Studies in Strawberry Bud Differentiation

By H. HILL and M. B. DAVIS

DIVISION OF HORTICULTURE DOMINION EXPERIMENTAL FARMS

W. T. MACOUN

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STUDIES IN STRAWBERRY BUD DIFFERENTIATION*

BY H. HILL AND M. B. DAVIS

Nutritional conditions within the plant, affected and modified by the nature of the soil solution, constitute one of the chief factors of fruit bud differentiation. An excess of carbohydrates, together with the absence of any limiting factor that interferes with vegetative growth, constitutes favourable nutritional conditions. The supply of available nitrogen is probably the most common limiting element. A knowledge of the time of fruit bud differentiation is of great importance in connection with the possibility of increasing their number by fertilizer applications.

In the Reports of the Dominion Horticulturist for 1924, 1925 and 1926 results were presented of our work with the time of application of nitrogenous fertilizers in the strawberry plantation. Our results gave evidence that spring applications as made, though of some slight value in increasing the size of fruit, were unable to increase the number of blossoms, and that the application of fertilizer on September 15 of the first year and August 15 of the first fruiting year gave the best results. In an endeavour to correlate and compare these results with the time of initiation and development of fruit buds, cytological studies were undertaken.

HISTORY

Goff (1), one of the earliest workers on the subject, found that the initial stage of blossom bud differentiation in the strawberry occurred on September 20. He considered that the slight irregularities in the growing point or crown of the bud were the first evidences that differentiation had taken place. He found that the order of development is the same in the different fruits, calyx, petal, stamens and finally the pistil.

Drinkard (2), working with the apple, also considered that corrugations on the crown were the first morphological evidences that a differentiation into flower buds had taken place.

Bradford (3), writing of the apple, says that the first evidence of fruit bud formation lies in the rapid elevation of the crown into a narrow, conical form, rounded at the apex, with the fibro-vascular connections and pith areas advancing concurrently.

Ruef and Richey (4) examined the differentiation of flowers in strawberry runners and found that the time varied with the position of the runner on the stolon, the flowers on the runners nearer the parent plant developing before those on the runners further away. In the same way the primary flowers of the inflorescence developed before the secondary or tertiary ones. Thus differentiation was spread over a period, the first signs of flower formation being visible in early September and the rudiments of the latest formed flowers not being formed until December.

^{*}The authors wish to acknowledge the assistance so generously given by G. F. Waldo of the U.S. Department of Agriculture, who assisted in the interpretation of some of the slides.

PROCEDURE

For this purpose runners of the variety Pocomoke, which were just becoming attached to the soil by roots, were staked at weekly intervals throughout the summers of 1925, 1926 and 1927. In this way we were able to obtain groups of runners rooted at intervals of one week from the 28th of June until the 10th of October. Runners from each of these groups were lifted every two weeks, when the group of runners attained an age of two weeks, and prepared for cytological examination. This provided us with material of comparative age, rooted at different times, and a range covering periodic development until fall.

TECHNIQUE

The crowns of the plants were taken and after being very carefully trimmed were placed in medium chromo-acetic acid killing solution for thirty hours. The buds were then washed, dehydrated and embedded in paraffin by the method usually employed in histological study. They were then sectioned on a rotary microtome with a thickness of twelve to fifteen microns. Despite extreme care taken in the handling of the buds, much difficulty was experienced in sectioning, owing to the presence of silicated hairs and bud scales. Safranin was at first employed for staining; later it was found that Erythrosin gave clearer and brighter sections.

PRESENTATION OF RESULTS

Even after the closest examination of numerous slides the initial stage at which morphological differentiation has begun is very difficult to determine. The initiation of differentiation appears to occur as a gradual transition rather than a sharp and sudden change. In this investigation it has been considered that slight irregularities in the growing point or crown, together with an elongation and flattening of the crown, constitute evidence of the first differentiation of the flower stalk.

Figs. 1, 2 and 3 show an undifferentiated crown, one which has barely commenced differentiation and one in which differentiation is quite definite, the crown pushed up and lobed.

GROUP 1

Rooted June 28, collected July 28, age one month:—

No sign of differentiation, growing crown enclosed by developing leaflets and protecting scales. Owing to scarcity of runners at the date of rooting this was the only sample of this group available. Similar in stage of development to fig. 1. See fig. 4.

Group 2

Rooted July 11, collected July 25, age 2 weeks:—

Small, poorly developed crown surrounded by developing leaflets and protecting scales. See fig. 5.

Rooted July 11, collected August 22, age 6 weeks:—

No flower bud differentiation, growing crown quite symmetrical, surrounded by developing leaf primordia. Runner primordium present towards the outside of the tissue. See fig. 6.

