. Analyses of a number of purified potato-starch samples ranging from 5 to 50 mg. in the 50-ml. aliquots furnished data for a factor curve applicable to the extremes of sample size.

Starting with weighed duplicates from uniform samples of powdered spur, bark, and wood tissues and carrying through extraction and enzyme digestion to the final reduction, the degree of accuracy was obtained as indicated by the following average percentage variations, calculated from starch percentage on basis of total dry matter: Between 68 pairs of duplicate samples, 3.0 percent; between the best 9 pairs of lot of 68, 0.02 percent; and between the poorest 9 pairs of lot of 68, 7.2 percent. The range of actual starch content was from 0.1 to 15.0 percent.

DETERMINATION OF SOLUBLE AND INSOLUBLE NITROGEN

From 1- to 2- gm. samples of the dry, powdered tissue were extracted 20 times with 5-ml. portions of 50 percent alcohol on filter papers. The extract was combined with a like aliquot of the original preserving alcoholic solution, slightly acidified, and evaporated to dryness in Kjeldahl flasks with a current of warm air. Nitrogen was determined on this dried material by the official Kjeldahl-Gunning-Arnold method.

The residue from the 50 percent alcoholic extraction was dried and transferred to Kjeldahl flasks, and nitrogen was determined by the Kjeldahl-Gunning-Arnold method.

EXPRESSION OF RESULTS

All analytical results are expressed in percentage of dry weight. Although it is desirable, whenever possible, to study and present analyses on the bases of fresh weights and absolute amounts, the tissues to be compared were in some cases in this study so dissimilar in moisture content and volume per unit that interpretations on these bases might not represent the true chemical picture. This is illustrated in table 3.

TABLE 3.—*Differences in total fresh weight per unit and in moisture content of the spur components of Yellow Newtown trees sampled at Wenatchee, Wash., May 17, 1935*

Leader type and sample No.	Spur components	Average fresh weight per unit	Water per unit	Moisture on fresh-weight basis
Nonbearing:		*Gram*	*Gram*	*Percent*
1	1935 growth	1.17	0.832	71.0
2	1934 secondary growth	.52	.303	58.6
3	1934 cluster base	.73	.427	58.6
Bearing:				
4	1935 growth	.55	.401	73.4
5	1935 cluster base	.57	.412	72.7
6	1934 vegetative growth	.60	.345	57.8

Chemical differences between samples 1 and 4, or 1 and 5, for example, could be interpreted accurately on the basis of fresh weight but not in absolute amounts. On the other hand, samples 2 and 4 could be compared as absolute amounts but not as percentages of fresh weight. Samples 1 and 2, 1 and 3, and 1 and 6 could not be compared on either basis.

It was therefore concluded that percentage of dry weight would be a more reliable basis to express the results of this study than either the percentage of fresh weight or absolute amounts per unit. Consideration was given to the expression of results on the basis of residual dry weight (total dry weight minus weight of sugars and starch), as this tends to reduce fluctuations due to seasonal changes. This method of presenting analytical results has considerable merit in many instances, although in the present investigation the comparative values were not altered by this procedure except to accentuate somewhat the maximum and minimum values.

RESULTS OF 1935 ANALYSES

The chemical composition of spurs initiating blossom buds as contrasted with those developing vegetative or leaf buds is shown in table 4. Calculations as percentage of fresh weight gave results much in line with those found in this table, although they showed more variability between tissue samples varying in moisture content. Likewise, when computed as absolute amounts per unit, the trend was similar to analyses expressed as percentage of dry and fresh weights, but the chemical content of spur components was generally in proportion to the actual volume of tissue comprising the component rather than to its possible physiological significance. In order to conserve space, results in percentage of fresh weight and absolute amounts are omitted from table 4.

TABLE 4.—*Free reducing substances, sucrose, starch, soluble nitrogen, and insoluble nitrogen in various components of bearing and nonbearing leaders of biennial-bearing Yellow Newtown trees sampled at Wenatchee, Wash., 1935*

[Calculated as percentages of dry weight]

FREE REDUCING SUBSTANCES[1]

Sampling date	Period before (−) or after (+) full bloom	Bearing leaders — Spur components: New secondary growths	New cluster bases	Old vegetative growths (1934)	Bark from 2- to 4-year-old branches	Wood from 2- to 4-year-old branches	Nonbearing leaders — Spur components: New vegetative growths	Old secondary growths (1934)	Old cluster bases (1934)	Bark from 2- to 4-year-old branches	Wood from 2- to 4-year-old branches
	Days	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent
Apr. 15	−18			1.06	1.22	0.43		0.93	0.54	1.44	0.47
May 1	−2		0.66	.74	1.27	.68	1.54	1.05	.66	1.56	.90
May 17	+14	2.30	.86	.90	1.04	.60	1.61	.98	.24	1.03	.44
June 4	+32	2.08	.34	1.15	1.58	.70	1.49	1.04	.60	1.45	.47
June 18	+46	1.76	.57	1.24	1.42	.59	1.39	1.18	.79	1.35	.35
July 8	+66	1.45	.34	1.42	1.56	.71	.92	1.01	.45	1.28	.42
Aug. 13	+102	1.11	.65	1.39	1.53	.59	.65	.84	.47	1.18	.31

SUCROSE[1]

Sampling date	Period	New secondary growths	New cluster bases	Old vegetative growths (1934)	Bark from 2- to 4-year-old branches	Wood from 2- to 4-year-old branches	New vegetative growths	Old secondary growths (1934)	Old cluster bases (1934)	Bark from 2- to 4-year-old branches	Wood from 2- to 4-year-old branches
Apr. 15	−18			0.85	2.04	0.33		1.21	1.83	1.78	0.43
May 1	−2		1.63	.51	1.65	.38	1.59	.91	1.83	1.83	.49
May 17	+14	1.33	2.12	.81	1.13	.15	1.10	.83	1.05	1.03	.44
June 4	+32	.02	1.16	.55	.79	.04	.61	.48	.62	.84	.10
June 18	+46	.58	1.33	.50	.87	.12	.54	.53	.72	.71	.21
July 8	+66	.51	1.65	.64	.98	.24	.64	.72	.99	1.05	.27
Aug. 13	+102	.63	1.44	.55	1.32	.34	.77	.70	.92	1.36	.39

STARCH

Sampling date	Period	New secondary growths	New cluster bases	Old vegetative growths (1934)	Bark from 2- to 4-year-old branches	Wood from 2- to 4-year-old branches	New vegetative growths	Old secondary growths (1934)	Old cluster bases (1934)	Bark from 2- to 4-year-old branches	Wood from 2- to 4-year-old branches
Apr. 15	−18			5.08	7.24	9.14		8.21	0.95	4.00	0.34
May 1	−2		0.00	1.05	1.20	1.20	Trace	3.88	4.24	1.37	3.45
May 17	+14	Trace	0	2.66	1.22	2.94	1.47	4.67	5.68	2.50	4.47
June 4	+32	1.50	Trace	1.59	.94	.74	3.56	5.99	4.65	4.21	2.70
June 18	+46	2.99	.86	2.66	1.25	.80	5.68	6.34	4.68	3.35	4.27
July 8	+66	6.41	2.59	3.96	1.86	1.28	9.54	8.53	7.47	4.42	4.82
Aug. 13	+102	11.95	10.85	6.57	3.25	3.27	15.15	13.15	13.45	7.92	8.86

SOLUBLE NITROGEN

Sampling date	Period	New secondary growths	New cluster bases	Old vegetative growths (1934)	Bark from 2- to 4-year-old branches	Wood from 2- to 4-year-old branches	New vegetative growths	Old secondary growths (1934)	Old cluster bases (1934)	Bark from 2- to 4-year-old branches	Wood from 2- to 4-year-old branches
Apr. 15	−18			0.26	0.16	0.03		0.24	0.54	0.11	0.11
May 1	−2		1.29	.37	.10	.11	0.81	.17	.49	.07	.03
May 17	+14	0.54	1.27	.23	.14	.08	.52	.21	.61	.14	.05
June 4	+32	.21	1.35	.14	.06	.02	.32	.13	.57	.08	.03
June 18	+46	.23	1.06	.19	.08	.05	.26	.14	.46	.06	.02
July 8	+66	.18	.95	.14	.05	.03	.24	.18	.58	.06	.03
Aug. 13	+102	.14	.69	.10	.07	.05	.17	.16	.40	.07	.05

INSOLUBLE NITROGEN

Sampling date	Period	New secondary growths	New cluster bases	Old vegetative growths (1934)	Bark from 2- to 4-year-old branches	Wood from 2- to 4-year-old branches	New vegetative growths	Old secondary growths (1934)	Old cluster bases (1934)	Bark from 2- to 4-year-old branches	Wood from 2- to 4-year-old branches
Apr. 15	−18			1.01	0.71	0.18		0.87	1.36	0.72	0.21
May 1	−2		2.37	.86	.80	.25	2.08	.80	1.11	.53	.16
May 17	+14	1.50	1.97	.70	.69	.30	1.40	.78	1.13	.63	.23
June 4	+32	.83	1.63	.56	.54	.18	.82	.67	1.05	.55	.18
June 18	+46	.71	1.60	.61	.57	.21	.71	.62	.97	.56	.18
July 8	+66	.65	1.57	.55	.53	.17	.69	.68	1.04	.61	.19
Aug. 13	+102	.58	1.22	.48	.57	.18	.43	.42	.90	.55	.17

[1] Expressed as dextrose.

The data (table 4) show some important chemical relationships between the various spur components. Pronounced chemical differ-

ences exist in the various morphological structures comprising the spur. This appears to give ample justification for the steps taken in excluding unlike tissues from samples in this investigation. Also, it may be noted that, with the exception of the starch analyses, samples of similar tissues, from leaders showing extreme physiological differences insofar as blossom-bud formation is concerned, show a striking parallelism in chemical composition. This reflects the uniformity of materials selected for sampling.

To assist in following the chemical changes in various tissues it might be well to point out that under the headings of bearing and nonbearing leaders the type of tissue in the samples, arranged from left to right, corresponds to the position they occupied on the tree in relation to the spur bud. For example, in bearing leaders the buds (leaf) were borne by new secondary growths which had their origin on new cluster bases. Old vegetative growths gave rise to new cluster bases. With nonbearing leaders, the buds (blossom) were on new vegetative growths, which in turn were borne by old secondary growths, etc.

Results of analysis for the various substances are discussed under their respective headings.

FREE REDUCING SUBSTANCES

In general, little seasonal change in reducing substances, as shown in table 4, was found to occur in structures showing but slight increases in dry matter; in other words, with those not having made extension growth. New secondary growths of bearing spurs and new vegetative growths of nonbearing spurs, on the other hand, show a gradual reduction in percentage as the season progressed, and the new secondary growths are at each date slightly higher in reducing substances than the new vegetative growths.

New cluster bases of bearing spurs show values considerably lower than those for new secondary growths throughout the period. This fact is probably worthy of special emphasis, for it illustrates that as intimately as these two components are connected they differ materially in chemical composition. Not only is this true of the new growths, but it may be seen that old 1934 cluster bases are also much lower in free reducing substances than new vegetative growths, old secondary growths, or bark of the nonbearing leaders. Bark tissues in branches of both bearing and nonbearing leaders are significantly higher in reducing substances than the wood tissues.

From the June 4 sampling date to August 13, free reducing substances were higher in comparable components from branches bearing fruit than from nonbearing branches. Thus the new secondary growth from bearing leaders was higher in free reducing substances on each date than the new vegetative growth from spurs of nonbearing leaders, although the latter were initiating flower primordia during this period and the former were not. Similarly, bark and wood of bearing leaders were higher in reducing matter than bark and wood of the nonbearing leaders on the same dates. Thus these analyses would indicate that a high concentration of the compounds included in free reducing sugars, as a group, is not responsible for the differentiation of blossom buds.

SUCROSE

No seasonal trend is evident in the sucrose content in any of the spur components which could be considered as having a direct bearing on the initiation of blossom buds. However, it is rather interesting to note that, in practically every case, the lowest percentages were found during the period in which blossom-bud initiation was assumed to take place.

At given dates new secondary growths of bearing spurs and new vegetative growths of nonbearing spurs are very similar in sucrose content. Wood samples of both bearing and nonbearing branches show the lowest sucrose content, and the values are very similar throughout the season. Corresponding analyses can be found in bark from bearing and nonbearing branches with gradients descending to the June 4 to 18 samples and ascending somewhat thereafter. The sucrose percentages of old vegetative growths and old secondary growths show nothing significant when contrasted, and little seasonal trend is evidenced. New cluster bases show a relatively high sucrose content as compared with other tissues at each sampling date. In relation to the new secondary growths the chemical picture of new cluster bases is just reversed from that of free reducing substances.

STARCH

Aside from the fact that spurs were separated into their components and analyzed as individual samples, the cycle of seasonal starch changes is in general agreement with analyses that have appeared in the literature on similar investigations.

With the exception of the April 15 sample of bark and wood, nonbearing spur components, bark, and wood were at all times higher in starch than comparable tissues of bearing leaders. The high values in the April 15 samples, of course, are due to reserve starch from the preceding growing season, and this shows a rapid decline by May 1, especially in the bearing tissues. In nonbearing leaders starch appears to accumulate immediately after full bloom, and in general it displays ascending gradients in all tissues, reaching quite high concentrations by August 13. Samples from bearing leaders, on the other hand, did not increase permanently in starch concentration until after May 17 in new secondary growths and not until after June 4 in all the other components.

Since leaf buds originate on the new secondary growths of bearing spurs, and blossom buds on new vegetative growths of nonbearing spurs, differences in starch percentage of these structures are of particular interest. The fact that growth structures resulting in the formation of blossom buds develop earlier, accumulate starch earlier, and contain a higher percentage of starch preceding, during, and following bud differentiation than those resulting in the formation of leaf buds, offers additional evidence of the association of the mechanism of starch synthesis and deposition with that of blossom-bud formation.

However, starch, as such, can hardly be the active principle in the initiation of flower primordia. For, were it so, the buds of new secondary growths should have differentiated blossom buds late in the season when the starch concentration equaled or exceeded that of nonbearing spurs at their differentiation period. If an association of

starch and fruitfulness exists, it is undoubtedly correlated with the physiological state or age of the bud meristem. This point is reserved for later discussion (p. 30).

Differences in starch percentage between spur components are again evident. Had new cluster bases of bearing spurs been included with new secondary growths the combined tissues would have shown lower starch concentrations at all sampling dates. If old vegetative growths had been included, the May 1 and May 17 samples would have shown values for starch when it was nonexistent in the new growths.

In samples taken August 13 the percentages of starch in both bearing and nonbearing tissues show a descending gradient from the structures bearing the bud to the more distant portions. This seems to indicate that, in the building up of reserves in the spur, dominance for starch deposition is correlated with proximity to the apical bud.

SOLUBLE NITROGEN

As calculated in percentage of dry weight the seasonal trend of soluble nitrogen in the main is of a descending order. This is not so evident in the old spur growths, bark, and wood, but quite uniformly so in the new growths of both bearing and nonbearing spurs. With the exception of new cluster bases, concentrations of soluble nitrogen in all samples, especially those of bark and wood, are rather low. The higher percentages found in new cluster bases are of interest. Even the old cluster bases of nonbearing spurs show relatively higher values. The possible physiological role of soluble nitrogen in cluster bases is perhaps a matter of conjecture.

The data in table 4 show that percentages of soluble nitrogen in the new secondary growths of bearing spurs and the new vegetative growths of nonbearing spurs, for a given date, are quite similar, though during the period of bud differentiation (June 4 to August 13) those on nonbearing leaders, and thus the ones differentiating flower parts, were always slightly higher. Other like tissues of bearing and nonbearing leaders, excluding cluster bases, were very similar in soluble nitrogen content.

INSOLUBLE NITROGEN

The values for insoluble nitrogen in general show a parallel seasonal trend with those for soluble nitrogen, although the actual percentages are substantially higher. Higher concentrations of nitrogen, included in this insoluble fraction, are again present in the new cluster bases as compared with new secondary growths, or for that matter, any other type of tissue sampled. Comparable tissues of bearing and nonbearing leaders sampled on the same date exhibit very similar analyses. This includes the new secondary growth and new vegetative growths; consequently no relationship can be found between percentage of insoluble nitrogen and blossom-bud differentiation.

