The Growth of Tree Twigs.

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Methods and Results.

During the summer of 1921 the writer made a series of measurements[1] of growing tree twigs. This was with the idea of throwing what light might be possible on the nature of the plants and on the nature of growth, but more specifically of attempting to determine definitely if in the absence of irrigation reliable data can be secured in humid regions for determining the normal course of the growth rate.

There were available two thrifty young peach trees, *Prunus Persica* (L.) Stokes, and some plants of flowering dogwood, *Cornus florida* L. The first peach tree was on a slight northern slope and was rather tardy in starting growth. The other was on a southern slope but was shaded considerably by tall forest trees some distance away. It started growth sooner than the other, and as the results to be presented show, stopped growing sooner. Neither bore any peaches, as the fruit was killed by a late spring freeze. Three of the flowering dogwoods were along the south edge of a patch of woodland where they were unshaded throughout the summer. A fourth was within the forest and was shaded as soon as the forest trees had developed their leaves. The dogwood is well known as a shade enduring tree, and there was no indication that the small shaded tree used in this study was diseased or weakened by reason of the shading. None of the dogwood trees were large enough to bloom this season. The measurements were made from the base of the shoot to the base of the terminal bud and were taken to the nearest one-eighth inch. They were subject to a maximum experimental error of about $\pm$ 0.125 inch, aside from the "probable" error (error of sampling), on the individual measurements. The experimental error of the averages is considerably less, but even the greater error would produce only a negligible alteration of the growth curve.

The shoots measured on the two peach trees were divided into two classes: (1) shoots which were not so situated as to be over-topped and shaded by others; and (2) shoots which were so situated as to be shaded. The means for the shoots of class one of the first tree and the corresponding growth increments are given in Table 1. The same data are shown graphically in Fig. 1. The weekly rainfall summations are also shown at the top of the figure. I am indebted for the rainfall records to the local co-operative Weather Bureau station. The number of twigs measured was eleven for all dates except March 29th, when it was seven, the seven shoots then measured being included in the population of eleven used on all succeeding dates. The data for class two of the first tree are given in Table 2, Fig. 2. The number of twigs was 19 for March 29th, and 22 for all succeeding dates.

[1] I am indebted to my wife, Mrs. Nelle McClurg Ludwig, for necessary aid in making and recording these measurements.

Table 1. Growth of unshaded shoots on peach tree No. 1.

Date	*Mean length*	*Mean increment*
March 29	1.49	....
April 5	2.44	0.95
April 12	4.22	1.78
April 19	5.19	0.97
April 26	7.71	2.52
May 3	11.06	3.35
May 10	15.14	4.08
May 17	19.97	4.83
May 24	25.53	5.56
May 31	32.15	6.62
June 7	38.03	5.88
June 14	43.26	5.23
June 21	48.38	5.12
June 28	52.16	3.78
July 5	55.05	2.89
July 12	56.91	1.86
July 19	58.47	1.56
July 26	59.61	1.14
August 2	60.33	0.72
August 9	60.98	0.65
August 16	61.32	0.34
August 23	61.51	0.19
August 30	61.58	0.07
September 6	61.57	—0.01
September 13	61.59	0.02

