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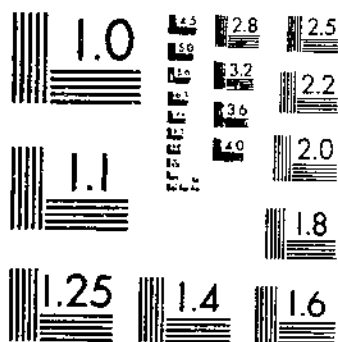
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GROWTH STUDIES ON GUAYULE (PARthenium ARGENTATIUM)

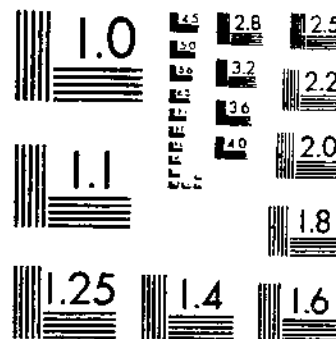
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**UNITED STATES
DEPARTMENT OF AGRICULTURE
WASHINGTON, D. C.**

Growth Studies on Guayule (*Parthenium argentatum*)¹

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INTRODUCTION AND SUMMARY

The selection of planting areas in which high-yielding varieties of guayule (*Parthenium argentatum* Gray) perform best is of great practical value, since the degree of field performance, expressed in pounds of rubber per acre, is dependent on the use of elite varieties and a congenial environment. The two important criteria in rating performance are external growth increment and percentage of rubber. By noting the progressive or fluctuating increase of the increments and changes in rubber content it is possible to obtain a fairly accurate estimate of the performance of a variety in a given environment without relating performance to anatomical structure. Since the storage of rubber, however, is restricted to certain tissues and since to all appearances maximum storage is contingent upon available storage space, information on the relative development of these tissues in different varieties and under different environmental conditions would put the interpretation of performance records on a broader basis. Lloyd *et al.* recognized the importance of such information and furnished data on the development of bark and wood and on the storage of rubber.

Very little is known about the developmental history of secondary tissues, especially the secondary phloem (²) for guayule. Such knowledge would have direct bearing on agronomic practices, especially the maintenance of proper moisture levels to assure maximum performance in pounds of rubber per acre.

The data presented in this paper give a detailed account of the

¹Submitted for publication, July 1944.

²Italic numbers in parentheses refer to Literature Cited, p. 19.

developmental history of the secondary tissues and rubber storage, the relative development of bark and wood under different irrigation practices, and retrogressive changes in the phloem.

Guayule plants developing under low soil-moisture stress show considerable seasonal shoot growth and a pronounced increase in the diameter of the branches. In contrast, with a restricted water economy the seasonal length increment is insignificant and the increase in diameter of the stems is reduced by approximately 50 percent. Expressed in tonnage the difference is considerable, and the rubber recovery from well-irrigated fields is much greater than from plots that are kept intermittently dry, despite a noticeable variation in the percentage of rubber in favor of intermittent irrigation.

Initial cambial activity is strictly centripetal; the differentiation of new phloem cells is belated and coincides with the initiation of inflorescences. The bulk of the new xylem is formed early in the season; on the other hand, phloem development is continuous and synchronized with the progressive inactivation of the old phloem through sclerosis. There is no carry-over of undifferentiated phloem cells into the new season, since the tissues in winter condition show fully matured sieve tubes adjacent to the cambium. Sclerenchymatization of the old active phloem begins before new phloem cells are formed by the cambium, but the two processes are usually so well synchronized that the width of active phloem tissue remains fairly constant. Sclerosis involves not only all of last season's active phloem but also imperceptibly overtakes the first-formed phloem of the current season to an extent that is not always easily determined, as the accumulation of rubber in the new phloem sector erases the demarcation line between old and new growth.

At first, no rubber is in the tissues of the new increment, because its synthesis is contingent upon the slowing up or repression of growth. Under a restricted water economy rubber appears first in the phloem as early as midsummer, but very much later in the xylem. The phloem rays show heavy deposits of rubber by the end of the growing season, and additional deposits are made throughout the winter months.