1936 ANALYSES

METHOD OF SAMPLING

To link chemical composition definitely with blossom-bud formation, the 1935 analyses in table 4 are subject to two main criticisms. First, a further separation of tissue is necessary. Heinicke found a con-

spicuous difference in chemical content between buds and the remaining portions of new spur growths (*21*). Therefore, samples of bud tissues alone would have been very desirable, but it was not possible to remove the large number of buds required in 1935. The second criticism pertains to the lack of information regarding the critical time of differentiation.

To obtain information relative to the latter, during the early summer of 1935, a large number of bearing and nonbearing spurs on the same tree but on different main leaders were tagged and measured at intervals for extension growth; and terminal-bud formation was also observed. It was found that on spurs making a final growth of 5 cm. in length, terminal buds were formed on nonbearing spurs in 23 days after full bloom, and on bearing spurs 25 days after full bloom. The proximity of time of terminal-bud formation on these different types of growth is of interest in view of the difference in time of the beginning of growth. Nonbearing spurs began growth about 10 days earlier than the secondary growths of bearing spurs. This indicates that in determining the periods of terminal-bud appearance, termination of elongation, and blossom-bud differentiation, the number of days after full bloom may serve as a more suitable index than, for example, days after beginning of growth.

Microscopic examination of buds from nonbearing spurs, 5 cm. in length, revealed the first indication of flower primordia 45 days after terminal-bud formation, or 68 days after full bloom. Since it has been shown (*19*) that blossom-bud differentiation on these biennial-bearing Yellow Newtown trees can be influenced by leaf adjustments as late as 44 days after full bloom, it was concluded that the interval between the latest day on which buds could be influenced by leaf adjustments and the appearance of flower primordia should be selected as the time to take bud samples for chemical analysis.

In 1936, 58 days after full bloom, samples of new secondary spur growths of bearing leaders and new vegetative spur growths of nonbearing leaders were taken for chemical analysis. Care was exercised in the selection of spurs for this study, and only those that closely approximated 5 cm. in length were included in the samples. It was felt that for this length of new growth, 58 days after full bloom closely approached the actual time of blossom-bud initiation.

Over 600 bearing spurs and over 400 nonbearing spurs were required to furnish sufficient material for analysis. Leaves were removed in the orchard, and the spurs were taken to the laboratory where bud tissues were separated from the remaining portions of the new growths. The meristematic tissue at the base of the bud was included in bud samples and was separated from the woody portion of the new growth by cutting thin slices of the soft tissue until cells encountered were somewhat resistant to cutting. Buds and basal portions of the new growth were preserved and analyzed separately. Methods of preserving, extracting, and analyzing were identical with those previously described (p. 5).

RESULTS OF 1936 ANALYSES

The analyses (table 5) are given as percentages of dry weight and of fresh weight and as absolute amounts per unit. In comparing the three methods of expression, due consideration should be given to the differences in weight of dry matter of the components, as misleading

interpretations may result if absolute amounts alone are considered. Differences in composition between samples on the basis of fresh weight follow those of dry weight rather closely and for these tissues would probably be equally reliable.

TABLE 5.—*Composition of buds and new growths of bearing and nonbearing Yellow Newtown apple spurs sampled 58 days after full bloom at Wenatchee, Wash., 1936*

Description of sample	Dry matter per unit	Free reducing substances			Starch			Soluble nitrogen			Insoluble nitrogen		
		Dry-weight basis	Fresh-weight basis	Per unit	Dry-weight basis	Fresh-weight basis	Per unit	Dry-weight basis	Fresh-weight basis	Per unit	Dry-weight basis	Fresh-weight basis	Per unit
Bearing spurs:	*Mg.*	*Pct.*	*Pct.*	*Mg.*	*Pct.*	*Pct.*	*Mg.*	*Pct.*	*Pct.*	*Mg.*	*Pct.*	*Pct.*	*Mg.*
Buds from secondary growth	20	1.62	0.65	0.32	1.89	0.76	0.37	0.22	0.09	0.04	0.98	0.39	0.19
New secondary growths minus buds	117	1.48	.61	1.74	5.21	2.17	6.12	.24	.10	.28	.66	.27	.77
Nonbearing spurs:													
Buds from vegetative growth	46	1.29	.55	.60	4.88	2.09	2.26	.20	.09	.09	.89	.38	.41
New vegetative growths minus buds	289	.77	.36	2.22	9.72	4.59	28.10	.22	.10	.63	.57	.27	1.04

Considering the data on either of the percentage bases, the composition of buds differs significantly from that of the corresponding new spur growths. Both bearing and nonbearing buds show higher percentages of reducing substances and insoluble nitrogen than the basal new-growth tissue. The differences in soluble nitrogen are probably within the limits of error and are therefore not considered as significant. The greatest contrasts are found in starch, and here the basal new-growth tissues are manifestly higher than bud tissues.

That buds containing or soon to develop blossom primordia differ in composition from those forming leaves alone is quite obvious. The differences are not great in reducing substances or soluble and insoluble nitrogens, although the buds (leaf) on bearing spurs show higher percentages than those on nonbearing spurs. Comparatively high concentrations of starch are again associated with the development of blossom buds. Although the starch content of buds is less than that of the spur tissues on which buds are borne, differences between the two types of buds are of a greater magnitude than when bud and spur tissues were combined in the sample (table 4).

It is therefore definitely concluded that the higher percentages of starch found in new spur growths of nonbearing spurs, as compared with those of bearing spurs, reflect a similar relative condition existing in buds at the time of blossom-bud initiation.

DISCUSSION OF RESULTS FROM CHEMICAL ANALYSES

The pronounced differences in chemical composition found in the various parts of the spur make it evident that, in analyses for carbohydrate and nitrogenous metabolites, it is highly desirable to determine, separately, rather restricted portions of the spur. By grinding

up and analyzing whole spurs, combining new and old growths or even dissimilar structures of the same year's growth, one may obtain an average composition that is quite unreliable from the standpoint of physiological interpretation. Disagreements in analyses and elucidations of chemical studies of fruit spurs, by many investigators in the past, have undoubtedly been due, in part, to the inclusion of materials having little or no relationship to the bud meristem.

Lagasse (29) previously found very marked differences in composition of new cluster-base and secondary-growth structures especially in the nitrogen fractions and suggested that these components be separated for analysis. Results obtained in the present investigation are in complete agreement with those of Lagasse. The high nitrogen content found in the new growth of bearing spurs by Harley (15) and many others was undoubtedly the result of including new cluster bases in the sample. Physiological significance heretofore attributed to high nitrogen in bearing spurs, as related to the initiation of vegetative buds, is therefore probably without foundation.

In this study high starch content appears to be correlated with the inception of blossoms. A slightly lower reducing-sugar content was also found in differentiating buds. In what way these correlations can be translated to account for the profound change that takes place in the bud meristem with the induction of floral primordia is not known. However, two possibilities, both of which may serve as useful working hypotheses, can be considered.

The first of these is based on the assumption that energy is required for differentiation and that this energy is supplied by the reserve carbohydrate, starch. It is somewhat difficult to conceive that a comparatively inert substance like starch could be the active principle in supplying this energy, but it is recognized that in living tissues starch is quite reactive and can be rapidly converted to soluble forms capable of furnishing energy. Soluble sugars are seldom stored as reserves in woody tissues of the apple. It is of interest, however, that reducing sugar is actually lower in the new vegetative growths of nonbearing spurs (table 4) that are differentiating blossoms than in similar tissues of bearing spurs.

Late in the growing season when bud cells are no longer meristematic, starch tends to accumulate in all tissues, especially the bud-bearing new secondary growths; however, no blossom buds are formed.

The other possibility to account for blossom-bud differentiation is that a specific hormonelike substance is produced in leaves and moves to certain regions of the stem where blossoms are initiated. This is but a new version of an old suggestion advanced by Sachs as far back as 1865, which, in the light of our present knowledge of plant physiology, is now highly probable. If a specific factor, or a group of factors, is the active principle in the inception of flower primordia, it can be concluded with reasonable certainty that the mechanism giving rise to this factor or hormone is very intimately related to the synthesis and deposition of starch. For all practical purposes, the concentration of starch in meristematic bud tissues can probably be used as an index of the fruiting potentialities of that bud. This starch-fruitfulness relationship is not limited to apple spurs but has been found in reproductive tissues of other species (8, 44).

PHYSIOLOGICAL STUDIES

Many attempts have been made to influence the formation of blossom buds in the apple by such cultural methods as pruning, fertilizing, and other field treatments (3, 17, 25, 30, 38). Much of this work was conducted on biennial-bearing varieties in an effort to discover a correction for the alternating habit by bringing trees into a nutritional balance corresponding to the fruitful class 3 of Kraus and Kraybill (27). In summarizing the results of a 12-year investigation, which represents in general the conclusions of others, Auchter and Schrader (3) state:

Various cultural, fertilizer, and detailed pruning treatments of York Imperial trees in Maryland have failed to materially influence the biennial bearing habit of this variety even though the growth conditions of the tree approached the vegetativeness which has been associated with annual cropping.

Under the growing conditions of the Pacific Northwest it was found (17) that, after formation of the terminal bud, variations in soil moisture and applications of nitrogenous fertilizers had no pronounced effect on blossom-bud formation in the Delicious variety. The soil in the experiments, however, was not permitted to remain at the wilting point for any appreciable time. Studies conducted elsewhere (2, 12, 32, 33) indicate that blossom-bud formation is increased as a result of rather prolonged periods of early summer drought.

Perhaps no approach to the problem has contributed as much to the present knowledge of the basic principles underlying blossom-bud initiation as has the full appreciation of the influence of leaf area on growth and reproduction in the tree. It has been demonstrated (1, 17, 18, 35) that unless apple trees possess enough leaf area above that necessary for fruit and tree growth, no blossom buds are formed for a crop the following year.

In view of the apparent vital importance of leaf function in reproductive processes, experiments were conducted by making leaf-fruit and leaf-bud adjustments in apple trees, to study the effects of such treatments on the development of blossom buds. Varieties studied were Yellow Newtown, Delicious, Jonathan, and Winesap.

BLOSSOM-BUD FORMATION ON SPURS WITH DIFFERENT LEAF AREAS

Magness (31) in 1917 and later Harvey and Murneek (20) and Roberts (39) found that removal of leaves from nonbearing spurs effectively prevented the development of flower parts in the bud. It was also shown that the bud of a spur was influenced primarily by the leaves of that particular spur. Results obtained in the present investigation with biennial-bearing Yellow Newtown trees are in agreement with these findings.

Alternate spurs on nonbearing main leaders were defoliated to 1 large leaf (immediately below the bud) per bud 33 days after full bloom; remaining spurs averaged from 6 to 10 leaves per bud. The average area of the leaves on defoliated spurs was 8.65 square inches. Bloom records the following spring revealed that 65.6 percent of the untreated spurs had blossomed. Only 3.6 percent of adjacent spurs with 1 leaf per bud had formed blossom buds. In some instances double spurs were encountered where 2 vegetative-spur growths originated from a single cluster base. When 1 of these was defoliated

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to 1 leaf per bud, but the other remained untreated, 17.5 percent of the buds on the defoliated part formed blossoms.

These results offer further evidence that single fruit spurs tend to function as individuals insofar as blossom-bud formation is concerned, and that differentiation is dependent largely on substances originating from leaves borne by the immediate new spur growth. With double spurs some movement of materials responsible for blossom-bud initiation from one branch spur to the other appears to take place. This apparent limited ability of the bud to obtain metabolites, other than those having their origin in the parent tissue, is in direct contrast with the power exhibited by apple fruits in obtaining nutrients from relatively distant sources (14). When records were taken it was noted that where blossoms occurred on defoliated single spurs the buds were invariably borne on spurs that had made rather short vegetative growths the preceding summer. This suggests that some differentiation might have taken place in these spurs prior to defoliation (43).

Further information on the effect of different leaf areas on blossom-bud formation was obtained from defoliation experiments during the growing seasons of 1934, 1935, and 1936. Again using the main leader method, nonbearing spurs of completely off-year trees were defoliated to 1, 2, 3, and 4 large leaves per spur on separate leaders. Whenever available, 1 leader was left untreated. Leaves were removed by cutting the petioles about midway between the leaf blade and spur with scissors or fruit-thinning shears. Injury to the spur or drying out of spur tissue was not observed to occur following this practice. The number of spurs on each leader varied from 800 to 1,200. Buds on terminal growths, although defoliated, were not included in the final averages in this study. After defoliation, especially on those leaders defoliated to 1 or 2 leaves per spur, the terminal buds would sometimes become vegetative and push out into second growth. Whenever this took place the spurs were either redefoliated and included in the data or tagged and omitted from the percentage figures. This second elongation growth will be discussed later (p. 20).

Results of these experiments on Yellow Newtown and Delicious trees are summarized in table 6. The relationship between leaf area and the development of blossom buds is again apparent. In general, the increase in percentage of spurs blossoming follows the increase in number of leaves borne by the spur the preceding summer, although in most instances the gradients are not uniform. The abrupt rise in percentage of spurs blossoming on leaders with three leaves per spur over that on those with two leaves per spur is of particular interest. That this sudden increase is not due to chance variation is evidenced by its occurrence to some degree on every tree. The performance of the Yellow Newtown tree defoliated 29 days after full bloom (table 6) is the only instance that could be considered as a deviation from the striking differences found between the two- and three-leaf spurs. The fact that this tree had somewhat larger leaves than the others might partially account for this apparent deviation.

TABLE 6.—*Effect of different leaf areas on blossom-bud formation on spurs of non-bearing main leaders of Yellow Newtown and Delicious trees at Wenatchee, Wash., 1934–36*

Variety	Period from full bloom to defoliation	Leaves per spur [1]	Average area per leaf	Spurs forming blossom buds
	Days	*Number*	*Square inches*	*Percent*
Yellow Newtown_____	24	1	8.6	0
		2		3.1
		3		56.5
		4		56.4
		8-10		96.6
Delicious_____	25	1	6.1	6.7
		2		11.5
		3		66.0
		4		97.4
		8-10		98.5
	26	1	8.7	0
		2		.2
		3		40.4
		4		38.0
		8-10		89.0
	28	1	9.1	1.3
		2		7.0
		3		72.3
		4		68.9
		8-10		88.9
	28	1	9.3	.5
		2		5.0
		3		28.8
		4		41.4
		8-10		97.0
Yellow Newtown_____	29	1	9.4	7.1
		2		32.0
		3		52.8
		4		50.4
		8-10		96.4
	31	1	8.7	2.1
		2		4.2
		3		51.5
		4		52.4
	31	1	9.3	.0
		2		8.4
		3		28.0
		4		50.4
	33	1	8.7	.3
		2		1.7
		3		29.0
		4		32.4
		8-10		97.2

[1] Spurs with 8-10 leaves were untreated.

The data as a whole indicate a basis for three important assumptions bearing on the formation of blossom buds. First, in trees where free movement of photosynthates is permitted, there is a quantitative relationship between leaf area and the development of blossom buds. Leaders used in this experiment bearing no fruit show a critical leaf area for blossom-bud differentiation somewhere between 17 and 28 square inches per spur bud. Second, since relatively few buds differentiated flower parts with one and two leaves per spur bud and a relatively large number resulted with three leaves, it is evident that the movement of the flower-producing substance is away from the bud until the requirements of other tissues have been met. When this movement was prevented, by bark-ringing smaller branches on the same leaders, an average of 86.8 percent of the spur buds on the girdled branches with two leaves per spur bud formed blossoms, whereas only 1.7 percent of those on the adjacent unringed branches formed them. Evidence that the flower-producing substance moves to the roots is found in the analyses of Davis (8) where, on May 7, June 9, and July 2, 1928, the roots of nonbearing prune trees showed a much

higher percentage of starch than did the nonbearing spurs. Third, the ability of a given leaf area to form the flower-producing substance appears to vary with the variety. It can be noted that a higher percentage of the spur buds formed blossoms on the Delicious than on the Yellow Newtown, although the area per leaf was less. This conclusion, however, could not be accepted as final on the basis of the present limited data if it did not have the support of other investigations (33).

