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A Preliminary Study

of the

FRUITING HABIT OF THE BLACK RASPBERRY

Rubus occidentalis

By George A. Beach

Colorado Agricultural College
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Most of the work in this field has been done where natural rainfall is depended upon to grow the crop. In Colorado, rainfall is usually insufficient and the crop is irrigated. In the East, brambles often suffer from drouth if too much fruiting wood is left in the plants after pruning. Possibly, where ample water is available at fruiting time, the blackcap would be able to support a greater amount of fruiting wood than it is otherwise advisable to leave.

The common practice in Colorado is to do no summer pruning. Some growers cut back the new canes just before picking. This practice is erroneously referred to as pinching; but being done so late, it encourages a weaker type of branching than proper pinching produces. It does facilitate picking to have this rank new growth removed, but it probably also reduces the yield and quality that might have been expected the next year. Whether to do no summer pruning and encourage growth of main canes, or to pinch properly and promote stout branches is another question that hinges upon knowledge of fruiting habit.

Since knowledge of fruiting habit is so fundamental, it will enable growers to solve many of their own particular problems. Such a basic study as the one reported here, should then, be more generally useful than a study of some special problem in growing the crop.

Literature Review

Many have investigated the merits of summer pinching, altho little apparently has been done toward determining the natural fruiting habit of blackcaps. Goff (3) said pinching was not commercially worth while. Card (2) indicates that, all things considered, pinching is the best commercial practice. Card tells how blackcaps are damaged by leaving too much fruiting wood in the plant. Marshall (8) shows that there is a direct relationship between rainfall and both size and yield of fruit for the season. Johnston (5) recommends short pruning to make even-sized pickings.

Aside from its value in interpreting past work, many problems that will arise hereafter are certain to hinge more or less closely upon a knowledge of the fruiting habit, of which we now know so little. Brierly (1) found that thick-set laterals on the red raspberry en-

*This bulletin is the second of a series started by R. V. Lott's Colorado Experiment Station Bulletin 367.

couraged formation of new xylem to a greater extent than where laterals were more widely scattered. This fact would probably hold with blackcaps and so offer a possible argument in favor of pinching, since pinching produces thick-set laterals.

Goff (3) says: "There seems to be evidence to show that in such plants as * * * raspberry * * * in which no flower buds can be distinguished in autumn, these plants unquestionably form their flower buds during that season." MacDaniels (7) cites fruit-bud differentiation in October in the variety Cumberland, which he studied by dissection with 15 to 20 X magnification. This question has a practical bearing on pruning practices. Spring pruning is essentially fruit thinning if differentiation of fruit begins before spring pruning is done; otherwise, it is simply a shaping of the plant. Marshall (8) says the season of fertilizer application makes no yield difference; (which it might be expected to make, if fruit bud differentiation were confined to any definite season).

Marshall's (8) statement that blackcaps are extremely sensitive to soil heterogeneity is borne out by the differences between hills selected for their relative uniformity in this experiment on soil apparently quite homogeneous.

NOMENCLATURE

L. H. Bailey's distinction between canes of different ages, before and after reaching bearing age—as *primocanes* and *floricanes*—is used here; and W. G. Brierly's (1) definitions of branch and lateral: *Branch.*—A division of the young cane, developed in the first year. Essentially the same as a young cane, but arising from it instead of from the crown or root. *Lateral.*—A leafy shoot of the old cane or branches, developing from a winter bud and usually bearing flowers and fruits. Many of the laterals may produce neither flowers nor fruits. To distinguish between them on the basis of performance they may be called fruiting laterals or barren laterals.

MATERIALS AND METHODS

Plants studied in the experiment were grown on clay loam with a slight slope to the north. An analysis from the station soils laboratory showed it to lack nothing with the exception of a very slight deficiency in potash. Three varieties were established by 2 years' growth on a tenth acre at the beginning of the experiment. These were Cumberland, Honeysweet and Plum Farmer; one north-south row (60 hills) of each variety, spaced 3 by 8 feet.