Group 3

Rooted July 18, collected August 3, age 2 weeks:—

Small growing crown surrounded by developing leaf primordia. See fig. 7.

Rooted July 18, collected August 15, age 4 weeks:—

Growing crown enclosed by protecting tissue and developing leaf primordia. See fig. 8.

GROUP 4

Rooted July 25, collected August 9, age 2 weeks:—

No sign of differentiation, growing point surrounded by developing leaf primordia. See fig. 9.

Rooted July 25, collected August 22, age 1 month:-

Crown enclosed by developing leaf tissue, no sign of differentiation, runner primordium present. See fig. 10.

Rooted July 25, collected September 6, age 6 weeks:-

Crown well developed, enclosed by embryonic leaflets, no sign of differentiation of flower bud. See fig. 1.

Rooted July 25, collected September 19, age 8 weeks:-

Initiation of fruit bud differentiation, crown or growing point pushing up, flattening and broadening out on top forming a flower stalk. See fig. 2. To one side of the developing flower bud is a runner primordium.

Rooted July 25, collected October 10, age 11 weeks:—

Differentiation of fruit stalk quite definitely begun, three growing points or crowns intended to develop into a primary and two secondary flowers. Crowns elongated and flattened out. Primary flower primordium with sepal and petal primordia. See fig. 11.

Rooted July 25, collected October 17, age 12 weeks:—

Primary bud with primordial sepals, petals and stamens. Two secondary flower buds with primary sepals and petals. See fig. 12.

Rooted July 25, collected October 31, age 14 weeks:—

Central or primary flower bud very well developed. Receptacle broadened and flattened out, bearing on the surface numerous pistil primordia. Anthers of stamens lobed with central vascular bundle and four locules. Secondaries with sepal, petal and stamen primordia and a tertiary with sepal and petal primordia developed. See fig. 13.

GROUP 5

Rooted August 3, collected August 22, age 21 weeks:

Growing crown enclosed by leaf primordia and protecting scales, no differentiation. See fig. 14.

Rooted August 3, collected September 12, age 6 weeks:-

Crown surrounded by enclosing developing leaflets, runner primordium present. See fig. 15.

Rooted August 3, collected October 1, age 9 weeks:—

Crown pushed up and flattened out. Initiation of primary bud and two lateral buds. Primary bud with sepal primordia beginning to arise from the side. See fig. 16.

Rooted August 3, collected October 17, age 11 weeks:—

Primary flower with sepal, petal and stamen primordia. Two secondary flowers arising from the base of the primary with sepal primordia just beginning to push up from the sides. See fig. 17.

Rooted August 3, collected October 31, age 13 weeks:-

Primary bud well developed, primordia of all flower parts present. Surface of receptacle corrugated, with primordial pistils beginning to appear. Two secondary flower buds with sepal and petal primordia. See fig. 18.

GROUP 6

Rooted August 17, collected August 31, age 2 weeks:—

Crown surrounded by young growing leaf primordia. See fig. 19.

Rooted August 17, collected September 12, age 1 month:—

Crown or growing point well developed, still even in contour, surrounded by developing leaflets and protecting scales, differentiation not yet commenced. See fig. 20.

Rooted August 17, collected October 10, age 2 months:—

Central primary flower bud with sepal, petal and stamen primordia. Two secondary buds with sepal and petal primordia. See fig. 21.

Rooted August 17, collected October 24, age 10 weeks:—

Primary bud with sepal, petal and stamen primordia, well developed. Two secondary buds smaller but with sepal and petal primordia. Tertiary bud just beginning to push up. See fig. 22.

Group 7

Rooted August 22, collected September 12, age 3 weeks:—

Crown quite symmetrical, no sign of fruit bud differentiation, enclosed by developing leaflets and protecting scales. See fig. 23.

Rooted August 22, collected September 19, age 4 weeks:—

Fruit bud differentiation definitely initiated. Crown pushed up, corrugated or lobed, contour uneven. Runner primordium present at one side. See fig. 3.

Rooted August 22, collected October 10, age 7 weeks:—

Primary bud with sepal and petal primordia showing but not very large. Two secondary buds with sepal primordia showing. See fig. 24.

Rooted August 22, collected October 17, age 8 weeks:—

Primary bud well developed with sepal, petal and stamen primordia. Two lateral secondary buds with sepal and petal primordia. See fig. 25.

Rooted August 22, collected October 31, age 10 weeks:—

Primary bud very well developed, surface of receptacle showing small lumps or tubercules, the beginning of the pistil primordia; stamens well developed, anthers lobed with locules.