The differences in blossom buds formed between the 3 and 4 leaves per spur bud in Yellow Newtown trees do not show any consistent quantitative relationship. In view of the extremely high percentages of fruit buds formed with 8 to 10 leaves per spur, a larger number of blossom buds are undoubtedly actually formed with 4 leaves, but in this study the percentage increments were probably not sufficiently great to overcome normal variation.

BLOSSOM-BUD FORMATION ON VEGETATIVELY ELONGATING DEFOLIATED SPURS

As stated previously, when entire main leaders were defoliated to one or two leaves per spur bud, a second apical growth sometimes occurred. This phenomenon is by no means rare in deciduous fruit trees, for mid- or late-season foliation has often been observed following leaf destruction by insects or other agencies. The fact that this second growth may be found on nonbearing spurs following defoliation is of interest from the standpoint of growth and reproductive relationships.

It was noted during the summer of 1935 that of the nonbearing spurs on off-year leaders defoliated to one and two leaves per spur bud about 40 percent pushed out into second growth. About 3 percent of second growth occurred with three leaves per spur bud, but none with four leaves or more. Leaf per spur bud adjustments were made 36 days after full bloom, and second growths were observed 38 days after defoliation or 74 days after full bloom. A relatively large leaf area developed on these new growths, followed by terminal-bud formation. Blossom records in 1936 disclosed that 58 percent of these second-growth spurs had formed blossom buds.

It can be conservatively estimated that flower buds in these second-growth buds were initiated more than 100 days after full bloom, and the results indicate that differentiation is possible over a rather long period if the buds are brought into the proper physiological state. The experiment also indicates that the bud meristem is primarily vegetative, and it will only develop flower primordia when associated with a given leaf area.

Additional studies on the effect of defoliation and bark-ringing on blossom-bud formation and vegetative elongation were made in 1936. Two large main leaders of a biennial-bearing Yellow Newtown tree in the off year were completely defoliated, except for two leaves immediately below each spur bud, 30 days after full bloom. Leader A received no further defoliation treatments, whereas leader B was redefoliated to two leaves per spur bud 63 and 93 days after full bloom. One large branch of each leader was bark-ringed 44 days after full bloom. Blossom development from these leaf per spur adjustments is shown in table 7.

TABLE 7.—*Effect of defoliation and bark-ringing on second-growth and blossom-bud development on two main leaders of a nonbearing Yellow Newtown tree at Wenatchee, Wash., 1936*

Branch treatment	Leader A; defoliated to 2 leaves per spur bud 30 days after full bloom; no redefoliation				Leader B; defoliated to 2 leaves per spur bud and redefoliated 63 and 93 days after full bloom			
	Spur buds making secondary growth		Spur buds making no secondary growth		Spur buds making secondary growth		Spur buds making no secondary growth	
	Portion of total spur buds	Spur buds forming blossoms	Portion of total spur buds	Spur buds forming blossoms	Portion of total spur buds	Spur buds forming blossoms	Portion of total spur buds	Spur buds forming blossoms
	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent
Unringed	67	77	33	1	42	0	58	2
Ringed	74	100	26	83	61	98	39	93

With only two leaves per spur bud, more than half the buds pushed out into second growth except on unringed branches of leader B. Similar to findings in the earlier experiments, a high percentage of second-growth spurs on unringed branches formed blossom buds, whereas but 1 percent of those that did not become vegetative (leader A) formed them. On ringed branches both types of spurs differentiated a very high percentage of blossom buds in both leaders A and B. On unringed branches of leader B (redefoliated), however, but 2 percent of the spurs that did not make second growth and none of those that did formed blossom buds.

These data again emphasize the relationship between leaf area and blossom-bud initiation. They also indicate that much less leaf area is required for blossom buds to form if the movement of photosynthates to other portions of the tree, presumably the roots, is prevented.

Aside from the effect of the above treatments on blossom-bud formation, the growth performance of defoliated spurs on ringed branches is of interest from the standpoint of growth-promoting factors. It can be seen that second growth took place on branches ringed as well as unringed, suggesting that the substance responsible for growth initiation is stored in tissues above the ring. A criticism of this assumption lies in the fact that the rings were made 14 days after defoliation, in which event the growth substance could have moved into the buds before the bark ring was made. To provide a further test for this possibility, branches from an off-year Yellow Newtown tree were both defoliated to one leaf per spur bud and ringed at four different periods after full bloom, as follows:

Period after full bloom: *Spurs producing second growths (percent)*
28 days -- 85.9
35 days -- 84.9
42 days -- 89.3
49 days -- 92.7

These results seem to indicate that, unless transported in the xylem, the growth-promoting factor is located above the ring, probably in the bud tissues, and its activity is apparently inhibited by leaf metabolism when a sufficient leaf area is present.

In the experiments of 1936 (table 7) the interval between the first defoliation and redefoliation was 33 days. Second growth following

the first redefoliation was in all cases vegetative, and these were again redefoliated 30 days later. No blossom buds were formed in any of the redefoliated spurs (leader B). Since blossom buds were formed on second growth when not redefoliated (leader A), it was of interest to determine when flower primordia were laid down and what the response of these buds would be to redefoliation after blossom differentiation.

In 1937 a large main leader of an off-year Yellow Newtown tree was defoliated to 2 large leaves per spur bud, 32 days after full bloom. Of the defoliated spurs, 230 made second growths, and these were redefoliated 45 days later. On August 18, or 25 days after redefoliation, it was found that 13 of the 230 redefoliated spurs were blossoming. This indicated that bud tissues were capable of growth even though blossom buds had already differentiated. Also, the critical time for the beginning of blossom-bud initiation was probably somewhat near 45 days after defoliation in these trees.

TIME OF BLOSSOM-BUD DIFFERENTIATION

Microscopic examination of bud meristems has been employed for many years in determining the first visible evidence of blossom-bud differentiation and at the present time is probably the only known effective method. Many excellent studies have been reported on the time flower primordia appeared in buds, and this information has been of incalculable value to the knowledge of fruit-tree reproduction. Unfortunately, these researches have had rather limited applications in many instances owing to the lack of a prescribed "physiological base line" for time measurements. Calendar dates of initial spring growth and blossoming are known to vary as much as 24 days from one year to another. This obviously precludes the use of calendar dates for bud-initiation studies except for the conditions that exist in a particular year and at a definite place.

Some growth indexes that may serve to date from are full bloom, cessation of extension growth, formation of the terminal bud, or, as suggested by Barnard and Read (6), the time when spur leaves have reached full growth. Throughout this and other investigations (17, 18, 19, 34) full bloom has been the physiological index, and all time records of treatment and response have been signified as the number of days from its occurrence. Full bloom, as here designated, refers to the day blossom petals begin to fall. In all cases records of full bloom apply only to the orchard in which the experiments were performed and to the varieties under study.

In summarizing the results of a comprehensive microscopic study on the time of blossom-bud differentiation in pome and stone fruits of Australia, Barnard in 1938 (5) stated:

In pome fruits the time of bud differentiation seems to be more closely related to the size of the current season's crop and to the *time of cessation of shoot elongation growth* [italics writers'] than to climatic conditions. * * * Generally speaking, all the evidence indicates that differentiation occurs latest in the trees of the one variety which are most vigorous and vegetative.

Barnard and Read (6) also found apple buds to differentiate from 5 to 6 weeks after the spur leaves reached full growth.

Here is convincing evidence that the time of differentiation of a spur bud depends primarily on the growth characteristics of that spur and that seasonal influences are operative only as they affect growth

conditions. The fact that differentiation occurred within a given time after cessation of extension growth suggests at once that this time interval is probably very similar in all spurs regardless of the time of growth cessation.

In the spring of 1935 a large number of spurs were tagged and elongation was measured at frequent intervals until it had ceased. These measurements were made on a Yellow Newtown tree that exhibited the main leader type of biennial bearing. Two leaders were definitely on year, while the remaining three were entirely off year. Both secondary growths of bearing spurs and vegetative growths of nonbearing spurs were included in the study. Terminal-bud development was recorded in all growths. After measurements were completed both types of spurs were divided into five classes according to their length growth. The results are graphically represented in figures 1 and 2.

The question might well be raised as to whether or not a length growth of 33 cm. could be considered as spur growth. The trees in this experiment were very vigorous, and growths of this length from fruiting structures were quite numerous. Account must also be taken of the fact that these biennial-bearing off-year leaders formed blossom buds on practically every new growth regardless of length or character.

It is quite evident from this study that the time of terminal-bud development in both bearing and nonbearing spurs varies with the length of growth made by the spur. The longer growths tend to form terminal buds later in the season. In view of the findings of Barnard and Read (6) on the relation of blossom-bud initiation to shoot growth, it is believed that length of growth, time of terminal-bud formation on the spur, and time of blossom-bud initiation are very closely correlated.

This offers an explanation for the observed behavior of certain varieties or of individuals of a given variety which tend to be annual bearers whereas others tend to be biennial. Rome Beauty, normally an annual-bearing variety, makes rather long spur growths, and it has been shown (34) that by leaf-fruit adjustments these spurs can be influenced to form blossom buds over a longer period than other varieties making shorter spur growths. Delicious trees in a high state of vigor were found to respond to similar treatments by the formation of blossom buds at a later date than less vigorous trees of the same variety (34).

Figures 1 and 2 are of interest also from the standpoint of selecting spurs for chemical analysis in blossom-bud studies. The desirability of selecting spurs of uniform length to represent accurately conditions within the spur in relation to blossom-bud initiation appears to be amply justified. For example, in figure 1, class *D* spurs represent an entirely different stage of bud development from those in class *A* at a given sampling date, and it is logical to expect that the chemical composition would also be different.

TIME DURING WHICH BUDS CAN BE INFLUENCED TO INITIATE BLOSSOM PRIMORDIA

It has been known since 1899 (11) that in the summer a critical period exists in buds during which the differentiation of the following season's blossoms can be seen. Only within comparatively recent

years, however, has the period during which buds could be influenced to form blossoms been brought to light (*2, 17, 34*), and therein lies the basis for the present method of attack on the problem of biennial bearing.

The technique employed in these investigations to determine the time during which buds could be influenced consisted of bark-ringing at intervals during the growing season and of making leaf-fruit adjustments on the ringed branches. In the following spring, detailed
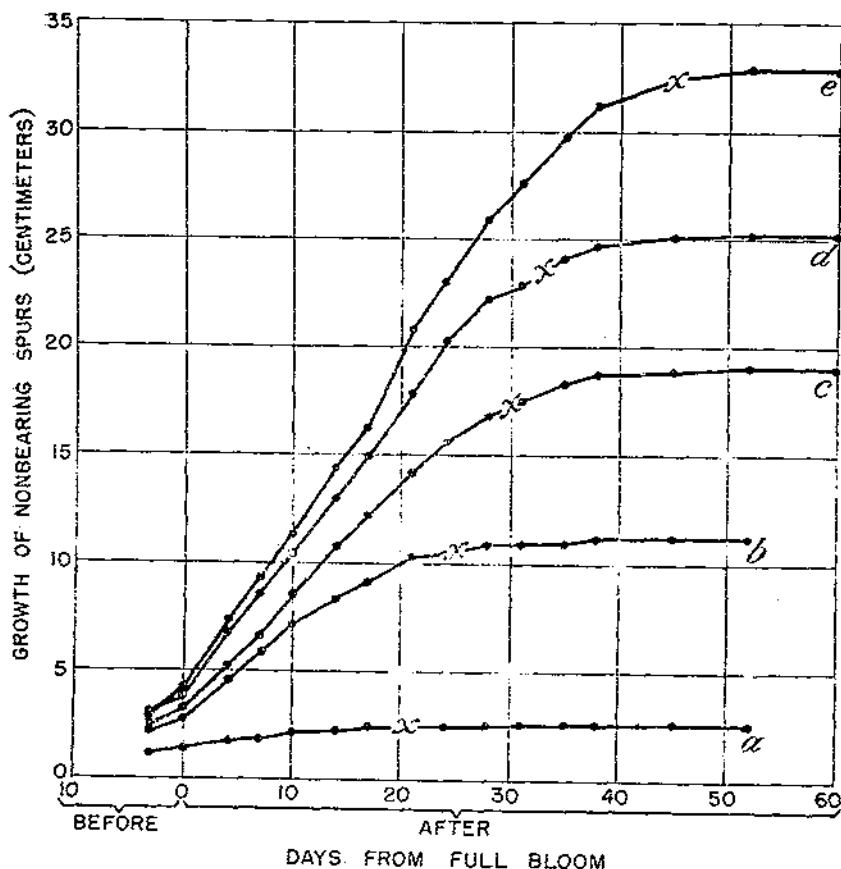

FIGURE 1.—Elongation growth of nonbearing Yellow Newtown spurs and its relation to time of terminal bud formation at Wenatchee, Wash., 1935. X indicates when terminal buds were formed.

records were taken of the number of blossom buds formed on these branches. If ringing was performed early in the summer, Magness and Overley (*35*) observed that Delicious branches with a ratio of only 10 leaves per apple formed no blossom buds, but with 40 to 50 leaves per apple almost every bud was a blossom bud.

In 1931, Harley, Masure, and Magness (*17*) conducted two systematic series of ringing treatments with Delicious, one series having leaf areas adjusted to 10 large leaves per apple and a parallel series having 70 large leaves per apple. In the former treatment any

blossom buds formed during the summer would have either differentiated before the treatment was given or failed to respond to the inhibiting effect of defoliation. On the other hand, with 70 leaves per apple, any increase in blossom buds over similar unringed branches was considered due to the influence of the excessive leaf area. Evidence was obtained that indicated that some blossom buds had normally differentiated as early as 47 days after full bloom, whereas others could be definitely influenced to form blossoms as late as about 90 days after full bloom, with a suggestion that a still later date was possible in some buds.

A summary of this study (17) is diagrammatically reproduced in figure 3. Here the percentages of growing points forming blossom buds as a result of treatment are plotted as ordinates, with the number
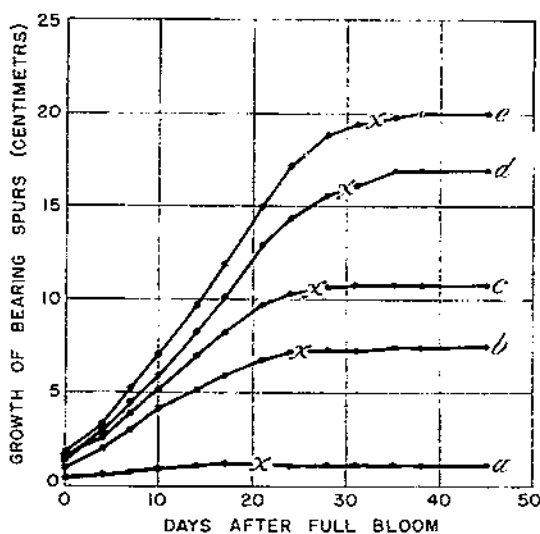

FIGURE 2.—Elongation growth of bearing Yellow Newtown spurs and its relation to time of terminal bud formation at Wenatchee, Wash., 1935. X indicates when terminal buds were formed.

of days after full bloom as abscissae. At 30 days after full bloom, reducing the foliage to 10 leaves per apple effectively inhibited the formation of blossom buds on ringed branches. Thinning the fruit to 70 leaves per apple on the same day caused almost all the growing points to form blossom buds. Seventeen days later, or 47 days after full bloom, however, with 10 leaves per apple, a few buds had already differentiated blossom buds, or the treatment failed completely to inhibit the differentiation processes already inaugurated. Similarly, with 70 leaves per apple adjustment made 47 days after full bloom, 16 percent of the buds had already passed beyond the stage in which increased leaf area per fruit could influence blossom-bud differentiation.