Plum Farmer, being a widely grown commercial variety, was chosen for detailed records, tho all varieties were prepared by pinching and thinning primocanes in the event that Plum Farmer should fail.

Fig. 1.—Tagging method.

Fig. 2.—Method of winter protection.

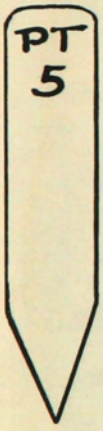
Treatments studied were: (1) "Pinched," in which all primocanes were pinched to 24 inches as soon as they reached 30 inches in length; (2) "pinched and thinned," in which all except the seven best primocanes per hill were removed in addition to the same pinching treatment described for (1); and (3) "unpinched and unthinned," where all canes were allowed to grow naturally.

Twenty hills of each variety were prepared for each treatment, a year prior to fruiting. All plants were covered for winter in November and uncovered the first week in April.

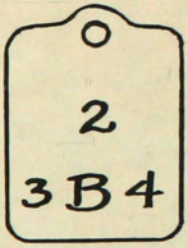
As soon as canes had been raised from winter cover, the five most representative hills of each treatment were selected and staked.

All plants of the same variety were in a single row. Each plant on which records were taken was considered a replicate. The five hills selected for each treatment were necessarily scattered by chance in selecting them for uniformity. Systematic replication was thus avoided; but for any one treatment, they were scattered only thru one-third of a single row.

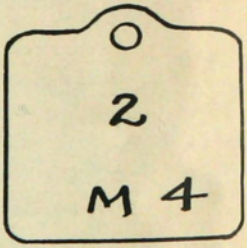
Cane numbers were assigned arbitrarily, starting at 1 in each hill. Beginning at the ground, a main cane tag was placed every 6 inches to mark the upper end of the section to which it referred. Branches were similarly tagged by placing the first tag 6 inches from the base of the branch and designating the lowest branch of each cane as branch No. 1. The lowest section of each main cane or branch was called section No. 1.



Stake



Branch Tag



Main Cane Tag

Pinched	P
Thinned	T
Hill No.	5

Cane No.	2
Third branch above ground	3
Branch	B
Sec. No.	4

(This tag hung 2 ft. or 4, 6-inch sections, from the base of the third branch of Cane 2.)

Cane No.	2
Main cane	M
Sec. No.	4

(Most branches arose from M4 sections, or 2 ft. from the ground)

Tagging was completed before shoot elongation was appreciable. In addition to tagging, the following notes were taken in April: Main cane diameter 6 in. from base; number of main cane section in which each branch originated; branch diameter 3 in. from base; length of live wood and total length of each main cane and branch.

All ripe berries were picked every 2 or 3 days into paper half-pints numbered to correspond with the section from which the fruit was gathered. A total of 10 pickings was made, both seasons. A tabulation was made showing the date, number of berries, and weight of each picking from every section.

After fruiting, a record was made of the number of fruitful and the number of barren laterals; the average length of laterals, and the total weight of each cane with its branches.

MICROSCOPICAL STUDY OF BUDS.—Median sections of buds taken at weekly intervals from June 10, 1931, to October 26, 1931, and from April 25, 1932, to June 10, 1932, were prepared as permanent mounts by standard histological methods and studied for manner and date of fruit-bud differentiation. From September 12 thru December, 1932, camera lucida sketches of fresh, freehand sections of buds at base, middle and near tips of branches were made weekly for comparison with permanent mounts.