Secondary bud considerably smaller, not so well developed but possessing sepal, petal and stamen primordia. Tertiary bud just beginning to push up. Quite similar to runner rooted July 25 but lifted at the same time. See fig. 26.

GROUP 8

Rooted August 29, collected October 1, age 4 weeks.

Initiation of fruit bud quite definitely commenced. Crown pushed up and irregular. Scpal primordia just beginning to show. See fig. 27.

Rooted August 29, collected October 10, age 6 weeks:—

Primary bud with sepal primordia. Two lateral secondary buds just beginning to develop. See fig. 28.

Rooted August 29, collected October 24, age 8 weeks:-

Primary or central bud with sepal, petal and stamen primordia present. Two secondary lateral buds much smaller than central bud; sepal and petal primordia present. See fig. 29.

GROUP 9

Rooted September 12, collected October 1, age 2 weeks:-

Differentiation of primary fruit bud well commenced, with sepal primordia arising from the base of knob-like receptacle. See fig. 31.

Rooted September 12, collected October 10, age 4 weeks:-

Primary flower bud with sepal and petal primordia. Secondary lateral buds pushing up with calyx primordia just showing. See fig. 32.

Rooted September 12, collected October 24, age 6 weeks:—

Primary flower bud well developed; sepal, petal and stamen primordia present. Two secondary buds much smaller with sepal and petal primordia present. See fig. 33.

GROUP 10

Rooted September 19, collected October 10, age 3 weeks:—

Primary or central bud with sepal and petal primordia. Two secondary buds just pushing up. See fig. 34.

Rooted September 19, collected October 17, age 4 weeks:—

Primary bud well developed with sepal, petal and stamen primordia. The differentiation of two secondary buds has just commenced with the pushing up and flattening of two growing points. See fig. 35.

Rooted September 19, collected October 31, age 6 weeks:—

Primary bud with sepal, petal and stamen primordia. Secondary buds just beginning to differentiate. See fig. 36.

Group 11

Rooted October 10, collected October 24, age 2 weeks:-

Central bud with sepal and petal primordia. Secondary bud with sepal

primordia. See fig. 37.

During the course of this study we examined several plants which had borne no bloom during their normal blooming season. Fig. 38 is a photograph of a section through the crown of one of these plants, showing an ordinary vegetative bud.

SUMMARY

In examining the data given above we find that the first sign of flower bud differentiation was observed to take place on the 19th of September. This is true for runners rooted both on July 25 (fig. 2) and August 22 (fig. 3), one month later, and intervening dates. That is, runners of eight weeks of age, up until the middle of September, were unable to commence differentiation of flower buds any sooner than four weeks-old runners. Runners two weeks of age on September 19 showed no signs of differentiation (fig. 30). In a consideration of runners rooted after this date we find that differentiation is evident when runners are but two weeks of age. Runners rooted September 12 (fig. 31), 19 (fig. 34) and October 10 (fig. 37) have begun differentiation on October 1, 10 and 24 respectively. It is also to be noted that runners rooted a week previous to September 19 are not so far developed as runners rooted after this date but collected at the same age. There is apparently a critical seasonal period before which the stimulus for flower bud formation is lacking, independent of the age of the runner. For this variety and locality the date is approximately September 19, the work of the three years giving approximately the same results.

Runners rooted the 25th of July showed the first signs of differentiation of flower buds on September 19, as evidenced by a pushing up and flattening out of the crown. On October 10 there were three growing points intended to develop into a primary and two secondary flowers. On the primary bud sepal primordia were beginning to push up from the sides. On the 17th of October the primary bud possessed sepal, petal and stamen primordia and the secondary buds sepal and petal primordia.

On October 31 the primary bud was very well developed, the receptacle bearing on the surface numerous pistil primordia. Anthers were prominent, lobed with four locules; secondaries with sepal, petal and stamen primordia and a

tertiary with sepal and petal primordia.

There is a general development of the floral part from the initiation of differentiation until late fall, with sepal, petal, stamen and pistil primordia appearing in the order named. The primary develops more rapidly than the secondary,

the secondary than the tertiary, etc.

The correlation between the results obtained with the time of fertilizer applications in the field and the initial date of fruit bud differentiation is quite marked. Spring applications of fertilizer as made had no effect in increasing the number of fruit buds. This is to be quite understood in the light of our cytological studies, which showed that the initiation of fruit bud differentiation is delayed until approximately September 19. Highest yields were secured with fertilizers applied on September 15 of the first year and August 15 of the first fruiting year, which dates are quite close to the beginning of fruit bud differentiation as determined by our microscopical studies.