As the curves tend to approach each other the effective influence of leaf adjustments becomes less, and at the point of intersection, or closest approach, susceptibility to influence is practically nil. Leaf adjustments on ringed branches of annual-bearing Delicious trees, in

a similar state of vigor, may then be expected to influence a considerable number of buds to form flower parts 89 or more days after full bloom, but this influence had almost terminated by 119 days.

Magness, Fletcher, and Aldrich (*34*) conducted similar investigations in 1931 and 1932 on different varieties, using 100 leaves per fruit on ringed branches and untreated branches as checks. The responses of different varieties as found by these investigators are of particular interest. The period during which Yellow Transparent, York Imperial, Oldenburg, and Delicious could be influenced after full bloom was relatively short as compared with Jonathan, Stayman Winesap, and Rome Beauty. This is in accord with the general behavior of these varieties relative to their bearing habit, the second group of varieties being much easier to maintain in regular production.
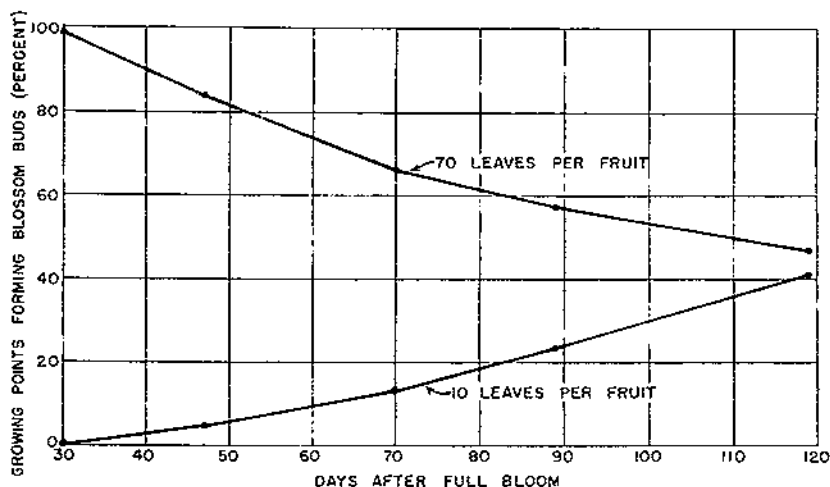

FIGURE 3.— Percentage of growing points forming blossom buds on Delicious trees with 70 leaves and with 10 leaves per fruit on periodically ringed branches at Wenatchee, Wash., 1931. Rings and leaf-fruit adjustments made 30, 47, 70, 89, and 119 days after full bloom.

Figures 4 and 5 show results of studies conducted at Wenatchee, Wash., in 1932 on the time during which spurs and terminal growths can be influenced to form blossom buds in the Jonathan and Winesap varieties, respectively. The method employed was very similar to those described previously (*17*).

A large number of branches, about 1½ to 2 inches in diameter, each carrying approximately the same amount of fruit in relation to leaf area, were selected after fruit set could be determined. Six branches of each variety were ringed and leaf and fruit adjustments were made beginning 37 days after full bloom and at 15- to 18- day intervals thereafter. Some of the Jonathan branches were thinned to 50 leaves per apple, and others were defoliated to 5 leaves per apple; the Winesap adjustments were made to 70 and 10 leaves per fruit. Six branches of each variety received no treatments and appear on the charts as checks. At blooming time in 1933 records were made of the percentage of all growing points forming blossom buds. Bud-performance records of terminal shoots were separated from those of spur buds.

The curves in figure 4 add further evidence to that already obtained (34) that Jonathan buds respond to leaf-fruit adjustments over a
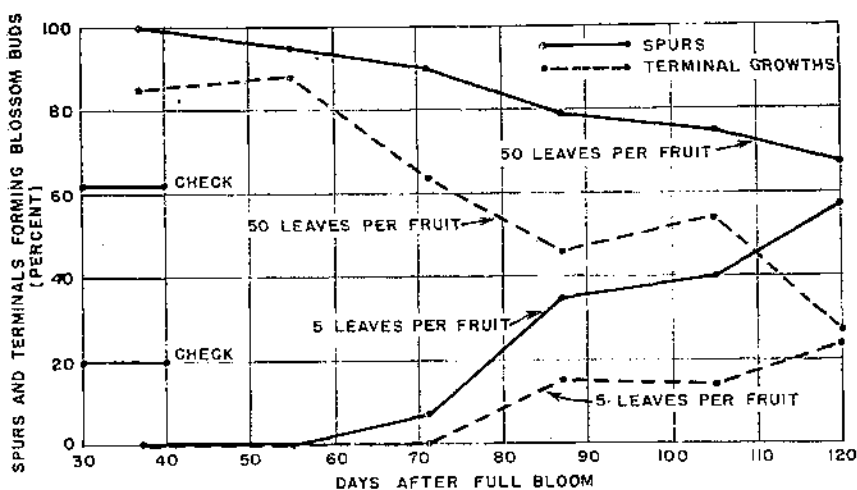
FIGURE 4.—Percentage of spurs and terminal growths forming blossom buds on Jonathan trees with 50 leaves and with 5 leaves per fruit on periodically ringed branches at Wenatchee, Wash., 1932. Rings and leaf-fruit adjustments made 37, 55, 71, 87, 105, and 120 days after full bloom.

relatively long period. A definite response can be noted as late as 105 days after full bloom in both spurs and terminals, and cessation
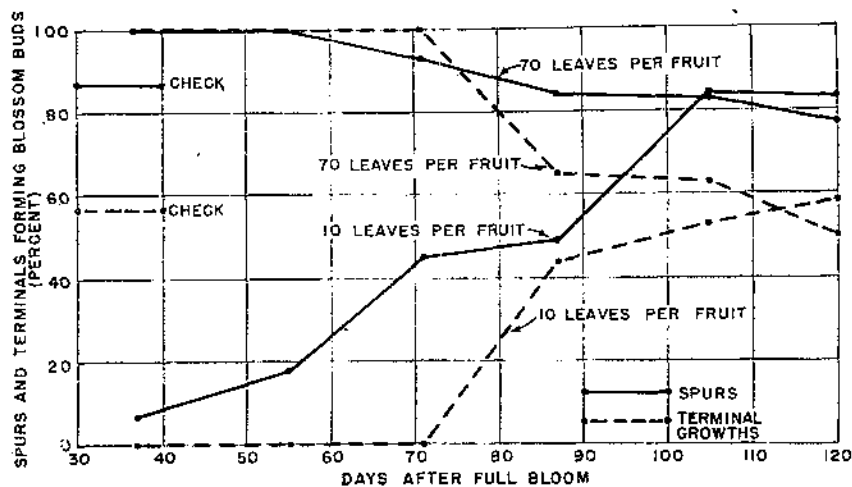
FIGURE 5.— Percentage of spurs and terminal growths forming blossom buds on Winesap trees with 70 leaves and with 10 leaves per fruit on periodically ringed branches at Wenatchee, Wash., 1932. Rings and leaf-fruit adjustments made 37, 55, 71, 87, 105, and 120 days after full bloom.

of response was not apparent until 120 days after full bloom. In contrast, Winesap spurs and terminals (fig. 5) show practically complete lack of response at 105 days and little, if any, significant response

at 87 days after full bloom in spurs and terminals thinned to 70 leaves per fruit. On the other hand, spurs with 10 leaves per fruit show response, as compared with untreated branches, at 87 days. There seems to be no obvious explanation for this rather wide divergence in performance except for inexplicable variability of the selected branches at this ringing date.

Although Jonathan buds apparently can be influenced to form flower parts later in the summer than Winesap buds, a more complete response to leaf-fruit adjustments earlier in the season, especially in terminal growths, is indicated in the Winesap curves. This may explain, in part, why under Pacific Northwest conditions both these varieties tend to bear heavy crops annually. Also, the fact that terminal growths can be more completely influenced later in the
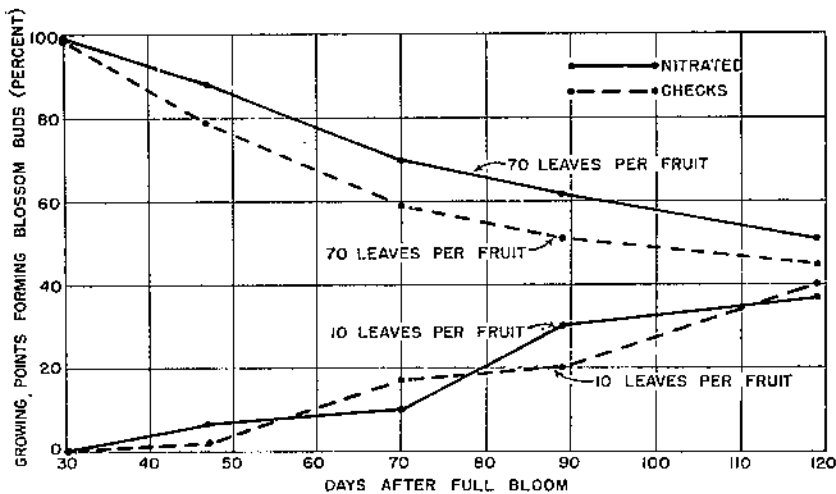
FIGURE 6.—Effect of soil applications of nitrate of soda on the percentage of growing points forming blossom buds on Delicious branches at Wenatchee, Wash., 1931. Branches ringed and leaf-fruit adjustments to 10 and 70 leaves per fruit made 30, 47, 70, 89, and 119 days after full bloom.

season than spur growths affords additional evidence for the concept that with equivalent leaf areas the time of blossom-bud initiation is governed primarily by the length of growth made by the bud-bearing shoot.

It was hoped that a comparison could be made in the time of bud influence with Yellow Newtown, a variety with strong biennial tendencies. Unfortunately, results of ringing and leaf-fruit adjustment experiments on Yellow Newtown were lost because the grower-cooperator inadvertently removed many of the ringed branches in pruning.

In addition to the studies in 1931 on the time during which buds could be influenced to form blossoms in Delicious, data were obtained on the effects of soil applications of nitrate of soda and varying amounts of soil moisture on the time buds could be influenced by leaf-fruit adjustments, as just described. The trees were 13-year-old Delicious in good vigor as interpreted by length of terminal growth, although the leaves were rather light green in color, indicating that at the time they were somewhat nitrogen deficient. The soil consisted

of 2 feet of light sandy loam with underlying coarse gravel. Trees included in this periodic ringing study received from 4½ to 9 pounds of nitrate of soda each. The nitrate was distributed in irrigation ditches and watered into the soil 27 days after full bloom. At this date apical buds had formed on all growing points with the exception of some terminal shoots in the upper portions of the trees.

The percentages of growing points forming blossom buds on periodically ringed branches with 10 and 70 leaves per fruit are shown in figure 6. Curves representing blossoms formed on trees receiving nitrate of soda are designated as nitrated and those formed on untreated trees, as checks.

The curves representing blossom buds formed on the branches with 10 leaves per fruit show no consistent effect of nitrate on the inhibition
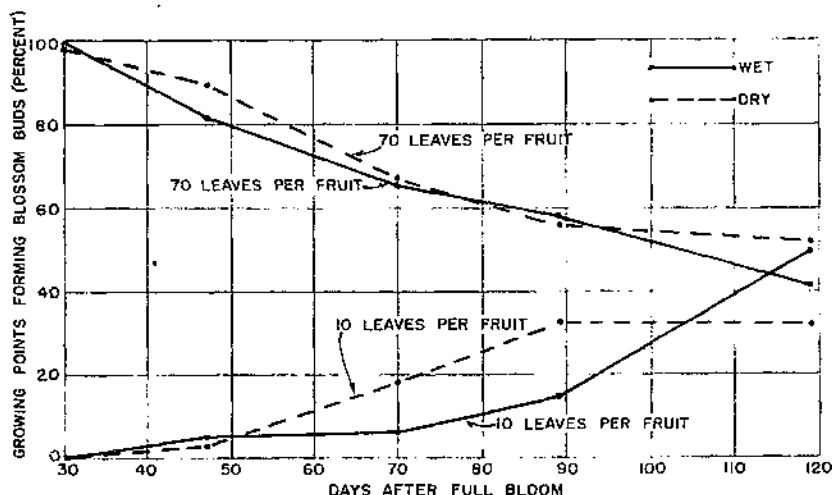
FIGURE 7.— Effect of differences in soil moisture on the percentage of growing points forming blossom buds on Delicious branches at Wenatchee, Wash., 1931. Branches ringed and leaf-fruit adjustments to 10 and 70 leaves per fruit made 30, 47, 70, 89, and 119 days after full bloom.

of differentiation over the unfertilized checks. With 70 leaves per fruit there is some indication that a slightly higher percentage of buds could be influenced to form blossom buds in the nitrated trees at all except the first ringing dates. Inasmuch as this increase in percentage of fruit buds on nitrated trees lacks supporting evidence in the curves for 10 leaves per fruit and in view of the possibility of rather high variability in treated branches, the effect of nitrogen on the time blossom-bud formation can be influenced in these trees is doubtful.

Figure 7 represents the effect of different moisture contents of the soil on blossom-bud formation, as influenced by 10 and 70 leaves per fruit on periodically ringed branches of Delicious trees. The plot designated as wet contained trees that received frequent irrigations, and the soil moisture was maintained near the field capacity. The dry plot was irrigated at the beginning of the experiment, and thereafter only when the soil had reached the wilting percentage and the

trees showed definite indications of wilting. Wilting percentages were reached in the dry plot 65, 85, and 122 days after full bloom.

The curves in figure 7 suggest that with 10 leaves per fruit, the restricted leaf area of the wet plot more completely inhibited the development of blossom buds than that of the dry plot at 70 and 89 days after full bloom. Here again, however, the evidence is not substantiated with 70 leaves per fruit, and it is therefore concluded that under the conditions of this experiment differences in soil moisture had little or no significant effect on the time spurs could be influenced to form blossom buds after terminal buds had formed.

In summarizing the results of this and other investigations on the time buds can be influenced to initiate flower parts by periodic ringing and leaf-fruit adjusting, several factors of fundamental importance have been brought out. First, the time range in which apple buds are physiologically capable of differentiating flower parts is not necessarily a short one, but may extend over a period of 2 to 3 months or more, depending on variety. Second, varieties that normally produce annual crops can, by leaf adjustments, be influenced to form blossom buds over a longer period than those less inclined toward regular cropping. Third, buds on trees of high vigor can be influenced to form blossom buds later in the season than those of low vigor. This is apparently due to the longer spur growths on vigorous trees which differentiate later than the buds on shorter spurs. Heinicke (21) reported that spurs on high-nitrogen trees did not form their terminal buds quite as early as on the low-nitrogen ones. Fourth, application of nitrogenous fertilizers after apical buds are formed or variations in soil moisture after apical buds are formed apparently have no pronounced effect on the time buds can be influenced to initiate flower parts in that year.

LEAF-FRUIT ADJUSTMENTS ON UNRINGED MAIN LEADERS

Although leaf-fruit adjustments on ringed branches are of value in determining when buds can be influenced to initiate flower primordia, it is desirable to know the degree of influence leaf-fruit ratios exert on blossom formation in structures where free movement of elaborated materials is not prevented by bark-ringing.

In the defoliation studies with a total absence of fruit, a larger leaf area was required to form blossom buds on unringed leaders than on ringed branches of the same leader, indicating the existence of a prior demand other than developing fruits for the flower-forming substance by certain tissues. Evidence from other chemical investigations (8) indicates that during the formative period of differentiation, the movement of this substance is mainly to the roots. These demands by fruit, roots, and possibly other structures must be recognized before the principles of leaf-fruit adjustments can be effectively applied to promote annual production through the practice of fruit thinning.

The experiments to follow have all been performed on unringed individual main leaders of biennial-bearing trees in their heavy crop or on years.