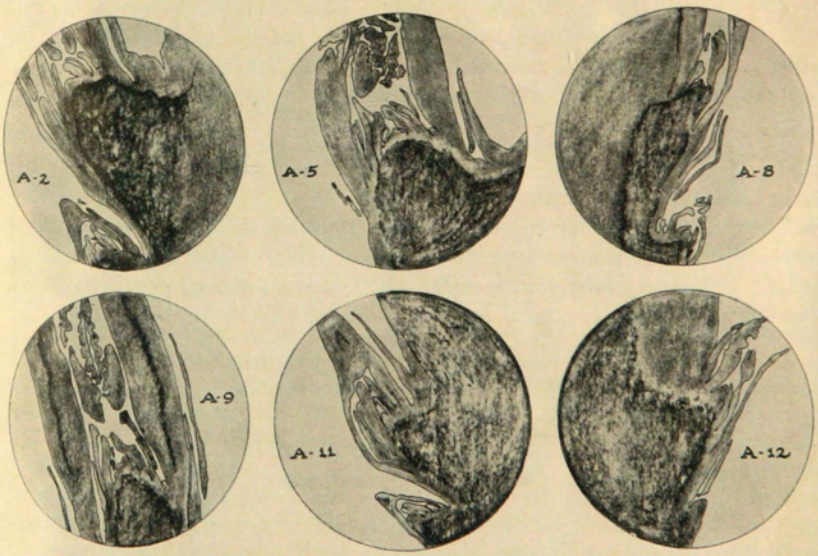


Fig. 3.—Camera lucida drawings (x 30) of axillary primocane buds of Plum Farmer, prepared the following dates:

A-2 June 12	A-9 July 3
A-5 June 19	A-11 July 10
A-8 July 3	A-12 July 24

In A-2, 8, 11 and 12, the primary and secondary buds were sectioned together. The secondary bud seldom continues development after midsummer except in case of accident to the primary bud.

A-2, 5, 8 and 11 are from canes pinched June 10. Canes of A-9 and 12 were unpinched. No consistent difference in bud development between pinched and unpinched canes was apparent in any of the sections.

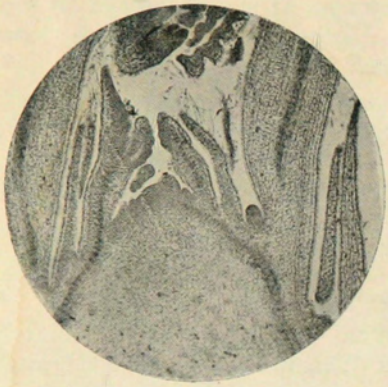


Fig. 4.—Microphotograph of section A-5 (X 50) shown in camera lucida drawings.

Buds taken in 1931 for permanent mounts were selected from the most fruitful portions of canes and branches, and all the Plum Farmer plants were used in an effort to obtain specimens representative of the stage of growth prevailing on the day of sampling. Three buds were taken each week from pinched plants and three more from unpinched plants.

Buds taken in 1932 for fresh, freehand sectioning were gathered as described above from two representative pinched plants of Plum Farmer.

Longitudinal sections were made to include the secondary bud in permanent mounts. Freehand sections were cut longitudinally, also, but at right angles to the plane which includes the secondary bud.

RESULTS

LOCATION OF FRUITFUL PORTIONS OF CANES.—The natural fruiting habit of Plum Farmer under the conditions of this experiment, is expressed by two seasons' performance of five unpinched, unthinned hills. Relatively long and slender plants are produced by this system. Ninety percent of the total crop in 1932 was borne on main canes.

In 1931, winter loss claimed about one-third of the total cane length. Untreated hills, with their short branches, sustained most of such loss on main canes. This lowered the proportion of total yield originating on main canes and explained the fact that in 1931 only two-thirds of the crop came from main canes of untreated hills.

Of the 33 canes studied in 1931, eight were unbranched or had only very short branches which bore no fruit. In 1932, 20 canes of 60 studied had no fruitful branches. The average point of origin of fruitful branches for the two seasons was 66 inches from the base of the cane on untreated hills.* (See Table 1.)

*Average height of branching probably fluctuates from year to year according to change in the proportion of floricanes to primocanes.