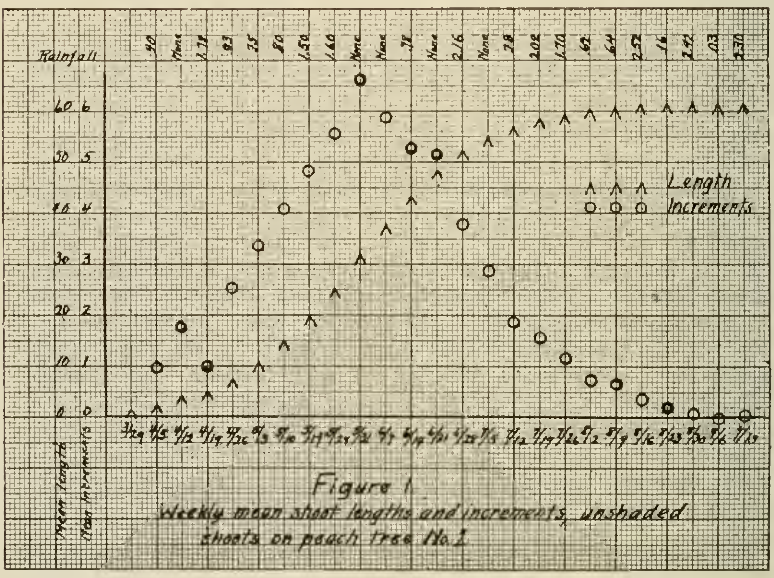

Figure 1
Weekly mean shoot lengths and increments, unshaded shoots on peach tree No. 1

Table 2. Growth of shaded shoots on peach tree No. 1.

Date	*Mean length*	*Mean increment*
March 29	1.23	....
April 5	2.11	0.88
April 12	3.58	1.47
April 19	4.59	1.01
April 26	6.59	2.00
May 3	9.23	2.64
May 10	12.34	3.11
May 17	15.53	3.19
May 24	18.89	3.36
May 31	22.85	3.96
June 7	25.89	3.04
June 14	28.34	2.45
June 21	30.15	1.81
June 28	31.41	1.26
July 5	32.23	0.82
July 12	32.72	0.49
July 19	32.95	0.23
July 26	33.11	0.16
August 2	33.13	0.02
August 9	33.14	0.01
August 16	33.08	—0.06
August 23	33.05	—0.03
August 30	33.09	0.04
September 6	33.07	—0.02
September 13	33.09	0.02

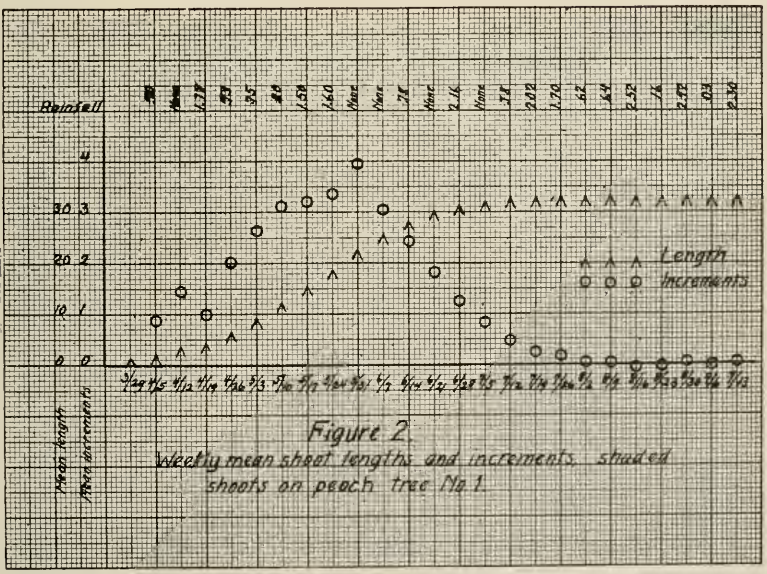

Figure 2.
Weekly mean shoot lengths and increments shaded shoots on peach tree No 1.

The corresponding data for peach tree No. 2 are given in Tables 3 and 4 and Figs. 3 and 4. The numbers of shoots involved in these cases are 7, 18 and 9, 10, respectively.

Table 3. Growth of unshaded shoots on peach tree No. 2.