To study the time during which buds of bearing spurs can be influenced to form blossom buds by establishing relatively high leaf-fruit ratios, an entire Yellow Newtown tree with 6 main leaders was selected. This tree was very vigorous but decidedly biennial, for

practically every growing point on each leader was bearing a cluster of fruits at the time of the first treatment. At intervals during the summer a single leader was selected and the number of fruits on that leader was reduced from a ratio of 3.5, to one of about 70 leaves per fruit. The average area of these leaves was 4.2 square inches, as determined by planimeter measurements of representative lots of leaves. Only well-developed leaves were included in counts and measurements; small leaves about the cluster bases were disregarded. Leaders were thinned to 70 leaves per fruit 33, 38, 54, 66, and 76 days
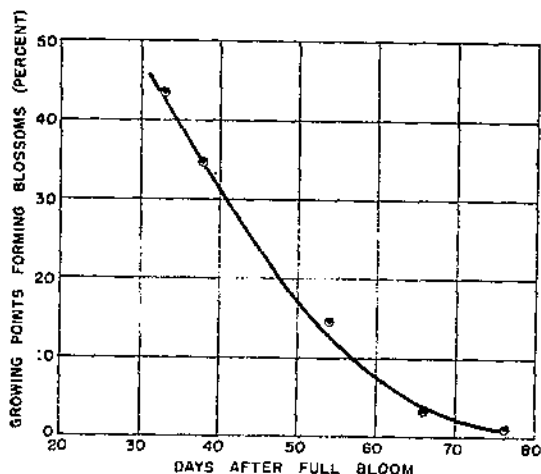
FIGURE 8.—Percentage of growing points forming blossoms on main leaders of a biennial-bearing Yellow Newtown tree following periodic fruit thinning to 70 leaves per fruit 33, 38, 54, 66, and 76 days after full bloom in the bearing year at Wenatchee, Wash.

after full bloom. One leader was allowed to remain unthinned. Percentages of growing points forming blossoms on the leaders the following spring are shown in table 8 and figure 8.

TABLE 8.— *Effect of fruit thinning to 70 leaves per fruit at different periods after full bloom on blossom-bud formation on individual main leaders of a biennial-bearing Yellow Newtown tree at Wenatchee, Wash.*

Leader designation	Period from full bloom to thinning	Average leaf area per fruit	Growing points counted	
			Total	Producing blossoms
	Days	*Square inches*	*Number*	*Percent*
A	33	209.3	755	43.8
B	38	283.7	907	34.8
C	54	270.2	650	14.6
D	60	333.1	878	3.1
E	76	296.0	868	1.1
F	(¹)	14.8	532	1.3

¹ Unthinned; 3.5 leaves per fruit before June drop.

The data show that with leaf-fruit ratios approaching 300 square inches of leaf surface for each fruit, blossom buds could be influenced to form in on-year spurs of biennial-bearing Yellow Newtown. The period of effective influence for this vigorously growing tree was about 54 days. As illustrated in figure 8, the percentages of bloom show a sharply descending gradient from 33 to 66 days. The curve suggests the possibility of the existence of a mathematical relationship between the time of thinning and the percentage of blossoms formed. From the 33- to the 54-day points, a reduction in blossoms of about 10 percent occurred for every 7 days thinning was delayed. This correlation, of course, would not be the same for all varieties or individual trees within the variety unless they were nearly identical in growth and crop with that used in the experiment. With trees of less vigor the period and degree of influence undoubtedly would have been less (16, 34). Basically, however, the data further substantiate the already existing evidence (1, 18, 19, 34) that if fruit thinning is performed within the range of effective influence and to a sufficient leaf area per fruit, the biennial-bearing habit of apple trees can definitely be broken.

At the time leader C (table 8) was thinned, 54 days after full bloom, it was observed that many of the small fruits had begun to show yellowing of the stems and a few had already dropped. This was interpreted as the beginning of the so-called June drop. When leader D was thinned, 66 days after full bloom, the drop had apparently reached its highest point. This indicates rather definitely that effective influence of fruit thinning in forming blossom buds cannot be expected if the thinning operation is delayed until the young fruits begin to drop.

TABLE 9.—*Effect of different leaf-fruit ratios established at different periods after bloom in 1933 on blossom-bud formation on main leaders of biennial-bearing Yellow Newtown trees at Wenatchee, Wash.*

Leader No.	Period from full bloom to thinning	Leaves per fruit after thinning	Spurs			Terminal growths	
			Total	Blossoming		Total	Blossoming
				1933	1934		
	Days	*Number*	*Number*	*Percent*	*Percent*	*Number*	*Percent*
3	36	70	786	87	61	25	44
6	37	70	389	89	10	10	5
9	37	70	544	61	65		
18	38	70	332	95	46	23	26
4	36	50	285	88	12	19	0
10	37	50	926	75	30	36	6
17	38	50	270	70	27	11	27
12	73	70	286	92	2	8	0
16	73	70	441	91	9	16	13
13	73	50	314	92	4	16	0
15	73	50	337	96	2	20	0
7	52	25	297	88	0		
8	52	25	191	95	0		
1	(²)	(³)	428	82	0	12	0
11	(²)	(³)	333	96	1.5	9	0
19	(²)	(³)	284	63	2	21	0
21	(²)	(³)	640	71	0	17	0
2		(⁴)	512		98	22	86
5		(⁴)	336	0	94		
14		(⁴)	434	1	95	18	78
20		(⁴)	342	0	98	20	100

¹ Low leaders on north side of tree.   ² Unthinned.   ³ On year.   ⁴ Off year.

The results of further studies on the relation of time and degree of fruit thinning to blossom-bud formation are found in table 9. These data were obtained from 4 vigorous Yellow Newtown trees having the individual main leader type of alternate-year cropping. Each tree had at least one off-year leader in 1933. Blossom records in 1934 fully substantiate those in table 8 and, in addition, suggest that a lower leaf-fruit ratio than 70 leaves per apple, if established sufficiently early in the season, could influence enough buds to form blossoms to produce a good crop the following year.

A comparison of the effect of varying leaf areas and periods of thinning after full bloom on blossom-bud formation in different varieties is presented in table 10. The leaf-fruit adjustments were made on main leaders of a single biennial-bearing tree of each variety. Tree vigor, as designated in this study, was evaluated on the basis of leaf characteristics at the time of thinning. Trees with large leaves for the variety and deep green in color were classified as high vigor. Trees with small, light green leaves for the variety were considered as low vigor. Numerical indexes of vigor on the basis of leaf characteristics, although desirable, would be rather involved and relative at best. Lengths of terminal growth have been employed as a measure of vigor, but this method is subject to much criticism in studies relating to blossom-bud formation. A given length of growth may indicate a high degree of vigor, while leaf injury by diseases, insects, or chemical injury from spray materials may, reduce the efficiency of the leaf to a point of blossom-bud reduction. For this reason all references pertaining to tree vigor in this report have been estimated in terms of leaf size and depth of color.

Table 10. *Effect of fruit thinning on individual main leaders of biennial-bearing Yellow Newtown, Winesap, and Delicious trees in 1935 on blossoming in 1936 at Wenatchee, Wash.*

Vigor and variety	Period from full bloom to thinning	Leaves per fruit after thinning	Average leaf area per fruit	Growing points blossoming
High vigor:	*Days*	*Number*	*Square inches*	*Percent*
	17	30	103	50.6
	17	50	172	68.0
Yellow Newtown	32	30	103	27.2
	32	50	172	20.0
	32	70	230	49.4
	60	[²] 25	77	.5
	32	30	48	18.0
	32	50	77	44.0
Winesap	32	70	108	77.5
	68	[²] 25	30	2.5
	68	[²] 25	39	4.0
	23	25	58	35.0
	31	30	69	28.2
Delicious	31	40	92	37.5
	39	25	58	12.3
	39	30	69	31.3
		[²]	12	1.5
Low vigor:				
Delicious	32	30	50	5.0
	32	50	83	3.0
	32	70	116	15.7
	68	[²] 20	33	0

[1] Leaders originally selected as unthinned checks but were later commercially thinned by grower-owner. Leaf-fruit ratios arrived at by counting a representative number of leaves and fruits after thinning was performed.
[2] Unthinned.

Differences in responses to thinning treatments in biennial-bearing Delicious trees of high and of low vigor are clearly evidenced in table 10. At 32 days after full bloom, a leaf-fruit ratio of 70 leaves per fruit was required to influence 15.7 percent of the growing points to bloom in the low-vigor trees. On the other hand, the Delicious tree high in vigor differentiated almost twice that percentage of growing points with only 30 leaves per apple at 31 days after full bloom. In fact, when thinning was performed 23 days after full bloom, a bloom on 35.6 percent of the growing points was obtained with but 25 leaves per fruit. A very definite response can be seen from thinning to 25 and 30 leaves per fruit even as late as 39 days after full bloom in this vigorous tree.

The difference in response to thinning treatments of trees of different vigor may be explained in part by the greater area per leaf of the vigorous trees. This apparently relates only to individuals within a variety, for it can be seen that on the vigorous Winesap tree a high percentage of growing points bloomed as compared with the low-vigor Delicious tree thinned at the same date, although the average area per leaf of the Winesap was somewhat less. That the leaf-fruit ratio necessary for blossom buds to form may be a distinct varietal characteristic is also suggested when the data for Winesap and Yellow Newtown are considered. Both trees were in a similar condition of vigor, but the ratio of leaf area to blossom buds formed is significantly higher for Yellow Newtown. The possibility of a greater leaf efficiency in Winesap, correlated with the time during which buds can be influenced, may explain why Winesap is usually an annual bearer whereas Yellow Newtown is, in general, notoriously biennial.

Perhaps the most important consideration of the results in table 10 from a practical and economic point of view is the fact that blossom buds, sufficient for a good crop, were formed on these biennial-bearing trees when ratios of 25 and 30 leaves per fruit were established early in the season. Leaf-fruit ratios as high as 70 or more leaves per apple, although more effective in breaking the biennial habit, necessitate the sacrifice of a large part of the current season's crop. With 25 or 30 leaves per apple a good production should be realized in the heavy crop year and still permit sufficient blossom buds to be formed for a crop the following year. As can be seen, however, this took place only when trees were in a highly vigorous condition and when thinning was performed within about 3 to 5 weeks after full bloom.

CONCLUSIONS DRAWN FROM PHYSIOLOGICAL STUDIES

Defoliation and leaf-fruit adjustment studies have provided evidence that the specific factor responsible for the initiation of flower primordia is a product of leaf metabolism. Just what particular substance constitutes this factor has not been determined, but it appears that the leaf area required to synthesize the necessary quantity to initiate a blossom bud is not particularly great. This suggests a hormonelike substance as the controlling factor. If a hormone, its specificity for buds seems to be quite limited, for apparently it is carried to structures making a greater demand than buds for carbohydrate substances. That developing fruits make the first and greatest demand for the blossom-bud-forming substance, followed by roots and finally by the spur, is strongly indicated in the leaf-fruit adjustment, defoliation

and ringing experiments. It remains then that, until these demands are met, movement of such a hormone would logically be in a direction away from the bud. The role of a blossom-forming hormone in root development or fruit growth would be highly speculative. If the hormone hypothesis be accepted, it would probably be difficult completely to dissociate the hormone from soluble carbohydrates in its synthesis and translocation, or from starch in its deposition. Factors that reduce the carbohydrate supply, such as heavy fruit set, defoliation (20, 35, 41), and shading (4, 13), invariably inhibit blossom-bud differentiation.

Together with the already existing evidence (1, 16, 18, 19, 36) the present results of leaf-fruit adjustments made on main leaders of biennial-bearing trees in the on year demonstrate that the biennial-bearing·habit can be broken by fruit thinning alone. The relative degree or severity of such thinning to influence the formation of blossom buds should be governed by vigor of the tree as interpreted by the size and color of foliage, and by the number of days after full bloom that thinning is performed.

Certain criticisms, notably by Roberts (40), have been directed toward the application of fruit thinning as a correction for biennial-bearing, on the premise that variety for variety the average area per leaf is in general greater for north-central Washington trees than for those of many other fruit-growing regions, and that thinning on the basis of certain leaf numbers per fruit would be applicable only to a special location. Obviously, leaf numbers alone cannot be comparable when leaves may vary greatly in size. Only with equivalent leaf areas can true comparisons be made, and, since it is highly impractical to measure all leaves to determine the leaf-fruit ratio, the number of leaves per apple has been used as the index of relative leaf area.

Other factors may be more important in favoring responsiveness to fruit thinning. Trees growing in the irrigated fruit districts of Washington may have a higher photosynthetic level than those grown in certain other localities. Relatively high sunlight intensities, long growing seasons, and extended lengths of daily light, which characterize these districts, may contribute to increased leaf efficiency. Under these conditions, leaf areas used in the present studies might influence the formation of blossom buds to a greater extent than equivalent leaf areas elsewhere.

The foregoing criticisms are timely and worthy of consideration, but it should be emphasized here that they relate only to problems arising in the wide or general application of thinning treatments as a corrective measure for biennial bearing. In no way do the criticisms apply to the principles involved in the relationship of leaf-fruit adjustment and blossom-bud formation. Accumulating evidence indicates definitely these principles to be fundamental and basically sound.

COMMERCIAL FRUIT-THINNING EXPERIMENTS

During the summers of 1936-38 records were taken on the percentage of growing points forming buds on biennial-bearing trees following early commercial fruit thinning. The principal deviations from the general commercial thinning practices in Wenatchee orchards consisted of establishing somewhat higher average leaf-fruit ratios, and all thinning was performed before the June drop. Common orchard

labor was employed to do the thinning under immediate supervision of the writers. Records obtained at the time of thinning consisted of the date each tree was thinned, the average number of large leaves per apple after thinning, and the relative vigor of each individual tree.

Bloom records the following spring were obtained by estimating the percentage of growing points bearing blossom clusters. These estimates were checked by frequent counts. All estimates were made separately by two individuals, and in all cases counts were made if estimates were not in good agreement. Varieties studied were Delicious, White Pearmain, and Golden Delicious apples, with a small experiment on Flemish Beauty pears.

EXPERIMENT ON DELICIOUS APPLE TREES

For this study an orchard was selected that had shown a decided biennial tendency since 1932. In the early summer of 1936 the Delicious trees were carrying an extremely heavy crop, practically every spur bearing a cluster of fruits. One hundred trees, approximately 22 years of age and the majority moderately to highly vigorous, were selected for early thinning treatments. About 30 percent, however, bore rather small light-green leaves and were classified as being low in vigor.

Table 11 shows these Delicious trees to have been very responsive to early thinning. When thinned within 31 days after full bloom, even trees classified as of low vigor blossomed sufficiently for a good crop in 1937. When fruit was thinned 39 days after full bloom, moderate-to high-vigor trees developed a relatively high percentage of bloom, but the low-vigor trees did not produce enough bloom for a crop the following season. Unthinned trees formed blossom buds on only 1 percent of the growing points. The amount of bloom was in relative proportion to the amount of foliage per fruit. An exception occurred in the moderate- to high-vigor tree thinned to 10 to 20 leaves per fruit 39 days after full bloom. As only one tree fell into this class, it is not surprising that such a deviation might be found.

TABLE 11.— Effect on blossoming in 1937, of fruit thinning of biennial-bearing Delicious trees of different vigor in 1936, at Wenatchee, Wash.

Period from full bloom to thinning (days)	Leaves per fruit after thinning [1]	Moderate- to high-vigor trees		Low-vigor trees		Both vigor classes	
		Trees treated	Growing points blossoming [1]	Trees treated	Growing points blossoming [1]	Trees treated	Growing points blossoming [1]
		Number	Number	Percent	Number	Percent	Number	Percent
Check [2]		2	1				2	1
23-31	10-20	12	22	11	23	23	22
	20-30	27	32	13	27	40	30
	30-40	17	43	2	33	19	42
39	10-20	1	30	2	1	3	11
	20-30	9	19	2	6	11	16
	30-40	2	45	0		2	45
Total or average bloom per thinned tree		68	32	30	23	98	29

[1] Estimated; see text (p. 36).
[2] Thinned after June drop.

Perhaps the most important feature of this study is the fact that these Delicious trees, although definitely biennial, were capable of forming blossom buds for a crop the following year with a relatively low leaf-fruit ratio. Thinning to 25 leaves per apple is not an uncommon practice for fruit growers in the Pacific Northwest, although it is seldom performed before the June drop.