Table 1.—Mean Point (M) of Origin of Branches

	1931			1932		
	M Inches	S.D. Inches	C.V.	M Inches	S.D. Inches	C.V.
Pinched	21.91	3.82	17.43	24.72	3.75	15.17
Pinched and thinned	22.44	3.84	17.11	24.36	3.19	13.09
Unpinched and unthinned	52.61	11.56	21.97	79.62	10.25	12.87

It is evident from this table, that branches are more widely scattered over the untreated plants than they are on pinched plants.

By departing from strictly natural growth only in the foreshortening of primocanes, and allowing fruiting to progress naturally thereafter, a plant is produced which is shorter, broader and much easier to handle, as it requires almost no support. Such foreshortening of primocanes (pinching) was practiced on two of the three treatments, ("pinched" and "pinched and thinned"). These two treatments were almost identical in fruiting response.

While main canes were more fruitful than branches if primocanes had not been summer pruned; the reverse was true when summer pruning had been done. No pinched treatment in either of the two seasons yielded more than 10 percent of the total number of berries on main canes, and one treatment bore less than 2.5 percent of its crop on main canes.

Observation of floricanes during the growing season showed pinched plants to be more vigorous vegetatively, thruout, and that the resulting competition for light was overcome to a considerable extent by the fact that the lowest buds gave rise to the longest laterals.

YIELD RECORDS.—In the Appendix is a calculation (Fisher's Variance Method) of the significance of the difference in number of berries produced, between the three treatments. Since little significance was found in 1931 and none in 1932, there is probably little, if any, actual difference between treatments in respect to number of berries produced.

A similar calculation was made for yield by weight, which showed no significant difference between treatments.

The relation of berry size to distribution is more clearly expressed by Figure 5 than by a calculated correlation. Largest berries were produced nearest the base of canes and branches. There is a fairly regular decrease in berry size as distance from base of cane or branch increases, except near the ends where size again increases slightly. Increased size of berries here, however, is negligible, because relatively few fruits are borne near cane ends.

The average berry size for each treatment and for the whole experiment is represented by straight lines on the graph in Figure 5.

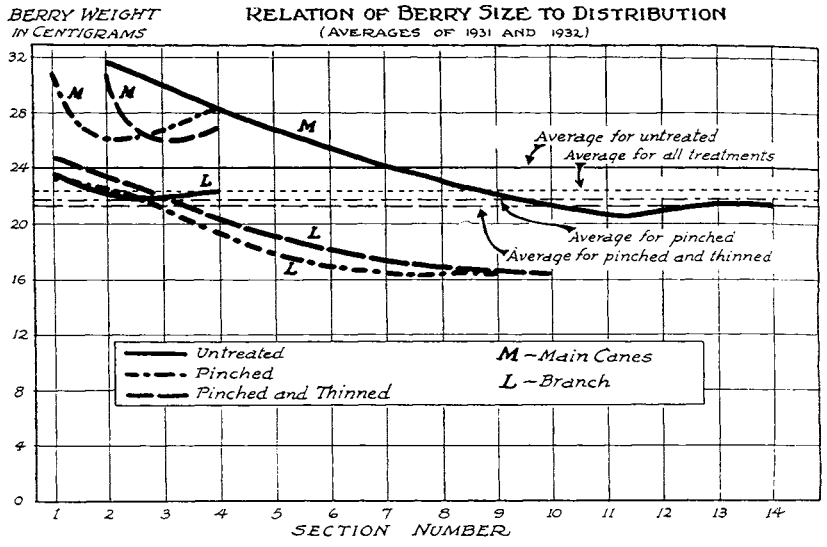


Figure 5.

On pinched plants, main-cane fruit, and that borne on the first 12 to 18 inches of branches was above average size. On untreated plants, only the first 7 sections, or 42 inches of main cane, produced berries above average size for the treatment. However, if the average berry size for all three treatments is considered, 9 sections or 54 inches of main cane and the first foot of branches on untreated plants produced above-average-sized berries.