Date	*Mean length*	*Mean increment*
March 29	3.64	....
April 5	5.98	2.34
April 12	9.72	3.74
April 19	11.31	1.59
April 26	14.56	3.25
May 3	18.08	3.52
May 10	21.39	3.31
May 17	24.17	2.78
May 24	27.28	3.11
May 31	30.73	3.45
June 7	32.89	2.16
June 14	34.08	1.19
June 21	34.27	0.19
June 28	34.30	0.03
July 5	34.36	0.06
July 12	34.34	—0.02
July 19	34.34	0.00
July 26	34.44	0.10
August 2	34.42	—0.02
August 9	34.47	0.05
August 16	34.38	—0.09
August 23	34.36	—0.02

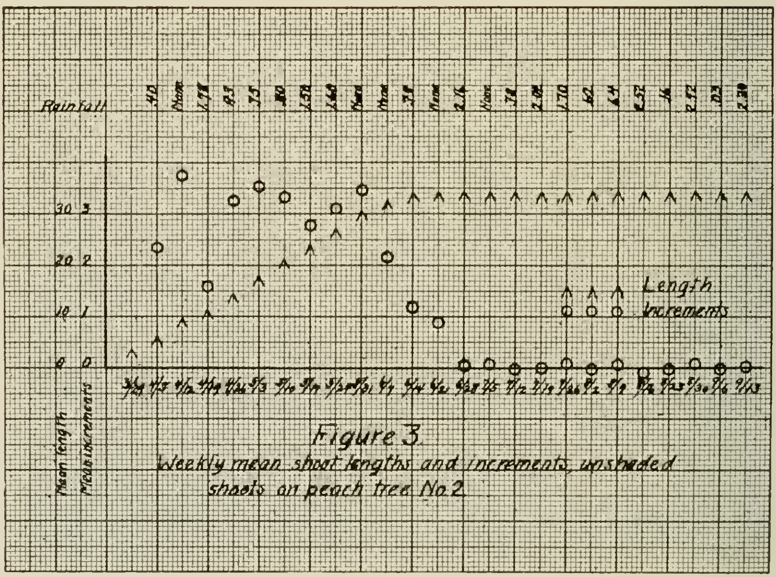

Figure 3.
Weekly mean shoot lengths and increments, unshaded shoots on peach tree No. 2

Date	*Mean length*	*Mean increment*
August 30	34.44	0.08
September 6	34.42	—0.02
September 13	34.42	0.00

Table 4. Growth of shaded shoots of peach tree No. 2.

Date	*Mean length*	*Mean increment*
March 29	2.61	....
April 5	4.54	1.93
April 12	7.53	2.99
April 19	9.08	1.55
April 26	11.56	2.48
May 3	13.56	2.00
May 10	15.00	1.44
May 17	15.91	0.91
May 24	16.74	0.83
May 31	17.36	0.62
June 7	17.68	0.32
June 14	17.86	0.18
June 21	17.91	0.05
June 28	17.89	—0.02
July 5	17.96	0.07
July 12	17.94	—0.02
July 19	17.94	0.00
July 26	17.98	0.04
August 2	17.98	0.00
August 9	17.96	—0.02
August 16	17.94	—0.02

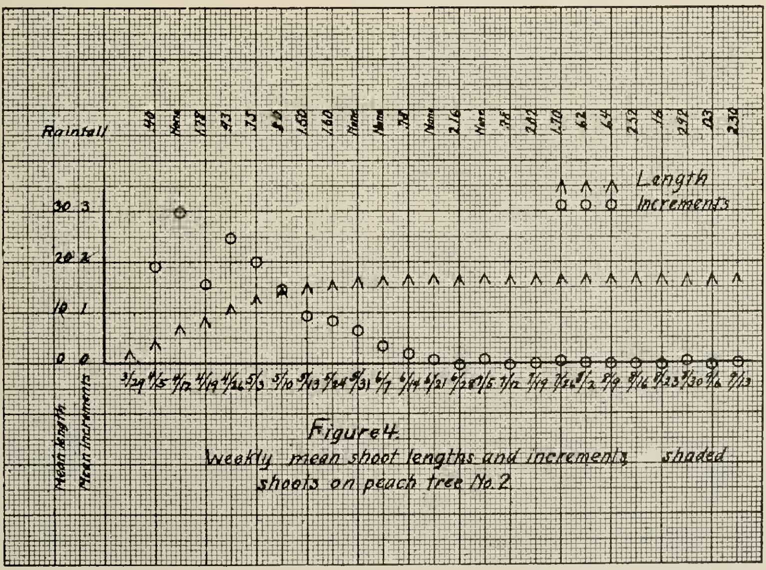

Figure 4.
Weekly mean shoot lengths and increments shaded shoots on peach tree No. 2