Total production of Delicious fruit from this biennial-bearing orchard from 1932 to 1938, inclusive, was as follows:

Year	Yield as equivalent of packed standard boxes
1932	6, 823
1933	1, 626
1934	7, 250
1935	850
1936 [1]	7, 920
1937	7, 439
1938	7, 000

[1] Thinned early; see table 11.

These yield figures were taken from the growers' harvesting and packing records, and some trees other than those in the experiment are included. For the most part, those outside the experiment were somewhat less inclined toward alternate cropping than the experimental trees. Production fluctuated greatly prior to the thinning in 1936, but was uniform thereafter.

EXPERIMENT ON WHITE PEARMAIN APPLE TREES

The effects of early fruit thinning on 36 White Pearmain trees were studied in 1936. These trees had been decidedly biennial bearers for several years. They were growing in the same orchard as the Delicious trees described in the foregoing test and were located immediately adjacent to them. The White Pearmain trees began to bear in alternate years just prior to 1932, and since the off and on years of Delicious and White Pearmain trees coincided, it is quite evident that pollination was the primary influence causing the Delicious trees to assume the biennial habit. The other variety adjacent to Delicious was Winesap, and these trees, depending on Delicious for pollen, were showing a similar trend of bearing in 1936.

The results of early fruit thinning on White Pearmain trees are shown in table 12. The data reveal that thinning to 25 leaves per apple 25 days after full bloom resulted in the formation of sufficient blossom buds to produce a good commercial crop for the following year on trees high in vigor. Unfortunately, no trees of low vigor were thinned on this date. The amount of bloom on trees thinned to 20 and 23 leaves per apple 39 and 46 days after full bloom was not great enough to produce a desirable crop. This is in contrast to the response of high-vigor Delicious trees at 39 days after full bloom (table 11) and indicates that Delicious trees can be influenced by leaf adjustments later than White Pearmain.

TABLE 12.—*Effect on blossoming in 1937, of fruit thinning of biennial-bearing White Pearmain trees of different vigor in 1936, at Wenatchee, Wash.*

Period from full bloom to thinning (days)	High-vigor trees			Low-vigor trees			Both vigor classes	
	Leaves per fruit after thinning	Trees treated	Growing points blossoming	Leaves per fruit after thinning	Trees treated	Growing points blossoming	Trees treated	Growing points blossoming
	Number	*Number*	*Percent*	*Number*	*Number*	*Percent*	*Number*	*Percent*
Check [1]............	....	2	1.3	....	....	....	2	1.3
25................	25	3	26.0	....	0	....	3	26.0
39................	20	6	5.8	23	9	4.7	15	5.1
46................	23	12	7.7	20	4	1.2	16	6.1

[1] Thinned after June drop.

EXPERIMENT ON GOLDEN DELICIOUS APPLE TREES

Under the conditions of the Pacific Northwest, Golden Delicious trees tend strongly toward alternate-year cropping. The habit is sometimes apparent in the early bearing years and increases in intensity as the trees grow older. In some instances it may appear only on main leaders or individual trees, but entire biennial orchards are commonly found. Since this variety has recently gained considerable favor, it is quite important that some attention be given to the possibility of maintaining annual production.

Early fruit-thinning tests were conducted on 43 extremely biennial Golden Delicious trees in 1936. These trees had been grafted over to Golden Delicious, and the grafts were about 14 years old. At the time of thinning, most of the trees were decidedly lacking in vigor. Leaves were quite small and light green and averaged only six per spur. Practically every spur, however, had set a cluster of fruits and when first thinned the fruit averaged three to each spur. At 44 and 45 days after full bloom a few fruits were beginning to drop. As in the two foregoing tests, hired orchard labor was employed to thin the crop.

Treatments in 1936 and blossom records of 1937 are given in table, 13. In no case was there bloom that could be considered sufficient for a good crop, except where moderately vigorous trees were thinned to 30 leaves per apple 28 to 31 days after full bloom. This seems to indicate that unless the trees exhibit a rather high degree of vigor Golden Delicious cannot be expected to respond to fruit thinning unless a relatively high leaf-fruit ratio is established very early in the season.

TABLE 13.—*Effect on blossoming in 1937, of fruit thinning of biennial-bearing Golden Delicious trees of different vigor in 1936, at Wenatchee, Wash.*

Period from full bloom to thinning (days)	Moderate-vigor trees			Low-vigor trees			Both vigor classes	
	Leaves per fruit after thinning	Trees treated	Growing points blossoming	Leaves per fruit after thinning	Trees treated	Growing points blossoming	Trees treated	Growing points blossoming
	Number	*Number*	*Percent*	*Number*	*Number*	*Percent*	*Number*	*Percent*
Check [1]	....	1	1	....	1	0	2	0.5
28–31	30	3	17	24	9	8	12	10.0
35–39	27	6	6	18	6	3	12	5.0
44–45	22	5	7	30	14	3	19	4.0
Off year	....	2	98	....	....	....	2	98.0

[1] Thinned after June drop.

EXPERIMENT ON FLEMISH BEAUTY PEAR TREES

The discovery of several biennial-bearing Flemish Beauty pear trees presented an opportunity to determine the effect of early fruit thinning on the fruiting response of these trees. Four decidedly biennial trees, in the on year, were thinned to 30 to 35 leaves per fruit, 23 and 24 days after full bloom. Two similar trees were not thinned until after the June drop (60 days after bloom). Another tree, No. 5 (table 14), with 3 main leaders was thinned to 35 leaves per fruit. One leader was thinned 23 days after bloom and the other two 61 days after bloom. All trees were of good vigor and very uniform as to the percentage of spurs bearing fruits.

TABLE 14.—*Effect on blossoming in 1937, of fruit thinning of biennial-bearing Flemish Beauty pear trees in 1936, at Wenatchee, Wash.*

Tree No.	Period from full bloom to thinning	Leaves per fruit after thinning	Growing points blossoming	Tree No.	Period from full bloom to thinning	Leaves per fruit after thinning	Growing points blossoming
	Days	Number	Percent		Days	Number	Percent
1	23	30–35	35	6	60	20–30	4
2	23	30–35	40	7	60	20–30	7
3	23	30–35	40	5 (1 leader)	23	35	70
4	24	30–35	25	5 (2 leaders)	61	35	5

Results of this thinning test (table 14) indicate that the biennial-bearing habit of these Flemish Beauty trees was completely broken by the early and somewhat severe thinning. When the operation was postponed until after the June drop the percentage of blossom buds formed was less than that required for a good succeeding crop.

EARLY FRUIT THINNING

GENERAL CONSIDERATIONS

The thinning of apples has long been recognized as a necessary adjunct to good orchard management, but in most instances the expected benefits from the practice had to do only with size improvement and quality for the immediate crop. As evidence accumulates it becomes more apparent that the beneficial effects of systematic fruit thinning are numerous and lasting.

Winter injury to the above-ground portions of fruit trees has often been observed to be more prevalent in trees that had an excessive crop the preceding season. Chandler (7) found low-temperature injury to buds greatly reduced on trees that had been thinned. Waring (45) studied the residual effects of fruit thinning on the Lombard plum and found beneficial influences on tree growth and behavior to the fourth year following 1 year's thinning. These consisted of increased trunk circumference, shoot length and diameter, spur growth, and foliage area.

Practical implications from the present investigations are rather definite that early fruit thinning provides the most essential basis for annual and uniform production. Thus, aside from such benefits as preventing breakage or injurious bending of branches by heavy crops, physiological effects of fruit thinning, as described above, assume im-

portance not generally attributed to the practice. Fruit thinning then could well be classified not only as a simple supplementary aid in the production of high quality fruit, but also as a principal factor in the production of annual crops and a potent influence in maintaining vigor and hardiness in structural tissues.

That biennial bearing in apple trees can be broken and annual production maintained thereafter through fruit thinning has been demonstrated in these and other investigations. Practical success in the application of this method cannot be attained however unless certain apparently fundamental rules are carefully adhered to. In the present experiments, failure of trees to respond to thinning has been directly traced to lack of one or more of the following requirements:

(1) A high degree of tree vigor should be maintained. A good healthy dark-green foliage is essential for best response to fruit thinning. Thinning necessary to break the biennial-bearing habit need not be so severe as to lower the quality of fruit or decrease production if the trees are highly vigorous. Biennial bearing can be corrected in trees of relatively low vigor, but in this condition very severe and very early thinning is apparently required.

(2) Thinning should be performed early in the growing season. It was found that in order to influence blossom-bud formation thinning should in all cases be completed some time before the June drop. In varieties where the biennial habit was not firmly fixed good response was obtained in most instances from 30 to 40 days after full bloom. With varieties having a strong tendency to alternate cropping there seems to be no date too early to commence thinning, from the standpoint of blossom-bud influence. Thirty days after full bloom appears to be the limit of time thinning should be deferred in biennial varieties if buds are to be influenced with 25 to 30 leaves per apple. On strongly biennial varieties, when thinning was delayed beyond 30 days after full bloom, or if trees were not highly vigorous, it required 40 or more leaves per apple to obtain sufficient fruit buds for a good crop the following year. Preliminary tests suggest that hand blossom thinning may be feasible with certain varieties such as Golden Delicious.

(3) Thinning must be relatively heavy. In these thinning experiments the distribution or spacing of fruits has been based entirely on the relation of leaf area, or on the number of large leaves per apple, rather than on a definite distance between fruits. This may be rather difficult or confusing to the orchardist attempting this method of thinning for the first time, but after a few trial counts it should be possible to estimate the number of leaves per apple about as readily and accurately as judging a given number of inches for spacing the apples.

The degree or severity of thinning necessary to influence blossom-bud formation on biennial-bearing trees seems to vary directly with tree vigor and the number of days after full bloom thinning is performed. The interrelationship of these factors is indicated in table 15. These data represent the average of a large number of observations made on main leaders and entire trees of biennial-bearing Yellow Newtown and Delicious varieties at Wenatchee, Wash., and they show the approximate number of leaves per apple required to influence 15 percent or more buds to differentiate blossoms at various intervals from full bloom, on trees of relatively high and of relatively low vigor. Under conditions in the Pacific Northwest fruit districts, if blossoms are evenly distributed throughout the tree, and conditions for pollination are good, this amount of bloom should be sufficient to produce a rather heavy crop.

TABLE 15.—*Approximate number of leaves per apple required to influence 15 percent or more buds to form blossoms on biennial-bearing Yellow Newtown and Delicious trees of high and low vigor at Wenatchee, Wash., 1931–38*

Period from full bloom to thinning (days)	Average large leaves per apple		Period from full bloom to thinning (days)	Average large leaves per apple	
	High-vigor trees	Low-vigor trees		High-vigor trees	Low-vigor trees
	Number	Number		Number	Number
20	22	31	34	44	57
28	30	43	40	70	100

As shown in table 15, the thinning should be increased proportionately with the increase in number of days after full bloom. Trees with relatively poor foliage systems required heavier thinning at a given date to produce sufficient bloom for a successive crop than did vigorous trees with good leaf areas. These figures, of course, represent means of a large number of observations, and a wide deviation from them might well be expected among individual trees in practical application. It is felt, however, that they serve to illustrate the fundamental relation between time and degree of thinning and the importance of tree vigor in the early thinning program.

DISADVANTAGES OF EARLY THINNING

Unless strict attention is given to thinning to an approximate number of leaves for each fruit, the orchardist attempting an early-thinning program for the first time will, as a rule, underthin. At 20 to 25 days after full bloom the apples are very small and it is difficult to visualize their size and position in relation to each other when they become fully developed. Also many small fruits may be hidden in the foliage and are likely to be overlooked resulting in too many fruits remaining on the tree for either sufficient blossom-bud formation or desirable fruit size. A second thinning later in the season has been found necessary in some instances.

With certain classes of orchard labor careful supervision and instruction may be required. This will tend to slow up the operation and also increase the cost.

The initial cost of thinning before the June drop can be expected to be considerably higher than that of late-season thinning. The added expenditure, however, should not be required beyond the first year if the alternate-cropping tendency has been corrected.

At harvest, apples from early-thinned trees are usually larger than those from similar trees thinned later. Also, if an extremely severe thinning is required to influence blossom-bud formation, the remaining fruits are very likely to grow too large. Large apples are generally more susceptible to certain disorders, such as water core and bitter pit, and the market value is often less than for medium-sized fruits.

The degree of thinning necessary for blossom-bud production may be such as to seriously reduce the current season's yield of fruit, although this has not necessarily followed when very early thinning was practiced on trees of high vigor.

Because of the fruit shape, certain varieties are extremely difficult to thin by hand when the apples are quite small. This is especially true

of Golden Delicious, and it was necessary to employ thinning shears to remove the small fruits at 20 to 28 days after full bloom.

SUGGESTIONS AND RECOMMENDATIONS

The results of blossom-bud differentiation studies along with observations on early leaf-fruit adjustments in commercial orchards provide the basis for this discussion. The suggestions, although founded on factual evidence, are tentative, for many questions remain to be answered. It is believed, however, that the following recommendations will assist materially in the promotion and maintenance of annual production in healthy apple trees:

(1) Within a given variety, trees with a heavy set of fruit should be thinned first. If alternate-year bearing exists in certain trees these should be thinned within 30 days after full bloom and the thinning should be relatively severe. In light-set trees, thinning should be delayed as long as possible or omitted entirely.

(2) In orchards containing mixed varieties and where biennial bearing is not evidenced, the varieties that differentiate early or in which the period of influence is short should be thinned first. Many growers thin varieties according to harvesting dates. Experiments have shown that from the standpoint of bud influence this would be a wrong practice in many instances. With the principal varieties of apples now grown in the Pacific Northwest the following order is recommended: Golden Delicious, Yellow Newtown or White Pearmain, Delicious, Winesap, Jonathan, and Rome Beauty.

(3) In order to grow fruit to a desirable size, maintain vigor in roots and tree structures, and form sufficient blossom buds for the succeeding year, the crop on the tree should be adjusted to the existing leaf area. This can seldom be accomplished effectively by space thinning. In the Pacific Northwest if a tree is vigorous and has healthy dark-green leaves, 25 to 30 large leaves per apple should form enough buds for a good commercial crop, provided thinning is performed within 25 days after full bloom. If foliage is injured or lacking in size and color, or if the fruit is thinned later than 25 days after full bloom, it may be necessary to thin to 40 or more leaves per fruit to influence blossom-bud formation in alternate-bearing varieties.

(4) Little or no influence on blossom-bud initiation can be expected if thinning is delayed to or until after the June drop. Unless there is a rather high percentage of nonbearing spurs in the tree during a heavy-set year, the following year's crop will undoubtedly be small if thinning is delayed until the June drop. Perhaps the benefits derived from late-season thinning do not extend much beyond increasing the size of fruit, although some increase in the accumulation of elaborated tree reserves probably does occur.

(5) The cost of early thinning for the correction of biennial bearing should be considered over a period of 2 years or more rather than the high initial expense. If regular bearing is reestablished the increased production should largely offset the additional cost of early thinning. Also, the cost of maintaining the trees in regular crops by thinning after the first year should not be in excess of that usually allotted for the practice. Information gathered from production and cost records of growers who have carefully employed early thinning to obtain and maintain annual bearing indicates that it is economically feasible; furthermore, considering the investment, few other orchard operations will do as much toward making the growing of apples profitable.

CONCLUSIONS AND SUMMARY OF INVESTIGATIONS IN PACIFIC NORTHWEST

Investigations have been conducted at Wenatchee, Wash., for 7 growing seasons within the period from 1931 to 1938, to study factors associated with blossom-bud initiation and the influence of early fruit thinning to correct biennial bearing in apples.

Chemical analyses of fruit spurs show that separate morphological components of the spur differ widely in composition. By the inclusion of old and new growth, or dissimilar structures of the same year's

growth, in a sample, an average composition quite unreliable as to physiological interpretation may result.

Of the chemical substances determined, a much higher starch percentage and a slightly lower one of free reducing substances were found in tissues initiating blossom buds as compared with similar tissues forming leaf buds. No explanation for this intimate association of starch and bud differentiation is apparent, but it appears that the factor or factors responsible for this change in the bud meristem are correlated with the synthesis and deposition of starch.