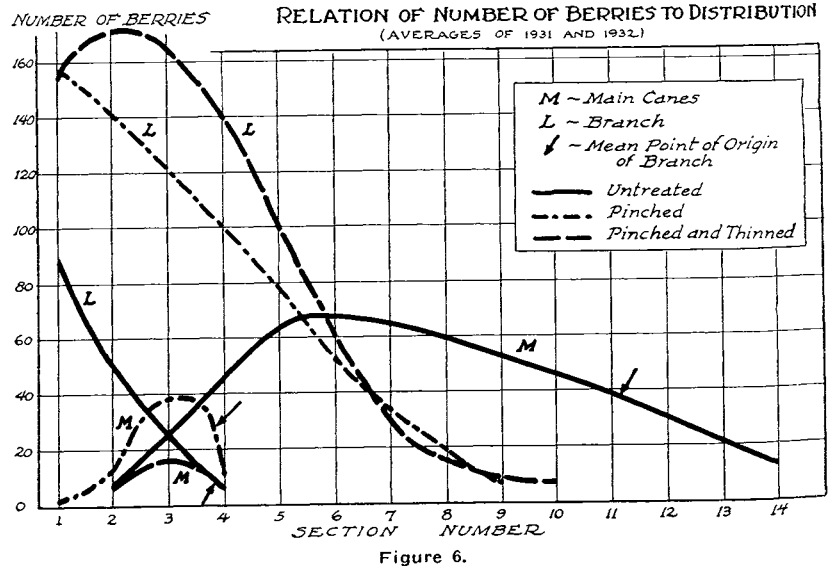


Figure 6.

The relation of number of berries to distribution is shown in Figure 6. The largest number of berries was produced near the base of branches and just below the mean point of origin of branches on the main cane.

The portions of cane which produced the largest numbers of berries coincided in every case, with those producing above-average-sized berries. But, as Tables 2, 3 and 4 show, the mean point at which fruit is borne is farther out on canes and branches in each case than the point (Fig. 5) where the berry size curve goes below average. The high coefficients of variability, make the mean fruiting point an unreliable figure, however, as a measure of the actual point of highest production.

Table 2.—Calculation (Harris' Method) of Mean Distance from Ground at Which Fruit Was Borne on Main Canes of Unpinched, Unthinned Hills.

In the following table, "V" is number of 6-inch section on main cane. Section 1 is 0 to 6 inches and bore no fruit; 2 is 6 to 12 inches from ground, etc.; "f" is season's total of berries borne on all canes in 5 hills, except branches.

V	f	X (= f V)	X^2 (= FV·V)
2	27	54	108
3	122	366	1,098
4	250	800	3,200
5	261	1,305	6,525
6	367	2,202	13,212
7	363	2,541	17,787
8	444	3,552	28,416
9	341	3,069	27,621
10	349	3,490	34,900
11	340	3,740	41,140
12	332	3,984	47,808
13	232	3,016	39,208
14	108	1,512	21,168
15	40	600	9,000
16	28	448	7,168
17	26	442	7,514
18	1	18	324
	N = 3,631	31,139	306,197

Mor X = 31,139/3,631

= 8.57

$$\text{S.D.} = \sqrt{\frac{306,197}{3,631} - 73.4449}$$

= 3.3

C.V. = 38.5

Converting 6-inch sections to inches from the ground: Fruiting range (6 in. to 9 ft.) = 8.5 ft.

Mean = 51.4 in.

S.D. = 19.8 in.

Table 3.—Calculation of Mean Distance from Main Cane, at which Branch Fruit was Borne in Pinched Hills.

In 1932, less than 10 percent of the yield of these five hills (and only 2.5 percent on pinched and thinned hills) was borne on main canes. Therefore, only the yield of branches is considered here.

V	f	X	X^2
1	1,100	1,100	1,100
2	684	1,368	2,736
3	655	1,965	5,895
4	440	1,760	7,040
5	523	2,615	13,075
6	368	2,208	13,248
7	221	1,547	10,829
8	157	1,256	10,048
9	71	639	5,751
10	11	110	1,100
11	1	11	121
	4,231	14,579	70,943

$M = 14,579/4,231 = 3.445$

$S.D. = \sqrt{\frac{70,943}{4,231} - 11.868} = 2.213$

$CV = 64.13$

Converting to inches:

Fruiting range = 5.5 ft.