Date	*Mean length*	*Mean increment*
August 23	17.91	—0.03
August 30	17.94	0.03
September 6	17.91	—0.03
September 13	17.91	0.00

The data for the dogwood shoots were divided into two groups. The first included those shoots from the trees on the edge of the forest and the second those on the shaded tree. The first had 41 members and the second group had 19. The mean lengths and growth increments for these two groups are given in Tables 5 and 6 and shown graphically in Figs. 5 and 6.

Table 5. Growth of unshaded shoots of dogwood.

Date	*Mean length*	*Mean increment*
March 29	0.42	....
April 5	0.72	0.30
April 12	1.17	0.45
April 19	1.43	0.26
April 26	1.79	0.36
May 3	2.33	0.54
May 10	2.69	0.36
May 17	3.42	0.73
May 24	4.18	0.76
May 31	5.00	0.82
June 7	5.40	0.40
June 14	5.75	0.35
June 21	5.82	0.07
June 28	5.86	0.04

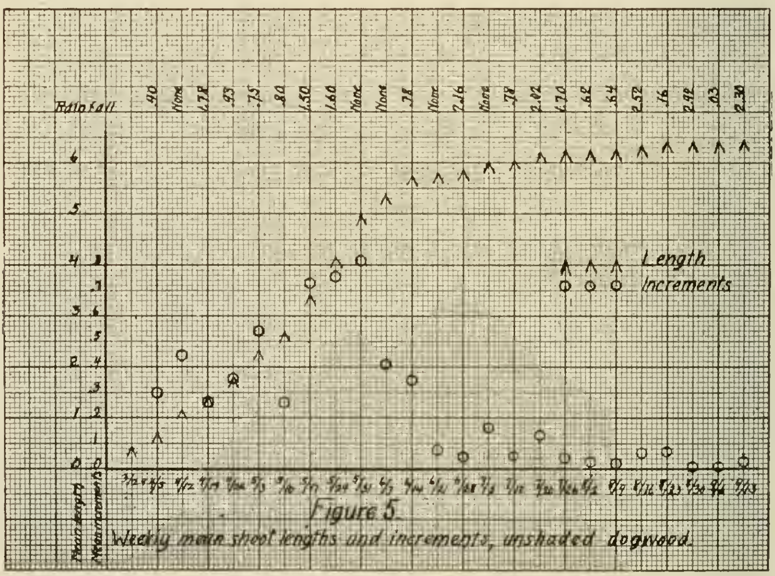

Figure 5.
Weekly mean shoot lengths and increments, unshaded dogwood.

Date	*Mean length*	*Mean increment*
July 5	6.02	0.16
July 12	6.07	0.05
July 20	6.21	0.14
July 26	6.25	0.04
August 2	6.28	0.03
August 9	6.30	0.02
August 16	6.36	0.06
August 23	6.43	0.07
August 30	6.44	0.01
September 6	6.45	0.01
September 13	6.48	0.03

Table 6. Growth of shoots of shaded dogwood bush.

Date	*Mean length*	*Mean increment*
March 29	0.42	....
April 5	0.68	0.26
April 12	1.00	0.32
April 19	1.20	0.20
April 27	1.41	0.21
May 3	1.45	0.04
May 10	1.53	0.08
May 17	1.56	0.03
May 24	1.61	0.05
May 31	1.68	0.07
June 7	1.70	0.02
June 14	1.74	0.04
June 21	1.73	—0.01