Defoliation experiments on off-year main leaders of biennial-bearing Yellow Newtown trees indicate that the substance responsible for the initiation of blossom primordia is synthesized mainly in leaves borne by the immediate new spur growth.

Differentiation of flower primordia in the bud meristem appears to bear a quantitative relationship to the foliage area. Between 9 and 17 square inches of healthy leaf surface was required to form blossom buds on ringed branches of off-year Yellow Newtown leaders; unringed branches required between 17 and 28 square inches of leaf surface in Yellow Newtown, and from 12 to 18 square inches in Delicious, for the initiation of blossom buds.

There was a strong implication that roots and other structural tissues make the first demand for the substance which carries the blossom-forming factor in trees devoid of fruit. With a good leaf area, requirements for roots and other parts are quickly met and blossom buds are formed. When present, the young fruits make a prior demand over all competing tissues for the blossom-forming principle.

Buds on spurs of nonbearing leaders defoliated to a leaf area apparently insufficient for blossom-bud formation often became vegetative and pushed out into a second elongation growth. Unless the accompanying leaves of this second growth were removed, blossom primordia were induced in the new apical bud. Following this differentiation there apparently was a critical time wherein bud cells were still meristematic, for upon further leaf removal a third growth often occurred and late blossoming sometimes resulted.

The time of bud differentiation apparently depends on the advent of terminal or apical bud formation. It was found that the time of terminal bud appearance in both bearing and nonbearing spurs was related to the length of current growth made by the spur. Short spurs formed buds early and longer spur growths relatively late in the season; therefore the time of differentiation can logically be expected to show a reciprocal relation to length growth and bud development.

Results of leaf-fruit adjustment studies on main leaders of apple trees demonstrate that blossom buds will be formed if a foliage area in excess of the demands made by developing fruits, roots, trunk, branches, etc., be established early in the growing season.

For a given leaf-fruit ratio the effective period of influence to form blossom buds is determined to a large extent by tree vigor, the time leaf adjustments are made, and the varieties under test. Buds from vigorously growing trees could be influenced to initiate flower parts over a longer period of time than those from weak or less vigorous trees, probably because of later differentiation on longer spur growths. The earlier the leaf-fruit adjustments were made, the greater was the

response in blossom buds formed. Varieties with biennial-bearing propensities could be influenced to initiate blossom buds over a relatively short period as compared with varieties that normally bear regular crops.

Neither nitrogen-carrying fertilizer nor soil-moisture variations had any pronounced effect on the time during which buds could be influenced to form blossom buds when sodium nitrate was applied after terminal buds had formed, and when soil moisture did not reach the wilting percentage until 65 days after full bloom.

By leaf-fruit adjustments on main leaders of biennial-bearing trees, and by practical early fruit thinning in commercial apple orchards, biennial bearing was definitely broken and annual production maintained thereafter.

The severity of such fruit thinning necessary for the formation of blossom buds was primarily governed by the vigor of the tree and by the number of days elapsing between full bloom and thinning.

INVESTIGATIONS IN THE POTOMAC VALLEY [5]

COMPARISON OF BIENNIAL-BEARING PROBLEMS IN THE EAST AND THE WEST

Growing conditions in apple orchards east of the Great Plains region in the United States vary greatly from conditions in the western irrigated districts. Because apple trees in general make less vigorous growth in the eastern areas and because environmental conditions are quite different, results of fruit-thinning tests to correct the biennial-bearing condition in western orchards are not directly applicable to eastern conditions. Although the underlying principles governing the initiation of flower parts in apples are undoubtedly the same everywhere they are grown, the results obtained from specific treatments may differ greatly. Some of the important factors governing conditions in the eastern orchards are discussed herein.

Most of the orchards are maintained in sod or with partial cultivation. Many are on rather shallow soils where periods of rainfall deficiency are quickly reflected in a shortage of the moisture supply to the trees. As a result of these conditions, most of the trees throughout the eastern part of the United States make much less vigorous growth than in the irrigated orchards of the Western States.

Pruning in bearing orchards, on the whole, is less severe and less detailed than in the western areas. This tends to result in a greater number of growing points per tree of similar size under eastern conditions as compared with western conditions. The amount of growth per growing point and the total leaf surface per growing point are less under the eastern conditions.

Control of apple scab requires the use of strong fungicidal sprays during the early part of the growing season in practically all eastern orchards. Liquid lime-sulfur sprays are generally used—at least prior to bloom. These sprays frequently result in foliage injury, reducing both the size of the individual leaves formed and their effectiveness in photosynthesis (22).

During the summer the light intensity is likely to average much less than in the Western States. At the United States Horticultural

Station, Beltsville, Md., approximately 80 miles from the district where the eastern investigations were conducted, average light intensity for the month of June has been from 60 to 70 percent of that of the brightest days during the past several years. While detailed light records are not available for Wenatchee, Wash., or other typical western apple districts, average light intensity there undoubtedly is very much higher. According to the results of Heinicke and Childers (*23*), photosynthetic activity of apple leaves with decreased light is reduced almost in proportion to the light intensity. Thus, because of less vigor of tree, the dwarfing of the foliage under many conditions by fungicidal sprays and reduced light supply, total photosynthetic activity per tree is greatly reduced under eastern conditions. This is reflected in the much greater average fruit production per tree in western irrigated orchards. It is also undoubtedly a vital factor in the greater tendency of the same varieties under eastern conditions to become biennial in bearing habit and to make a less favorable response in many cases to treatments to control biennial bearing than in the West. Thus in many eastern orchards such varieties as Jonathan, Delicious, and Winesap are strongly biennial, whereas these same varieties in western orchards are generally annual producers.

Although the basic relationship of leaf area and fruit production to the formation of blossom buds outlined in the first part of this bulletin apply under eastern conditions, the exact values in terms of foliage areas necessary to obtain blossom-bud formation may be very different. Also, response under eastern conditions to similar fruit and foliage adjustments may vary from year to year because of fluctuation in moisture or light conditions, or in the amount of injury to foliage from fungicidal sprays.

As heretofore discussed (p. 23), the time during which the buds are sufficiently meristematic to form flower parts, if other conditions are favorable, varies with the amount of growth the spur or shoot may make. Thus the much shorter growth on individual spurs in most eastern orchards would be reflected in a shorter time after full bloom during which blossom-bud formation might be affected.

Since 1931 extensive field tests have been conducted to determine the practical value and limitations of fruit thinning to correct the biennial-bearing condition in orchards in the Potomac Valley area. These orchards and trees are typical of those in many eastern fruit districts. In many of the experiments detailed records have been made of the number of growing points on large "record" limbs on many trees. The number of fruits in relation to approximate numbers of leaves before and after thinning, and the percentage of growing points that formed blossom clusters following the various treatments, have been recorded. Not all of these experiments are discussed in this bulletin, but sufficient detailed data are included to indicate the trends. A discussion of each experimental set-up will be made in connection with the presentation of the results.

FRUIT-THINNING EXPERIMENTS ON YORK IMPERIAL TREES

THINNING IN 1932

Since York Imperial is one of the most pronounced biennial-bearing varieties and it is also one of the most widely grown varieties in the Potomac Valley area, it has been more extensively used than any other

in experiments to correct the biennial-bearing habit by fruit thinning. An extensive experiment was established in 1932 in a block of large York Imperial trees about 27 years of age at the time the experiment was started. Twenty trees were selected in which an attempt was made to determine fairly accurately the total number of growing points per tree, the leaf area per growing point, and the number of fruits set per growing point before the occurrence of the June drop. As some of the experimental thinning was done before the time of the June drop, all records on numbers of growing points per fruit before thinning were necessarily based on the relationship before the time of the June drop.

As there was considerable variation in the set of fruit on various branches of the tree, records were made on an individual branch basis and are so reported in table 16. All the record limbs listed had more than 500 growing points per limb. These individual limbs were so marked that blossom records could be taken on the same limbs the following spring.

TABLE 16.- *Effect of fruit thinning of 27-year-old biennial York Imperial trees in 1932 on blossoming in 1933, Hancock, Md.*

Approximate degree and date of thinning	Period from full bloom to thinning	Trees treated	Limbs recorded	Approximate growing points¹ per fruit before thinning	Growing points blossoming
	Days	*Number*	*Number*	*Number*	*Percent*
Unthinned checks		4	5	1.0-2	0.4
			37	2.1-4	1.3
			22	4.1-6	1.0
			10	6.1-8	2.9
1 fruit to 10 growing points:					
June 5	35	4	9	1.0-2	2.8
			36	2.1-4	0.3
			11	4.1-6	7.3
			9	6.1-8	12.8
June 20	50	4	20	1.0-2	1.2
			59	2.1-4	3.5
			26	4.1-6	3.0
				6.1-8	14.0
July 5	65	4	10	1.0-2	.1
			53	2.1-4	.6
			21	4.1-6	3.6
			13	6.1-8	3.3
1 fruit to 20 growing points:					
June 20	50	4	11	1.0-2	2.4
			56	2.1-4	4.4
			24	4.1-6	8.1
			13	6.1-8	20.2

¹ Measurements on 1,100 spurs from 11 different trees averaged 13.8 square inches total leaf area per spur.

The limbs are classified according to the amount of fruit carried in 1932 in relation to total growing points. Only limbs that carried more than 1 fruit per 8 growing points are listed. Most of the limbs with less than this amount of fruit in 1932 were at the bottoms of the trees where the effect of shading in reducing productiveness of the branches was pronounced.

Four of the 20 trees received no thinning and were used as checks. The other trees were thinned to the degree and at the time shown in table 16.

It is of interest to compare the leaf surface on these trees per growing point with that on the very vigorous and more heavily pruned Yellow Newtown trees used at Wenatchee. In many respects

the Yellow Newtown and York Imperial varieties are quite similar in habit of growth and in type of foliage. The foliage per growing point at Wenatchee averaged about 50 square inches. The average leaf system on these York Imperial trees averaged between 13 and 14 square inches per growing point.

It is apparent from table 16 that there was little bloom on the check trees in the spring of 1933. Trees thinned to 10 growing points per fruit 35 days after full bloom had considerably more bloom in 1933 than limbs having a comparable set of fruit on the check trees. The amount of bloom on these trees, however, was not sufficient to produce nearly a full commercial crop in 1933. Under conditions of fairly good fruit set, bloom on approximately 20 percent of the growing points would be required for a full crop on York Imperial. The bloom on these trees averaged a little less than 10 percent, or not more than half enough for a full fruit crop.

Thinning to 1 fruit to 10 growing points 50 days after full bloom had little effect on the initiation of flower parts for the next year. Thinning to 1 fruit to 20 growing points 50 days after full bloom in this experiment was about equal to thinning to 1 fruit to 10 growing points 35 days after bloom.

Thinning the crop to 1 fruit to 10 growing points 65 days after full bloom, which would constitute a fairly heavy thinning at the date normally practiced commercially, had no significant effect on the amount of bloom for 1933.

THINNING IN 1933

Only one small experiment on thinning fruit on York Imperial trees was conducted in 1933. Six trees, all completely biennial and carrying a very heavy crop of fruit, were used. These trees, which were about 22 years of age, were growing on relatively shallow soil and were in moderate to rather low vigor. Actual leaf area per growing point was not obtained in this experiment, but it is probable that it was not greater than in the York Imperial trees used in the 1932 experiments. Results obtained on these trees are shown in table 17.

TABLE 17. *Effect of fruit thinning of 22-year-old highly biennial York Imperial trees in 1933 on blossoming in 1934. Dillon orchard, Hancock, Md.*

Approximate degree and date of thinning	Period from full bloom to thinning	Tree No.	Approximate growing points per fruit before thinning	Growing points blossoming
	Days		*Number*	*Percent*
Unthinned checks		1	3.6	0
		2	3.2	0
1 fruit to 10 spurs, June 10	38	3	2.6	.2
		4	3.8	1.6
1 fruit to 20 spurs, June 10	38	5	2.6	1.3
		6	2.4	1.4

Two trees having an average of approximately 3.6 and 3.2 growing points per fruit, respectively, were used as checks without thinning. Neither of these trees produced any blossoms in 1934.

Two trees were thinned to 10 growing points per fruit 38 days after full bloom, and 2 other trees were thinned to 20 growing points per fruit on the same date. While all of these thinned trees had a few

scattered blossom clusters in the spring of 1934, none had sufficient to produce an appreciable crop. Thus the thinning of these relatively weak growing and biennial trees 38 days after full bloom was not sufficiently early or heavy to break the biennial-bearing habit.

THINNING IN 1934

In 1934 the same block of trees used in the 1932 experiments was again used for fruit thinning. Half of the trees in this block had not received nitrogen fertilizer after 1931; the remainder had received moderate applications (about 8 pounds per tree) of nitrate of soda each year. Data on these trees are shown in table 18.

TABLE 18.—*Effect of fruit thinning of 29-year-old nonnitrated and nitrated partially biennial York Imperial trees in 1934 on blossoming in 1935, Hancock, Md.*

NONNITRATED TREES

Approximate degree and date of thinning	Period from full bloom to thinning	Trees treated	Limbs recorded	Approximate growing points per fruit before thinning	Growing points blossoming
	Days	Number	Number	Number	Percent
Unthinned checks		4	6	1.0-2	0.4
			15	2.1-4	.4
			2	4.1-8	6.5
1 fruit to 10 growing points:					
June 4	30	2	1	1.0-2	15.6
			7	2.1-4	52.5
			4	4.1-8	17.9
July 4	60	2	0	1.0-2	....
			16	2.1-4	1.5
			8	4.1-8	3.6
1 fruit to 20 growing points:					
June 4	30	2	7	1.0-2	14.7
			16	2.1-4	12.0
			6	4.1-8	3.5
June 20	46	2	8	1.0-2	16.1
			15	2.1-4	19.3
			4	4.1-8	.7

NITRATED TREES

Unthinned checks		4	16	1.0-2	1.4
			14	2.1-4	9.7
			4	4.1-8	15.0
1 fruit to 10 growing points:					
May 24	19	1	3	1.0-2	18.0
			6	2.1-4	28.1
			6	4.1-8	12.7
June 3	29	2	3	1.0-2	12.1
			7	2.1-4	4.1
			7	4.1-8	16.3
July 3	50	1	0	1.0-2	
			2	2.1-4	11.2
			5	4.1-8	12.4
1 fruit to 20 growing points:					
June 3	29	2	3	1.0-2	100.0
			12	2.1-4	76.5
			8	4.1-8	62.5
June 20	46	2	6	1.0-2	36.9
			9	2.1-4	29.7
			4	4.1-8	51.9

On the whole, the nonnitrated trees tended to form somewhat fewer blossom buds than the nitrated trees, as shown by percentage of points blossoming in 1935. Nonnitrated check trees had but little bloom, whereas the nitrated check trees had an appreciable amount of bloom in 1935.

All of these trees thinned in 1934 appeared to form blossom buds somewhat more readily than in the 1932 experiments on the same trees. Nonnitrated trees thinned to 1 fruit to 10 growing points 30 days after bloom produced sufficient bloom for a good commercial crop in 1935. Two other trees thinned even more heavily on the same date (1 fruit to 20 growing points) did not bloom so heavily in 1935. Similarly, nonnitrated trees thinned to 1 fruit to 20 growing points 46 days after bloom had a moderate bloom in 1935, but less than the 20 percent average, which is considered essential for a full commercial crop.

With the nitrated trees, 1 tree thinned 19 days after bloom to 1 fruit to 10 growing points produced a moderate bloom in 1935. Two trees thinned 10 days later to the same degree carried a lighter bloom. However, 2 trees thinned to 1 fruit to 20 growing points 29 days after bloom had a heavy bloom in 1935, and even trees thinned 46 days after bloom produced a moderately heavy bloom in 1935.

Although the results of the 1934 thinning appear to indicate that thinning up to 30 days after bloom was quite effective in increasing blossom-bud formation, results were somewhat variable and not wholly consistent. Some of the check trees and the trees thinned 59 days after bloom when other results would indicate that thinning had no effect on blossom-bud formation carried a moderate bloom. Hence, it must be assumed that some of the blossom-bud formation on the thinned trees might have occurred had no thinning been done.