M = 20.67 in.

S.D. = 13.28 in.

Table 4.—Mean Distance from Main Cane at which Fruit was Borne on Branches of Pinched and Thinned Hills.

V	f	X	X^2
1	923	923	923
2	835	1,670	3,340
3	744	2,232	6,696
4	602	2,408	9,632
5	342	1,710	8,550
6	392	2,352	14,112
7	171	1,197	8,379
8	117	936	7,488
9	80	720	6,480
10	68	680	6,800
	4,274	14,828	72,400

$M = 14,828/4,274 = 3.469$

$S.D. = \sqrt{\frac{72,400}{4,274} - 12.03}$

$= 2.216$

$C.V. = 63.88$

Converting to inches:

Fruiting range = 5 ft.

M = 20.81 in.

S.D. = 13.30 in.

MICROSCOPICAL STUDY OF BUDS

Camera lucida outline sketches of fresh freehand sections (Fig. 3) gave a means of comparing bud development on different dates thru the fall of 1932, with permanent mounts of sections made in 1931. Branching was evident in these sketches, which shows the compound nature of the primary bud (more properly called an "eye"). Six months before the several laterals appear on the cane with a common origin, this compoundness is noticeable in the sections. Examination of floricanes during the growing season shows that from one to a half dozen laterals commonly arise from a single eye. One or several of these may be fruitful, or all may be barren.

Branching, therefore, does not indicate the beginning of flower-bud differentiation in this compound type of bud, as it might in single buds which give rise to only one shoot with a compound inflorescense.

The appearance of lobing at and near the growing point at first seemed to indicate flower primordia (as noted by Watkins (9) in

gladiolus, and Goff in fruits.) It later became evident that three-lobed primordia in floricane buds of this plant may develop into either flowers or leaves. Elongation of the central lobe produces unmistakable leaf primordia, while a modification of the side lobes forms equally unmistakable flower primordia. (Fig. 7.) The latter type of modification was noted only in spring, after new laterals had started from the buds.

Figure 7a

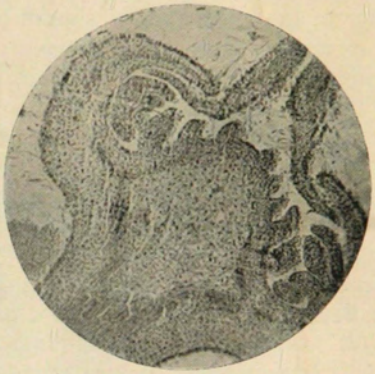


Figure 7b

Fig. 7a.—Median section of Plum Farmer floricane bud prepared May 9. (X75). Primordia of sepals and petals may be seen in the bud at the left. Just prior to this stage, leaf and flower primordia are identical in appearance.

Fig. 7b.—Section of a single flower bud prepared only 8 days after date of Fig. 7a showing rapidity of development. (X80).

DISCUSSION

Nearly 25,000 berries were counted and weighed in obtaining these data. Single yields (per 6-inch section per picking) were seldom greater than a dozen berries and averaged around four, while hundreds of yields consisted of a single berry. Sampling was, therefore, near the ultimate possibility.

While two seasons may not be a representative sample of the climate, it seems reasonable to expect that continuation of the experiment would confirm these results, since a significant difference in favor of one treatment in 1931 was contradicted by the next year's results. (See Appendix). Calculation showed little or no significance in the difference between treatments with respect to both numbers and weights of berries.

Distribution of fruit in relation to both size and quantity are important considerations in a study of fruiting habit. Pinching affected distribution chiefly in causing most of the fruit to be borne on stout branches, while the natural habit is for most of the crop to be borne on main canes which have relatively small and unfruitful branches.