Winter synthesis of rubber may be from current products of photosynthesis if climatic conditions are favorable; if they are not, the rubber must be synthesized from prerubber reserves previously stored.

The volume of rubber-bearing tissue in the stem varies with thickness of bark and total stem diameter and with the percentage composition of ray tissue, sclerenchyma, and active phloem. A large sieve-tube complement, especially if typified by broad tangential bands, has a depressing effect on the available storage space for rubber, and plants showing this structural configuration should be eliminated from breeding stock. Within certain limits, however, the anatomical picture of the bark of plants relatively high or low in rubber may show little variation, indicating that storage space is only partly utilized. A factor to be reckoned with is the variation in physiological efficiency from the standpoint of rubber synthesis.

MATERIALS AND METHODS

The material for study came from the indicator plot at State College, N. Mex., which is on an alluvial fan, or bench, lying some 30 feet above the flood plain of the Rio Grande. The soil is a light grayish-brown

calcareous heavy sandy loam of moderate fertility and moderate water-holding capacity. The mean annual precipitation is about 8.7 inches. The monthly irrigation schedule, with dates of irrigation and natural rainfall, is given in table 1. This shows that the control plot was irrigated once a month; plot 0 received additional water during June, July, and August; and water was withheld from plots 1, 2, 3, and 4 at varying periods of 1 to 3 months during the 4 months May to August. Although the inflow of water was not accurately controlled, the plots received similar volumes with a given irrigation.

TABLE 1. *Monthly irrigation schedule (showing rainfall on guayule experimental plots, State College, N. Mex.*

[Blank spaces indicate no irrigation.]

Plot	Distribution of irrigations (days)							Total
	March	April	May	June	July	August	Sept. 1st	
Control	23	28	21	21	26	18	26	165
0	23	28	21	8, 21	7, 21	18, 26	26	165
1	23	28	21		26	18	26	125
2	23	28				18	26	72
3	23	28					26	54
4	23	26	21				26	96
Natural rainfall	Rainfall, inches			Rainfall, inches				

All studies were made on fresh material obtained at different intervals from the indicator plot at State College. Supplementary material was received now and then from indicator plots in New Mexico, Texas, and California.

Rubber deposits were studied in hand sections stained with Sudan III or osmic acid; for tissue differentiation the common phloroglucin-HCl technique was employed. Counterstaining with chloriodide of zinc was effective in bringing out sieve tubes in the active phloem and newly differentiated xylem cells, staining the latter a bright blue. Photographs were taken directly on sensitized paper.

STEM TISSUES IN WINTER CONDITION

The structure through the base of a branch of a 1-year-old transplant, taken in January when growth activities are suspended or are at a minimum, is shown in figure 1, A. Because of the variation in growth of the two sides of the branch, the pith is eccentric. This differential growth is mostly reflected in the length of the radii of the xylem strands, but the cortical region on the side of greater xylem development is also broader.

The bark, composed mainly of secondary phloem, forms a broad band of tissue exceeding the xylem in area. Conspicuous within the bark are discrete, occasionally confluent groups of fibers, arranged in a concentric ring along the periphery of the functional phloem.

The primary cortex is very narrow and abuts on the primary resin canals. A clearly defined endodermis densely filled with large, compound starch particles sets it off from the secondary phloem (fig. 1, B). This tissue (2), which consists of a concentric ring of sclerotic and functional phloem, usually encloses the first set of secondary resin canals. The latter may abut on the groups of fibers, or varying quantities of active sieve-tube tissue may be found above the canals.



FIGURE 1. A, Cross section of branch of a 1-year-old transplant. $\times 14$. B, Part of cross section, showing starch-filled endodermis above the groups of sclerenchyma but several cell layers away from the primary resin canals. $\times 100$.



FIGURE 2. —A, Cross section through region of active phloem (winter condition), showing fibers at apex and along upper flanges of bundles. $\times 500$. B, Cross-section through basal branch (winter condition) when cortex and rays are filled with rubber. $\times 50$. C, Cross section through basal branch, taken April 16; new xylem increment measures 0.25 mm.; no activity as yet shown in the phloem. $\times 100$.