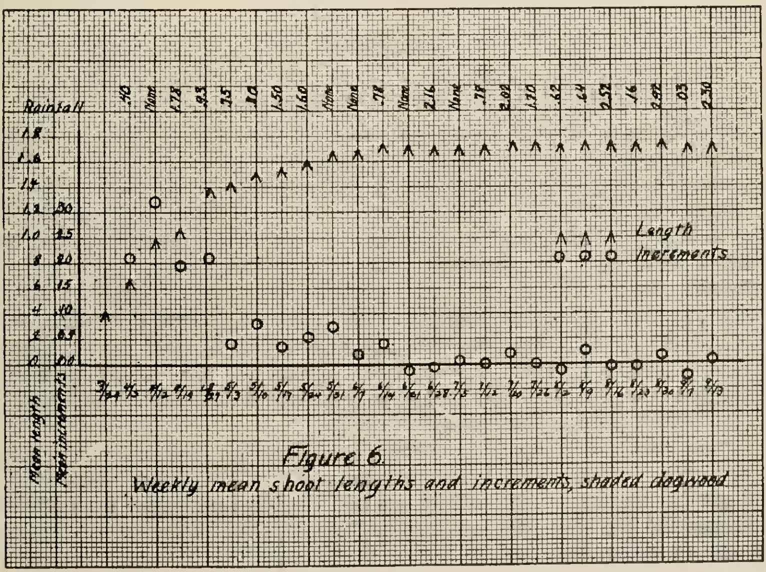

Figure 6.
Weekly mean shoot lengths and increments, shaded dogwood

Date	*Mean length*	*Mean increment*
June 28	1.72	—0.01
July 5	1.73	0.01
July 12	1.73	0.00
July 20	1.75	0.02
July 26	1.75	0.00
August 2	1.74	—0.01
August 9	1.76	0.02
August 16	1.76	0.00
August 23	1.75	—0.01
August 30	1.76	0.01
September 7	1.74	—0.02
September 13	1.74	0.00

The dogwood shoots which developed from terminal buds were further divided on the basis of whether they were true terminal branches or were lateral branches of the pseudo-whorl which develops from the terminal bud in the spring. The mean final lengths of these branches were determined for each group and for the two groups combined. The results are shown in Table 7.

Table 7. Final mean length of the true terminal branches and of lateral branches from terminal buds in dogwood.

Group	*Type of shoot*	*Number of shoots measured*	*Mean length*
1	True terminal	12	4.40
1	Lateral	21	7.44
2	True terminal	6	.54
2	Lateral	13	2.30
All	True terminal	18	3.11
All	Lateral	34	5.47

Discussion.

Since the data secured come from a limited number of trees and shoots under different and varying environmental conditions it will not be possible to reach conclusions concerning the normal seasonal course of the growth of tree twigs under uniform outside conditions. Furthermore, it is probably not possible to obtain such curves in humid regions without recourse to irrigation unless an exceptionally good year should happen to be found, or if the observations should be extended over a sufficiently large number of seasons to equalize variations in rainfall. Even then one season's observations under irrigated conditions ought to be more reliable. The present season's rainfall was fairly uniform, and yet the growth curve seems to have been affected rather definitely by rainfall variations. However, the variations in the conditions give certain advantages in interpretation which would not be secured were the conditions uniform.

The curves all show the same general type. The growth rate at first is slow, it increases to a maximum, and then decreases to zero as the season advances. The initial slowness of growth is not very clearly indicated by the data for the shaded dogwood bush, nor for the shaded shoots on peach tree No. 2, but it would doubtless be more evident if it had been practical to take one or two earlier sets of measurements. The type of curve is shown best of all in the unshaded shoots of peach tree No. 1.

It will be noted that peach tree No. 1 and group 1 of the dogwoods reached their maximum growth rate during the week ending on May 31st. These trees were under very similar conditions. However, peach tree No. 2 grew much more rapidly early in the season but ceased growing sooner. The shaded dogwood reached its maximum earlier than the other but because of an earlier decline in growth and not because of a more rapid early growth.

The behavior of these two peach trees seems to point toward the conclusion that the early spring rate of growth is influenced a great deal by the temperature. Tree No. 2 had a considerably warmer location than No. 1. It should also be remarked in this connection that there was freezing weather on one or two occasions after these measurements were begun. It may be possible that if optimum temperature conditions had prevailed early in the season the growth rate would quickly have approximated that found later, after making due correction for the number of working hours per day which the plant has at the two periods.