Quality in this fruit is largely a matter of size. Largest fruit is borne lowest on main canes and branches. Since decrease in size or quality, as well as quantity, shows a tendency to continue with increased length of cane and branch (except for a negligible increase of berry size near ends) it seems that spring pruning should remove wood which produces the low-quality fruit.

Taking average berry size as the smallest consistent with good quality, Figure 5 indicates that when primocanes have not been summer pruned, main canes should be pruned in spring to 54 inches with the remaining branches shortened to 12 inches; and that when primocanes have been pinched, plants should be pruned in spring so as to leave branches 12 to 18 inches long. The high coefficients of variability found in calculating the mean fruiting point, show the mean to be capable of such wide fluctuation that even more pruning might be done without greatly reducing the yield.

This procedure requires testing to determine whether such spring pruning would have any other effect than simply removing potentially undesirable fruit. As mentioned in the Literature Review, date of fruit-bud differentiation has a practical bearing on this question, for if it takes place before spring, such pruning definitely reduces the yield by removing potentially undesirable fruit; but, if it does not occur until after spring growth has begun there may be as much fruit formed on the stub of a branch left after spring pruning as would normally be produced over the entire branch, had it been left unpruned.

Lott (6) shows that cane heading removes undesirable fruit in red raspberries. Branching is not common with red raspberries in Colorado as it is with blacks, and this may alter the effect of heading upon blackcaps as compared to the reds.

As flower and leaf primordia are indistinguishable until relatively late, differentiation may actually take place before primordia become distinguishable by the simple inspection employed here. Microchemical determinations might reveal a method of making the distinction between primordia identical in form, or definitely prove that differentiation does not take place until it is apparent upon inspection.

CONCLUSIONS

1. There is little or no significant difference in yield between pinched, pinched and thinned, and untreated plants of Plum Farmer blackcaps, with respect to either numbers or weight of berries produced under the conditions of this experiment.

2. Pinching concentrates between 1 foot and 3 feet from the base of canes, the bulk of the fruiting area, which is otherwise widely scattered over the entire length of cane.

3. Largest-sized fruit is borne lowest on canes and branches in all three treatments mentioned in 1.

4. The largest number of fruits and the highest-quality fruits are borne nearest the base of branches, and just below the lower branches on main canes, in all three treatments.

5. Pinched plants produced above-average-sized fruit on main canes and the first 12 to 18 inches of branches. Unpinched plants produced above-average-sized fruit on the first 54 inches of main cane and the first 12 inches of branches. All wood beyond these limits produced below-average-sized fruit.

6. Differentiation may possibly begin before flower primordia are distinguishable by simple microscopic examination of bud sections, but flower primordia are indistinguishable by form alone, until relatively late because of their similarity to the three-lobed leaf primordia.

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APPENDIX

NUMBER OF BERRIES IN 1931

P = pinched. PT = pinched and thinned. When new canes reached 30 in. in height, they were pinched to 24 in. Thinning consisted of removing all but the seven best canes per hill. U = Untreated.

	P	PT	U	Tr Total
	661	940	541	2,142
	428	926	348	1,702
	747	1,163	506	2,416
	546	817	836	2,199
	873	678	844	2,395
Tv	3,255	4,524	3,075	10,854

	P^2	PT^2	U^2	Tr^2 Total^2
	436,900	883,600	292,700	4,589,000
	183,200	857,500	121,100	2,897,000
	558,000	1,353,000	256,000	5,837,000
	298,100	667,500	698,900	4,835,000
	762,100	459,700	712,300	5,735,000
				23,893,000 = Σ Tr^2
Tv^2	10,590,000	20,470,000	9,455,000	40,515,000 = Σ Tv^2

$\Sigma X^2 = 8,540,600$
$T^2/MN = 7,853,954$
$T^2 = 117,809,316$

Total $= \Sigma(X)^2 - T^2/MN = 686,646$
Varieties $= \Sigma(Tv)^2/N - T^2/MN = 249,046$
Replicates $= \Sigma(Tr)^2/M - T^2/MN = 108,379$