Sclerenchymatization of the phloem usually proceeds centrad from the periphery, but frequently phloem fibers mature in advance along the flanges of the active phloem (fig. 2, A). They may even differentiate in the middle of a phloem group. Usually one concentric ring of the secondary resin canals develops before the onset of winter, but a second and even a third ring (fig. 2, B) may be initiated in the region of the secondary phloem on the side of greater xylem development. The last-formed canals may not open completely until the following spring, and the sieve-tube tissue below is then only a few cells wide. When secondary resin canals do not develop during the first year, the seasonal increment of phloem unbroken by canals and their jacket cells is relatively broad (fig. 3, E).

The vascular rays, of which the primary ones connect directly with the pith, are narrow, but they flare out fanlike in the cortex. They comprise the important storage tissue for rubber.

Even in midwinter the cambium is composed of several rows of thin-walled cells (fig. 3, A). The contour of the xylem is even or irregular; usually the last cells to mature are fibers. Outwardly, the cambium abuts upon the mature sieve tubes of the active secondary phloem.

The xylem, inclusive of pith, constitutes approximately 40 percent of the cross-sectional area of the branch, whereas the bark makes up 60 percent. The fibers and the cells of the active phloem contain no rubber and reduce the potential storage capacity of the bark by about one-third. These figures are only relative, their magnitude depending on such factors as total width of cortex, area occupied by fibers, and active phloem.

The rubber content of the storage tissues is at a maximum late in winter (fig. 2, B). Microscopic examinations of young plants made in summer show only a few particles of rubber, except for the jacket cells around the resin canals. With the coming of cold nights late in September or early in October, the cells of the phloem rays suddenly appear to be filled to capacity. Additional rubber, however, is deposited in winter.²

GROWTH DATA OF CONTROL PLOT

The record of the growth of the plants on the control plot, made from time to time during the experiment, follows:

March 9, 1943.—The cambium zone of most of the bundles has become broader, and some of the cells facing the xylem show enlargement (fig. 3, B). In some bundles vessel differentiation is evident (fig. 3, C, D, E). The walls of the newly formed xylem cells are already quite thick, but as yet un lignified.

March 20, 1943.—Xylem differentiation is continuing. Connecting the newly formed vessels is a narrow tangential band of "infill" wood parenchyma or vesicentric parenchyma. The bulk of the new tissue is composed of fibers, which remain thin-walled and unlignified much longer than the vessels. The cambium cells of the ray have lengthened or even divided. There is as yet no activity in the phloem region.

April 16, 1943.—The xylem increment, consisting mostly of vessels and fibers (fig. 2, C), measures 0.25 mm. Cell division in the ray cells has kept pace with xylem differentiation, and since the new portion of the ray contains no rubber, the current growth contrasts strongly with the old wood (fig. 2, C). Cell activity on the phloem side of the cambium is still questionable. Mature sieve tubes are seen adjacent to the cambium, and the phloem rays are densely filled with rubber down to the level of the cambium. In some bundles, however, new cells as yet little dif-

² Rubber analyses from indicator plots, Salinas, Calif., 1942-43.