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- 3. Bradford, F. C. Fruit Bud Development of the Apple, Oregon Agr. Exp. Bull. 129: 1-16: Plates I-VI.
- 4. Ruef, J. U. and H. W. Richey. A Study of Flower Bud Formation in the Dunlap Strawberry. Am. Soc. Hort. Sci., 1925, p. 252.



Fig. 1.—Rooted July 25, collected September 6. Note the even contour of the crown with no sign of fruit bud differentiation.

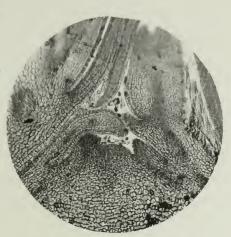


Fig. 4.—Rooted June 28, collected July 28.

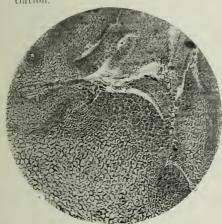


Fig. 2.—Rooted July 25, collected September 19. Note the slight raising of the crown indicating initiation of fruit bud differentiation.

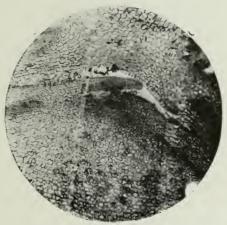


Fig. 5.—Rooted July 11, collected July 25.

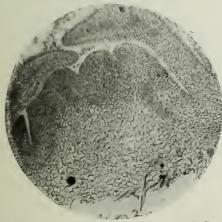


Fig. 3.—Rooted August 22, collected September 19. The deep corrugations of the crown indicate definite differentiation.

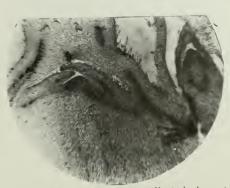


FIG. 6. Rooted July 11, collected August 22. Showing undifferentiated crown with runner primordium showing on the right.

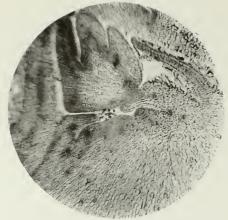


Fig. 7.—Rooted July 18, collected August 3.

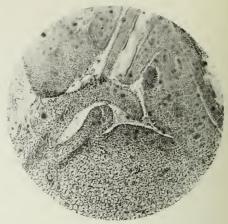


Fig. 10.—Rooted July 25, collected Aug. 22.

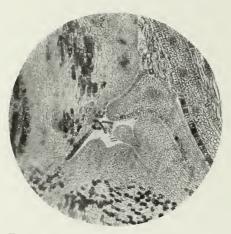
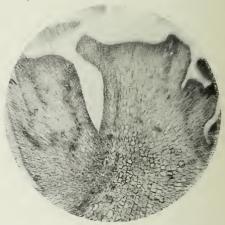


Fig. 8.— Rooted July 18, collected Aug. 15. Fig. 11.—Rooted July 25, collected Oct. 10.



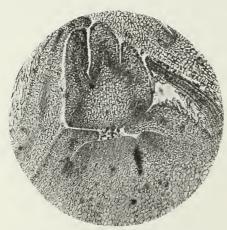


Fig. 9.—Rooted July 25, collected August 9.

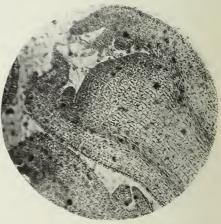


Fig. 12.—Rooted July 25, collected Oct. 17. Sepals, petals and stamens are all in evidence at this stage.

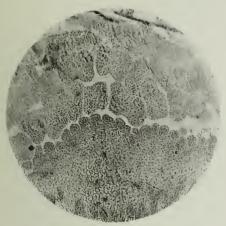


Fig. 13.—Rooted July 25, collected Oct. 31. Authors and stamen primordia clearly evident.



Fig. 16.—Rooted August 3, collected Oct. 1.

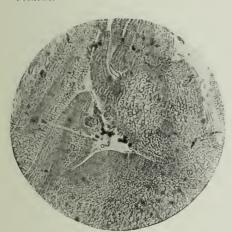


Fig. 14.—Rooted August 3, collected Fig. 17.—Rooted August 3, collected Oct. 17.

August 22.



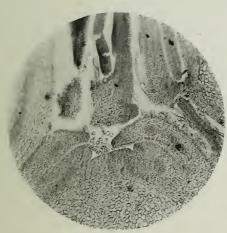
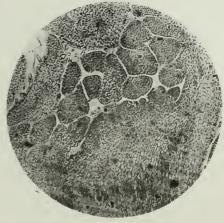


Fig. 15.—Rooted August 3, collected September 12. Fig. 18.—Rooted August 3, collected Oct. 31.