Variance	Sum of Squares	Deg. Freedom	Mean. Sq.	S.E.
Repl.	108,379	4		
Var.	249,046	2		
Er.	329,221	8	41,153	202.8
Total	686,646	14		

General mean $= T/MN = 10854/15 = 723.6$
S.E. ea. treatment $= SE./\sqrt{N} = 202.8/2.236 = 90.7$
S.E. of a Dif. $= 90.7 \times \sqrt{2} = 128.25$
2 S.E. = 256.5

Mean number of berries:

PT = 905	651 (Number berries on P treatment)
P = 651	256 (2 S.E.)
U = 615	907 (Approximate number berries on PT treatment)

Odds are 30 to 1 that PT is a better treatment than either P or U. There is no significant difference between P and U.

NUMBER OF BERRIES IN 1932

P	PT	U	Tr Total
1,205	1,565	978	3,748
430	188	541	1,159
832	788	1,152	2,772
1,265	836	662	2,763
953	1,048	706	2,707
Tv 4,685	4,425	4,039	13,149

P^2	PT^2	U^2	Tr^2 Total^2
1,452,025	2,449,225	956,484	14,047,504
184,900	35,344	292,681	1,343,281
692,224	620,944	1,327,104	7,683,984
1,600,225	698,896	438,244	7,634,169
908,209	1,098,304	498,436	7,327,849
			38,036,787 = Σ Tr^2
Tv^2 21,949,225	19,580,625	16,313,521	57,843,371 = Σ Tv^2

$\Sigma X^2 = 13,253,245$

$T^2/MN = 11,526,413$

$T^2 = 172,896,201$

Total $= \Sigma(X)^2 - T^2/MN = 1,726,832$

Varieties $= \Sigma(Tv)^2/N - T^2/MN = 42,261$

Replicates $= \Sigma(Tr)^2/M - T^2/MN = 1,152,516$

Variance	Sum of Squares	Deg. Freedom	Mean Sq.	S.E.
Repl.	1,152,516	4		
Var.	42,261	2		
Er.	532,055	8	66,507	257.9
Total	1,726,832	14		

General Mean $= T/MN = 13149/15 = 876.6$

S.E. ea. treatment $= SE/\sqrt{N} = 257.9/2.236 = 115.3$

S.E. of a Dif. $= 115.3 \times \sqrt{2} = 163.0342$

2 S.E. = 326

Mean number of berries:

P = 937

PT = 885

U = 808

808 (Number berries on lowest producer)

326 (2 S.E.)

1,134

No significant difference between treatments.

SUMMARY

Determination of the fruiting habit of blackcaps in Colorado was considered necessary as a basis for determining the proper pruning practices for the state.

Fruiting habit was studied under three different sets of conditions: (1) "Pinched," in which primocanes were shortened to 24 inches when they reached 30 inches; (2) "pinched and thinned," the same as "pinched" except that only the seven best canes were allowed to remain in each hill; and (3) "untreated," where all canes were allowed to grow naturally. Lengths and diameters of canes and branches were measured at the beginning of each growing season (1931 and 1932). Numbers and weights of fruits from each 6-inch section of canes and branches were recorded for each picking. Ten pickings were made both seasons, 2 to 3 days apart.

Statistical interpretation of the data shows little or no significant difference between treatments in either weights or numbers of fruits produced; but a decided difference in distribution of fruit on pinched and unpinched plants. The largest size as well as the greatest numbers of fruits were produced on the lower portions of plants. This habit, coupled with the fact that pinching makes the plant shorter and broader, concentrates the bulk of yield on branches and between 1 foot and 3 feet from the ground on pinched plants; while unpinched plants bear the bulk of their crop on main canes and more widely scattered.

Several hundred buds taken periodically, summer and winter, over both seasons, were studied from permanent mounts and fresh freehand sections.

Leaf and flower primordia were found to be indistinguishable, by form alone, until spring. Evidence indicates that differentiation may begin before any change of form takes place in the primordia.