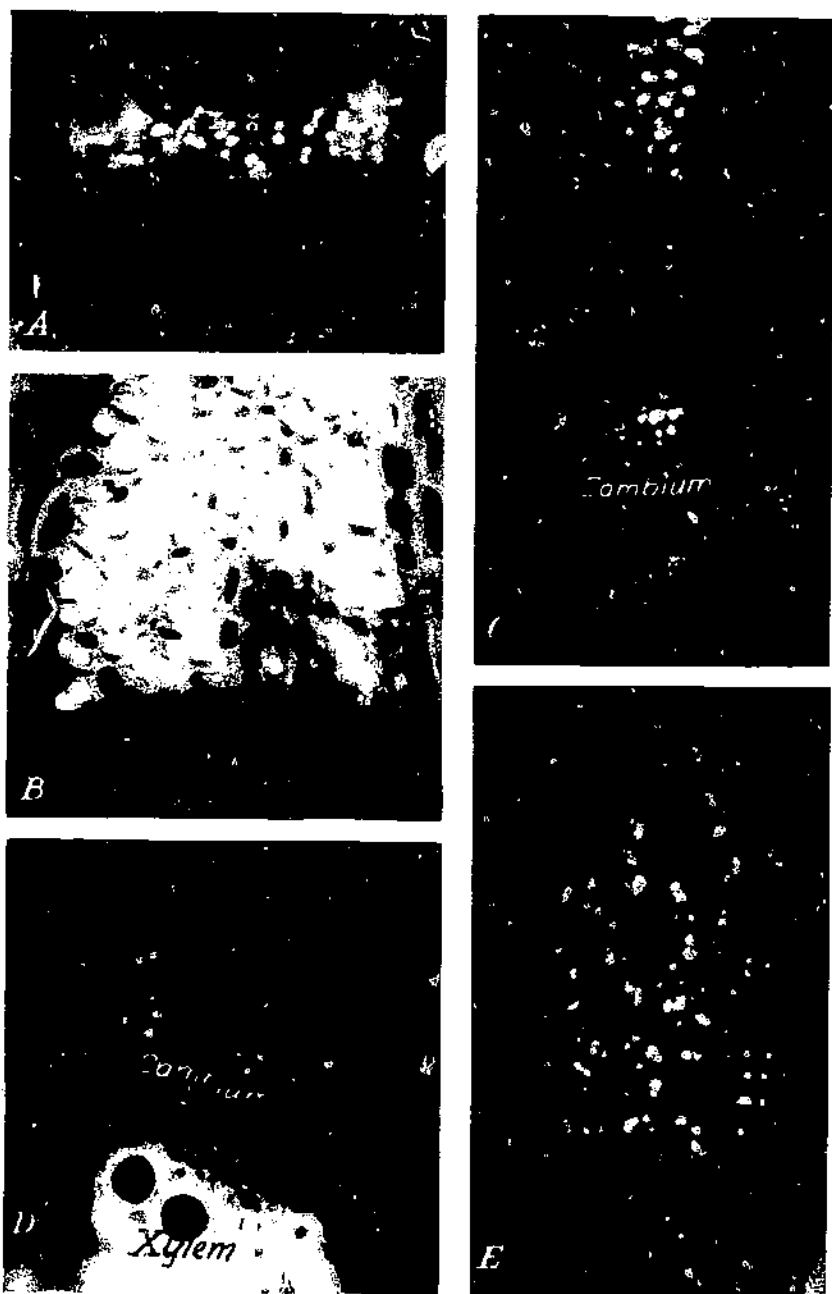


FIGURE 3. A, Cambium of basal branch in winter condition. B, Beginning of cambial activity on the xylem face of the bundle. C, Differentiation of three large vessels. D, Differentiation of two large vessels and fibers. E, Active phloem above cambium without secondary resin canal; differentiation of three large vessels below cambium. All $\times 250$.

ferentiated are observed central to the old phloem. The fiber initials on the periphery of the old phloem have greatly increased in size, but their walls have only slightly thickened. Resin canals that formed but did not completely open before the advent of winter are now oval or circular.

May 2, 1943.—The new xylem increment measures 0.48 mm. Phloem fiber differentiation in the 1942 season's increment is progressing more rapidly. In the process of sclerenchymatization entire masses of fiber initials enlarge almost simultaneously (fig. 4, A), thereby crushing all adjacent sieve tubes and companion cells; subsequent thickening and lignification, however, are more gradual processes.

Cell differentiation is becoming increasingly evident on the phloem side of the cambium, resulting in the formation of an ever-widening band of secondary phloem. In contrast to the xylem, where new cells in various stages of differentiation comprise a relatively broad band of tissue, the maturing of new phloem cells is confined to a relatively narrow zone. Furthermore, the time element in differentiation and maturing of sieve tubes is much shorter than in the xylem, as mature sieve tubes are found within 2- to 4-cell layers of the cambium even during most active growth. In bundles where no secondary resin canals had differentiated (fig. 3, B) before cessation of growth in winter, canals make their appearance after only a few rows of sieve tubes have been formed, while normally their differentiation is preceded by the formation of a fairly broad band of phloem. The appearance of new resin canals is foreshadowed by deposits of rubber aggregates in the potential epithelial cells of the canal.