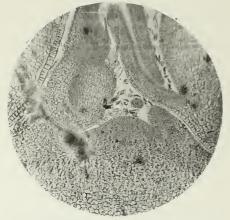


Fig. 19.—Rooted Aug. 17, collected Aug. 31. Fig. 22.—Rooted Aug. 17, collected Oct 24.



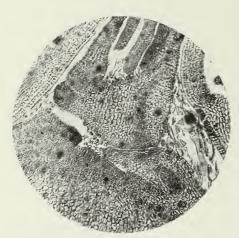


Fig. 20.—Rooted August 17, collected September 12. Fig. 23.—Rooted August 22, collected September 12.

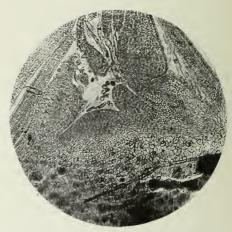




Fig. 21. Rooted Aug. 17, collected Oct. 10.

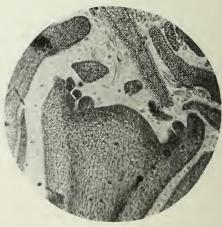


Fig. 24.—Rooted Aug. 22, collected Oct. 10.

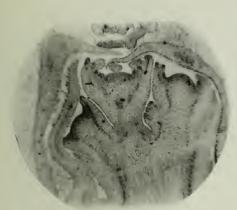


Fig. 25.—Rooted Aug. 22, collected Oct. 17. Primary and two lateral secondary buds.

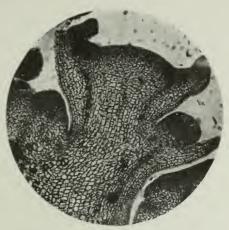


Fig. 28.—Rooted Aug. 29, collected Oct. 19.

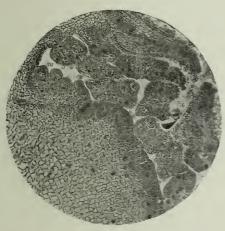
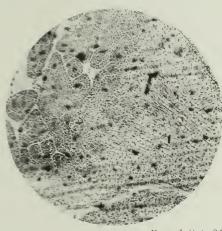


Fig. 26.—Rooted Aug. 22. collected Oct. 31. Fig. 29. Rooted Aug. 29. collected Oct. 24.



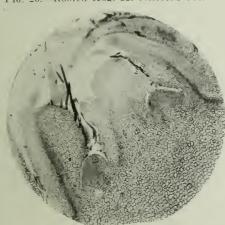


Fig. 27.—Rooted Aug. 29, collected Oct. 1.

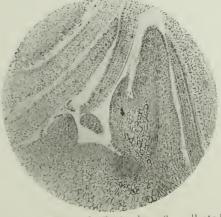


Fig. 30. Rooted September 6, collectedSeptember 19. The same age as in Fig.8, but lifted earlier. Note that there is no sign of differentiation.

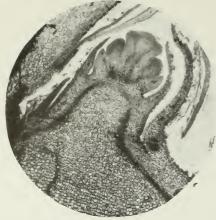


Fig. 31.—Rooted September 12, collected October 1 Note age, only 19 days, sepal primordia clearly evident.

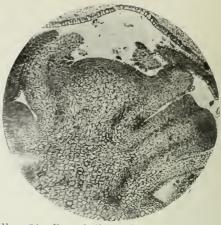


Fig. 34.—Rooted September 19, collected October 10. Note the two secondary buds just starting, one on either side of the main bud.



Fig. 32. Rooted September 12, collected October 10.



Fig. 35. Rooted September 19, collected October 17.

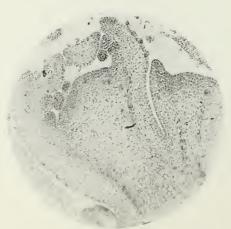
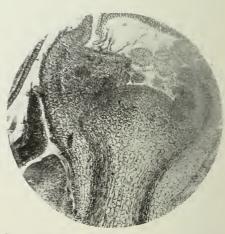


Fig. 33.—Rooted September 12, collected Fig. 36.—Rooted September 19, collected October 24.



Ocober 31.



Fig. 37.—Rooted October 10, collected October 24. Only two weeks of age, but note the sepal and petal primordia of central bud.

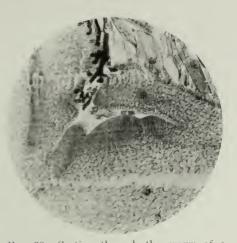


Fig. 38.—Section through the crown of a plant which had no bloom during its normal blocming period, i.e., vegetative bud.





DIVISION OF HORTICULTURE

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