The cause of the onset and continuation of a decreased growth rate was clearly not lowered temperature, however, because growth had stopped while the temperature was still at a point at which rapid growth occurred earlier in the season. The evidence from the rainfall is that variation in the water supply was at least partially responsible. It seems reasonable to suppose that in the case of peach tree No. 1 and dogwood group No. 1 the growth rate would have continued to augment for some time longer but for the onset of drier weather. In the case of the shaded dogwood the decrease in growth was probably caused by shading. Although no record was made of the time when the forest trees had expanded their leaves sufficiently to produce full shade it was noted that growth in the shaded dogwood seemed to stop shortly after this occurred. It was also noted on the peach trees that as soon as a branch became shaded it quickly ceased growing. This was true whether the shoot came from a last season's bud or was a lateral on a shoot of this season's growth. This observation would account, at least partially, for the more rapid decrease in the growth rate of branches which became overtopped, as shown by the curves for the two peach trees.

In view of the work of Garner and Allard[2] on the effect of the relative length of day and night on the onset of the flowering stage of plants it is worthy of suggestion that this factor also may be operative in such cases as this. It is a common observation that hardy woody plants usually cease growing and harden their twigs while the weather is still warm enough for good growth, whereas in the spring they begin growing very shortly after the weather warms up sufficiently.

[2] Garner, W. W., and H. A. Allard. Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. Jour. Agr. Res. 17:553-606. 1920.

Owing to the lag of the seasonal curve of temperature the days of given length in spring are much cooler than days of the same length in the fall.

This study has suggested a few interesting points concerning the dogwood which do not have to do directly with the growth rate. The dogwood is well known as a shade enduring tree. The quickly declining growth rate of the shaded tree in this study suggests that this ability on the part of the dogwood is not due to an unusual power to grow in the weak light of the forest, but rather to an ability to grow for a few weeks in the spring and then spend the entire remainder of the season slowly storing up food for another few weeks' growth the next spring.

Another interesting fact, which is shown by Table 7, is that, contrary to the condition in most trees, the terminal shoot in the dogwood is shorter than the laterals of the same season's growth. Each terminal shoot, as it starts growth in the spring, produces one or more very short internodes and sends out one or two lateral branches from each of the closely spaced nodes. There are thus from one to about six laterals produced in an arrangement which simulates a whorl. The measurements mentioned above show that the average final length of these laterals exceeds the final length of the terminal. Additional observations (without measurements) show that in upright, unshaded, rapidly growing stems the terminal exceeds the laterals, but that in the case of stems growing at an angle the lowermost branch grows the longest and becomes the leader, while the rest of the branches decrease in size till the innermost (or uppermost) one is reached, and the terminal is still smaller. Thus every year a new branch becomes the leader and each successive true terminal finally assumes the role of a minor branch. The result each season is to produce a more or less eccentric umbel shaped group from each terminal bud which opened that spring.

Summary.

A number of woody shoots were measured during one season's growth period. The results showed an initial slow growth rate, which then increased to a maximum, and later decreased to zero before the temperature had dropped to the point at which growth started in the spring. The slow initial rate in this case is believed to have been due to the cool weather at the time. The onset of the decrease in growth rate is believed to be due to a decrease in available moisture for at least part of the trees, and it is therefore considered impossible to get dependable curves for the normal course of a season's growth in tree twigs without having recourse to irrigation. For one of the trees and for some shoots on others the onset of the decrease in growth rate is believed to be due to shading, and it is suggested that in all cases the variation in relative length of night and day may have influenced the course of the cycle. The ability of the dogwood to live and develop in shady situations seems not be due to an ability to grow in poor light but rather to an ability to endure shade most of the season and at the same time to store food slowly for use in a spurt of growth in the fol-

lowing spring before the forest develops full shade. In branches growing at an angle the terminal shoot of dogwood grows less than any of the closely spaced laterals which start growth at the same time. The lowermost (outermost) branch grows the most and becomes the future leader of the branch.

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