May 31, 1943.—The width of the total and xylem increments measures 1.28 mm. and 0.96 mm., respectively. Secondary resin canals have differentiated in practically all bundles. The canals are at first slitlike and partly closed; those initiated earlier are now oval or circular. Each canal is surrounded by several rows of jacket cells that are densely filled with rubber. Starch (fig. 4, D) is usually present in the second cell layer, especially on the sides bordering the rays. Peripherally, the sieve tubes approach within two cell layers of the canal, while central as many as four rows of jacket cells may be present. Occasionally canals fail to form, or at least they do not open, causing a break in the radial continuity of the sieve-tube tissue. The cells in such areas as the normal jacket cells of canals are densely filled with rubber.

Thus, during 12 weeks of active growth, the stem increased in radius by 1.28 mm. and the xylem by 0.96 mm. The addition to the bark through cambial activity was relatively small. In other words, cambial growth activities in guayule favor xylem development both in priority of differentiation and in tissue mass. The growth curve during March and early April was rather flat, but it rose sharply early in May, then leveled off for the rest of the month. While formation of new phloem tissue has been limited, retrogressive changes resulting in sclerosis of a large part of the 1942 season's active phloem were conspicuous.

June 15, 1943.—The new xylem increment measures 1.26 mm.; total increment, 1.42 mm. Expressed in terms of area, this increment represents an increase of more than 100 percent. This increase is due to cambial activity and enlargement and division of older cells in the outer bark. The periphery of the stem cross section has lengthened considerably; the groups of fibers have moved farther apart, while new cells have been added to the flanges of the groups of fibers and to the sides of the phloem rays. All of the active phloem produced during the season of 1942 is now sclerotic, and the fibers extend central to the level of the rubber-free phloem ray (fig. 4, B) or slightly beyond. The rapidity of xylem differentiation is forcibly illustrated in material from the biweekly irrigated plot. Here the cambium zone and the area occupied by xylem tissue are very broad. A few solitary vessels are embedded in thin-walled fibrous tissue, which extends as far as 10 cell layers inward. A small quantity of rubber is evident in the new phloem ray, chiefly in the vicinity of the new resin canals (fig. 4, B). As yet there is no rubber in the rays of the new xylem increment.

June 15, to October 15, 1943.—Measurements on growth increments on plants from the control plot as well as from plots 0 to 4 are given in table 2. It is evident that while cambial activity continues throughout the summer, little new xylem is formed after the middle of July. The bark, however, continues to increase somewhat in width and relative weight. In the early part of the growing season the weight of wood and bark in the basal part of the main branches is about equal. As the season advances, the bark becomes increasingly heavier. This is to be expected, since during the early part of the growing season xylem is mostly differentiated. There is often considerable variation in the size of the coefficient of bark to wood in branches of equal thickness and age (table 3). Samples taken from the base of branches always have a smaller coefficient than stem pieces higher up.