Measurements made on several thousand growing points on these trees in 1936 showed an average of 13.3 square inches leaf surface per growing point for nonnitrated trees and 14.8 for the nitrated ones. These differences probably are similar to those in 1934 when the fruit-thinning work was done.

THINNING IN 1935

Since the earlier results with York Imperial trees had indicated that fruit thinning more than 30 days after bloom usually had but little effect in influencing blossom-bud formation, two experiments were set up in the summer of 1935 to determine the effects of very early fruit thinning. The first of these (table 19, Dillon orchard) was in a block of relatively small 20-year-old York Imperial trees which had set a heavy crop, as indicated by the number of growing points per fruit before thinning. Three of the thinned trees carried a heavier crop than the check tree. In 1936 all of the thinned trees had a good bloom, ample for a commercial crop. There was a scattered bloom on the check tree.

TABLE 19.—*Effect of fruit thinning of 20-year-old and 18-year-old York Imperial trees in 1935 on blossoming in 1936, Hancock, Md.*

20-YEAR-OLD DILLON ORCHARD

Approximate degree and date of thinning	Period from full bloom to thinning	Tree No.	Approximate growing points per fruit before thinning	Growing points blossoming
	Days		*Number*	*Percent*
Unthinned check		5	4.8	4.5
1 fruit to 10 growing points: May 31	28	1	3.0	33.3
		2	2.2	37.0
1 fruit to 20 growing points: May 31	28	3	2.6	32.4
		4	6.2	26.1

18-YEAR-OLD CASPER ORCHARD

Unthinned check		4a	6.2	2.5
		5b	5.2	0
		17a	8.4	12.0
1 fruit to 10 growing points: May 20	17	1a	4.0	16.0
		2a	3.8	27.0
		1b	5.8	33.0
		2b	4.0	15.0
June 20	48	9	7.6	12.9
		11	5.6	6.6

The same experimental setup in another orchard with trees about 18 years of age is shown in table 19. The set in this orchard was somewhat variable. Of the 3 check trees used, 1 had approximately 8.4 growing points per fruit before thinning, and it formed blossoms on 12 percent of the growing points in 1936. Four trees thinned 17 days after full bloom to a ratio of 1 fruit to 10 growing points all formed sufficient blossom buds to give a moderate to good commercial fruit crop in 1936. These 4 trees all carried a heavier set of fruit prior to thinning than did check tree 4a, which had bloom on only 2.5 percent of its growing points in 1936.

Two trees thinned to 1 fruit to 10 growing points 48 days after full bloom appeared to have slightly more bloom than comparable trees that were not thinned.

SUMMARY OF RESULTS ON YORK IMPERIAL TREES

Results of these thinning experiments conducted during several years indicate that, as in the western work, thinning must be done very early to obtain dependable results in increased blossom-bud formation. York Imperial trees thinned more than 30 days after bloom did not consistently produce sufficient bloom for a commercial crop the following season. Thinning within 20 days after bloom appeared to be more consistently successful than thinning 30 days after bloom in obtaining adequate blossom-bud formation. Thinning to 1 fruit per 10 growing points or approximately 1 fruit per 140 square inches of leaf surface was almost as effective as thinning twice as heavily if it was done sufficiently early. If thinning was postponed more than 30 days after bloom, even the heavier degree of thinning did not consistently result in increased blossom-bud formation.

All of these experiments were performed on what might be considered typical biennial-bearing York Imperial trees. All of the trees were characterized by abundant development of relatively short spurs, each carrying only a moderate leaf surface, totaling slightly under 15

square inches on the average. It seems highly probable that very vigorous trees would respond to thinning somewhat later in the season than the trees used in these tests, although the additional time would not be more than a few days.

FRUIT-THINNING EXPERIMENTS ON YELLOW TRANSPARENT TREES

The Yellow Transparent under conditions in the Potomac Valley is, on the whole, perhaps the most biennial variety. The trees form a moderate number of spurs, but the blossoms tend to set very heavily—frequently three to four apples setting from each blossom cluster. Investigations to determine the time during which buds could be influenced to form flower parts (34) indicated that the interval after bloom during which Yellow Transparent could be influenced was less than for the other varieties studied.

The first thinning experiment to correct the biennial-bearing habit in Yellow Transparent was established in 1933. Trees were approximately 20 years old, relatively small for their age, closely planted in the orchard, and in a completely biennial condition. More than 80 percent of the growing points blossomed on all trees in the test in the spring of 1933, and the set of fruit prior to the June drop was generally two to three fruits per blossom cluster. Results of the thinning test are shown in table 20.

TABLE 20.— *Effect of fruit thinning of highly biennial Yellow Transparent trees on blossoming the next year, Hancock, Md.*

DILLON ORCHARD (THINNED 1933; BLOOM RECORDS 1934)

Approximate degree and date of thinning	Period from full bloom to thinning	Tree No.	Growing points blossoming
	Days		*Percent*
Unthinned checks		1	0
		1	0
		3	0
		4	0
1 fruit to 10 growing points:			
May 26	30	1	.6
		2	6.5
		3	1.3
		4	4.2
June 19	54	1	2.8
1 fruit to 20 growing points:			
May 26	30	1	7.0
		2	8.3
		3	13.4
		4	9.1
June 19	54	1	1.1

TONOLOWAY ORCHARD (THINNED 1936; BLOOM RECORDS 1937)

Unthinned checks		1	[1] 2.8
		9	.1
		11	.5
1 fruit to 7 growing points:			
May 25	27	3	[2] 1.9
		8	6.4
		5	.4
June 4	37	7	[3] 12.5
1 fruit to 14 growing points:			
May 25	27	2	[2] 10.7
		10	[2] 5.6
		4	.6
June 4	37	9	[2] 7.6

[1] Practically all on 1 limb. [2] Well distributed. [3] Fairly well distributed.

On the 4 unthinned trees that served as checks, no blossom buds were present in 1934. Four trees thinned to 1 fruit per 10 spurs 30 days after bloom formed a limited number of blossom clusters in 1934. In 1934, 7 to 13.4 percent of the growing points bloomed on trees thinned on the same date to 1 fruit to 20 spurs.

Because of the very heavy set that usually occurs on Yellow Transparent when well pollinated, bloom on 15 to 20 percent of the growing points is usually ample for a full crop. Thus on these 4 trees the bloom in 1934 was sufficient for from half to almost a full crop. These trees produced 3 to 6 bushels per tree in 1934. The fruit was of large size and required practically no thinning.

Trees thinned 54 days after bloom developed a small amount of bloom, but not sufficient to produce an appreciable portion of a crop in 1934.

The four trees that produced a moderate crop in 1934 bloomed heavily in 1935, but there were many nonblossoming spurs in 1935. Heavy early thinning was repeated in that year with the result that these trees again produced a good commercial crop in 1936. Under the conditions of this test, it was possible by very early thinning to obtain good annual production of large-size Yellow Transparent apples. Thirty days after bloom, at which time the first thinning was done on these trees, appeared to be the latest date that effective results could be expected. Had the thinning been done even earlier, it is probable that better results would have been obtained.

Another experiment on Yellow Transparent apples (also reported in table 20) was started in 1936. The 3 unthinned check trees produced practically no bloom in 1937 except on 1 branch on 1 tree. Two trees were thinned to 1 fruit to 7 spurs 27 days after full bloom. One of these trees produced approximately half enough bloom for a crop in 1937, with the bloom well distributed over the tree; the other produced only a scattered light bloom. Two trees thinned on the same date to 1 fruit to 14 spurs had sufficient bloom in 1937 to produce about a half crop of fruit.

Four trees were thinned on June 4, 1936, 37 days after full bloom. Two of these failed to respond with additional bloom in 1937, and two formed a moderately well-distributed bloom sufficient for about a half crop.

Because of the very heavy bloom that normally develops on biennial Yellow Transparent trees, foliage buds are usually late in developing during the on year, and the foliage system is limited during the early part of the growing season. Results of these experiments indicate that heavy thinning, leaving from 15 to 20 spurs per fruit, done within 30 days will usually result in a fair bloom for the following season. To be effective in producing a full crop for the following year, such thinning on Yellow Transparent should apparently be done not more than 20 to 25 days after full bloom.

FRUIT-THINNING EXPERIMENT ON STAYMAN WINESAP TREES

Stayman Winesap is one of the more regularly producing varieties in the Potomac Valley area. Normally, the fruit does not set heavily, and the ratio of fruit set to foliage is usually such that at least some bloom forms following the moderate crops that are usually produced. However, frequently the trees alternate from a heavy crop to a light

crop of fruit. An experiment in such a block of trees, not completely biennial but alternating from a light to a heavy crop, was established in 1935. The trees were approximately 30 years of age, of rather small size, and only moderately vigorous. The results of the thinning experiments are shown in table 21.

TABLE 21.—*Effect of fruit thinning of partially biennial Stayman Winesap trees in 1935 on blossoming in 1936, Tonoloway orchard, Hancock, Md.*

Approximate degree and date of thinning	Period from full bloom to thinning	Tree No.	Approximate growing points per fruit before thinning	Growing points blossoming
	Days		*Number*	*Percent*
Unthinned checks		1	8.4	19.0
		2	3.8	5.0
1 fruit to 10 growing points:		3	5.6	37.4
May 22	22	4	5.0	29.6
		5	4.8	23.7
May 31	31	6	10.0	27.2
		7	3.4	54.0
June 19	50	8	5.0	43.9
		9	6.7	11.4
July 1	62	10	4.0	31.2
1 fruit to 20 growing points:		11	3.6	23.8
		12	8.4	51.3
June 1	32	13	5.2	11.4
		14	4.4	23.1
		15	6.2	8.4
June 19	50	16	4.8	41.1
July 1	62	17	4.0	9.3

Two check trees were left unthinned. The three trees thinned July 1, 62 days after full bloom, were probably not affected by the thinning treatment. Of these five trees only one produced blooms on as many as 20 percent of its growing points in 1936.

Two trees were thinned to 10 growing points per fruit 22 days after full bloom; 2 additional trees were thinned similarly 31 days after full bloom; and 4 additional trees were thinned to 20 growing points per fruit 32 days after bloom. Of these 8 trees only 1 had less than 20 percent of its growing points with bloom in 1936. Thus it would appear that the thinning treatments had been effective in increasing the amount of bloom on these partially biennial trees. The variability that occurred in individual trees, however, must be considered in evaluating the results of this experiment.

Four additional trees were thinned 50 days after full bloom, three of which carried heavy bloom in 1936. These results might indicate that blossom-bud formation could be influenced later on the Stayman Winesap than on the other varieties studied. Such a result would be expected from the studies on the time during which blossom-bud formation could be influenced (34). An appreciable number of buds of Stayman Winesap apparently could be influenced to form flower parts up to 85 days after full bloom, as compared with 55 days with Yellow Transparent and 51 to 62 days with York Imperial.

FRUIT-THINNING EXPERIMENT ON JONATHAN TREES

Results of a small experiment with Jonathan trees are shown in table 22. These trees were approximately 25 years of age, of small size, and in only moderate vigor. They were completely biennial, a rather unusual condition for Jonathan. An experiment conducted

in 1933 consisted of only 6 trees, 2 of which were unthinned, 2 were thinned to 10, and 2 to 20 growing points per fruit, all on June 6, 37 days after full bloom. No blossoms were formed on either of the check trees. The growing points with bloom in 1934 on the thinned trees ranged from 3.5 percent to 7.6 percent. Thus while there was clear evidence of increased blossom-bud formation following thinning, it was not sufficiently great to result in a commercial crop in 1934. Also, there was little difference in results in the trees thinned to 10 and those thinned to 20 growing points per fruit. Apparently in such completely biennial trees thinning as much as 37 days after full bloom failed to cause a large amount of blossom-bud formation in Jonathan. However, there was distinctly more blossom-bud formation following the thinning on Jonathan than on the York Imperial trees (table 17), which were in an adjoining row in the same orchard and thinned at approximately the same interval following bloom.

TABLE 22.—*Effect of fruit thinning of highly biennial Jonathan trees in 1933 on blossoming in 1934, Dillon orchard, Hancock, Md.*

Approximate degree and date of thinning	Period from full bloom to thinning	Tree No.	Approximate growing points per fruit before thinning	Growing points blossoming
	Days		*Number*	*Percent*
Unthinned checks		1	3.8	0
		2	3.2	0
1 fruit per 10 growing points, June 6	37	3	3.4	3.5
		4	3.2	7.6
1 fruit per 20 growing points, June 6	37	5	3.4	5.0
		6	2.6	3.5

GENERAL DISCUSSION OF FRUIT THINNING IN THE EAST

Results of these thinning investigations conducted during several years indicate clearly that blossom-bud formation can be influenced under conditions prevailing in the Potomac Valley area by sufficiently early thinning with trees in moderate vigor, generally used in these tests. Such thinning was usually quite effective if done within 20 to 25 days after full bloom and if sufficiently heavy to leave as much as 150 to 200 square inches (10 growing points or more) of leaf surface per fruit. If thinning was delayed as much as 30 days after bloom, a much smaller quantity of bloom usually resulted. Thinning with most varieties more than 30 days after full bloom was not generally effective, although in some experiments some increased bloom resulted.

These results are in general accord with those obtained in the western areas, except that the time interval during which the thinning must be done is apparently shorter than with the more vigorous trees in the Western States.

Because of the very early thinning required and the large numbers of fruits that must be removed when all the thinning is done prior to the June drop, such treatments would appear to be of doubtful practicability when applied to large orchards, particularly on sites subject to frost, where the biennial-bearing condition might be reestablished relatively soon. Since no other means of correcting the biennial-bearing habit are now available, such thinning might be feasible with such varieties as Yellow Transparent which, because of

their tendency to set so heavily in the on year, frequently fail to attain market size. The maintenance of such a variety in regular bearing with the more moderate sets and larger size of fruit might be feasible even though the costs were high.

Summary of Investigations in the Potomac Valley

Experiments to determine the response of biennial-bearing apple trees to fruit thinning at different intervals of time following bloom were conducted in commercial orchards in the Potomac Valley from 1932 to 1937, inclusive.

Moderately vigorous biennial York Imperial trees thinned during the bearing year in these experiments formed sufficient blossom buds for a crop the following year when thinning was completed within 30 days after full bloom and when 10 or more growing points, carrying an average of 13 to 15 square inches of leaf area, were present for each fruit remaining after the thinning. Similar trees, thinned 35 to 40 days after full bloom, generally developed more blossom buds than unthinned check trees, but not enough for a full crop the following year. Thinning 50 days or more after full bloom had no consistent effect on blossom-bud formation.

The greater the vigor of the tree the greater in general was the response from early fruit thinning.

Yellow Transparent trees, thinned within 30 days after full bloom to 14 or more growing points per fruit, formed blossoms on only about 10 percent of the spurs. Apparently 30 days from bloom was the limit for fruit thinning to be effective in correcting biennial bearing in this variety.

Stayman Winesap trees, only partially biennial, apparently showed some response in increased blossom-bud formation following thinning up to 50 days from full bloom.

Completely biennial Jonathan trees formed some blossom buds when thinned to 10 and 20 growing points per fruit 37 days after full bloom, although bloom was not sufficient for a full crop the following year.

Earliness of thinning appears to be more important than degree of thinning in inducing blossom-bud formation in biennial trees under eastern conditions.

Possibilities in Other Types of Approach to Biennial-Bearing Problem

The basic principles established in this and other work for the control of biennial bearing, based on adjustment of fruit to the foliage system, suggest the possibility of other less expensive methods of approach to the biennial-bearing problem. Possibly the most promising of these is to reduce the set of fruit during the heavy crop years by early caustic sprays, which will prevent the set of a large proportion of the blossoms. At the present time, special emphasis is being placed on studies of this character. Evidence has been accumulated to indicate that the year during which the heavy crop is produced can be changed by such spray treatments. Whether or not such treatments can be used to reduce the set without almost entirely eliminating the crop can only be determined by further experiments.

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