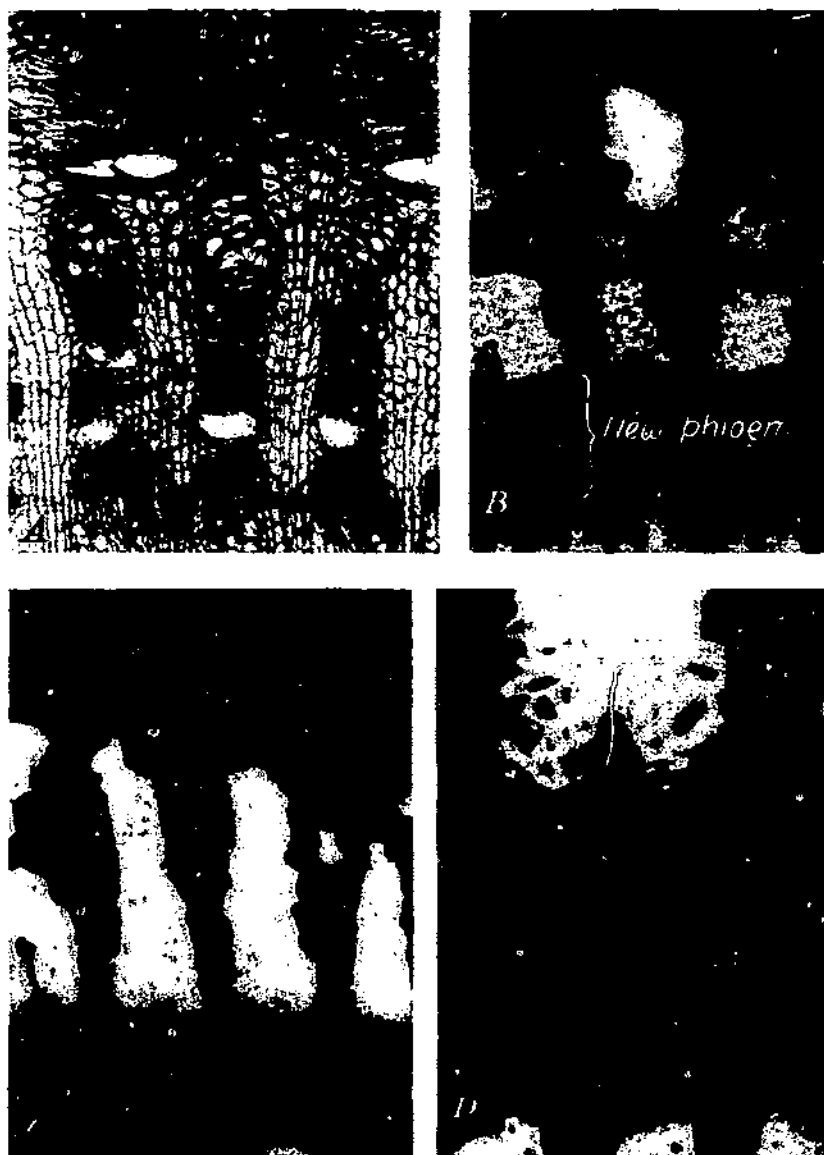


FIGURE 4.—*A*, Sclerenchymatization of peripheral part of active phloem (May 2). $\times 75$. *B*, Rubber deposit in ray and basal line of sclerenchyma on same tangent, showing that all of the active phloem increment for the season of 1942 has become sclerotic. $\times 50$. *C*, Rubber deposit in ray extends down to cambium line; only one secondary resin canal formed during entire season (Oct. 11). $\times 50$. *D*, Starch in jacket cells around secondary resin canal. $\times 100$.

TABLE 2.—Average radial measurements, in millimeters, of branches, showing total increments and xylem increments, June to October 1943

Plot No.	June		July		August		September		October	
	Total	Xylem	Total	Xylem	Total	Xylem	Total	Xylem	Total	Xylem
	<i>Mm.</i>	<i>Mm.</i>	<i>Mm.</i>	<i>Mm.</i>	<i>Mm.</i>	<i>Mm.</i>	<i>Mm.</i>	<i>Mm.</i>	<i>Mm.</i>	<i>Mm.</i>
Control	1.70	1.31	1.76	1.37	2.09	1.63	2.08	1.62	2.48	1.82
0	1.76	1.31	2.21	1.73	2.72	2.08	2.78	2.11	2.91	2.21
1	1.81	1.02	1.52	1.17	1.79	1.39	1.87	1.42	2.08	1.60
2	1.60	1.28	1.72	1.29	1.79	1.37	1.95	1.53	2.14	1.79
3	1.31	1.18	1.36	1.01	1.51	1.10	1.67	1.19	1.76	1.28
4			1.58	1.20	1.85	1.21	1.83	1.12	1.76	1.21

TABLE 3.—Relative volume of bark and wood in quagyle and comparison of ratios of bark to wood by weight, Oct. 18, 1943

HEIGHT OF PLANT, 17 INCHES; WEIGHT, 1,29 GRAMS

Plot No.	Length of branch	Diameter of branch	Diameter of wood	Width of bark	Weight of bark	Weight of wood	Ratio of bark to wood by weight
	<i>Cm.</i>	<i>Mm.</i>	<i>Mm.</i>	<i>Mm.</i>	<i>Gm.</i>	<i>Gm.</i>	
Control	3.40	10.9	6.5	2.20	1.110	1.082	1.30
	2.93	10.2	5.8	2.20	1.060	.823	1.29
	3.18	9.5	6.1	1.70	1.148	1.081	1.07
	3.48	9.3	5.9	1.70	1.238	1.000	1.17
	2.60	8.5	6.5	1.00	.797	.765	1.01
	3.11	8.1	6.0	1.05	1.117	.824	1.36
	2.52	8.1	6.1	1.00	.872	.712	1.25
	2.70	8.0	5.5	1.25	.851	.601	1.23
	3.75	7.2	4.8	1.20	1.013	.688	1.47

HEIGHT OF PLANT, 21 INCHES; WEIGHT, 1,820 GRAMS

0	2.71	13.0	9.0	2.00	1.778	1.785	1.00
	2.50	11.5	8.6	1.45	1.363	1.721	.79
	2.68	11.2	7.5	1.85	1.289	1.428	.81
	2.46	11.1	7.7	1.70	1.360	1.209	1.13
	2.71	11.0	8.1	1.45	1.528	1.439	1.06
	2.32	11.0	7.6	2.00	.996	1.120	.89
	2.60	10.6	8.0	1.30	1.361	1.482	.92
	2.50	10.3	8.1	1.10	.928	1.300	.71
	2.46	10.0	7.4	1.30	1.129	.991	1.13
	2.07	9.5	5.9	1.80	.836	.767	1.09
	2.50	9.0	5.9	1.55	.972	.797	1.09
	3.11	9.0	5.5	1.75	.921	.991	.92
	2.71	8.2	5.4	1.40	.912	.769	1.20

HEIGHT OF PLANT, 20 INCHES; WEIGHT, 1,275 GRAMS

1	3.00	12.2	8.9	1.65	1.080	1.819	1.09
	3.20	11.5	7.7	1.90	1.761	1.637	1.08
	3.42	11.1	7.3	2.05	1.536	1.412	1.09
	3.21	11.1	6.8	2.15	1.903	1.241	1.53
	3.23	10.9	6.9	2.00	1.441	1.295	1.18
	3.24	10.7	6.6	2.05	1.485	1.242	1.19
	2.47	9.7	6.3	1.79	1.110	.933	1.23
	2.55	8.8	5.7	1.45	.863	.642	1.31
	2.57	8.8	5.0	1.90	.880	.519	1.31
	2.54	8.2	5.7	1.25	.741	.622	1.19
	2.57	7.7	5.6	1.05	.691	.580	1.01

HEIGHT OF PLANT, 16 INCHES; WEIGHT, 1,090 GRAMS

2	2.53	9.0	5.4	1.80	.955	.611	1.56
	2.49	8.8	6.0	.96	.953	.760	1.25
	2.34	8.6	5.4	1.60	.774	.555	1.39
	2.50	8.4	5.4	1.60	.876	.571	1.53
	2.39	8.2	5.3	1.45	.763	.593	1.29
	2.47	7.8	4.7	1.55	.712	.515	1.38
	2.60	7.7	5.2	1.25	.763	.579	1.32
	2.44	7.7	4.8	1.41	.712	.427	1.66

TABLE 3.—*Relative volume of bark and wood in guayule and comparison of ratios of bark to wood by weight, Oct. 18, 1943—Continued*

HEIGHT OF PLANT, 17 INCHES; WEIGHT, 1,000 GRAMS

Plot No.	Length of branch	Diameter of branch	Diameter of wood	Width of bark	Weight of bark	Weight of wood	Ratio of bark to wood by weight
	<i>Cm.</i>	<i>Mm.</i>	<i>Mm.</i>	<i>Mm.</i>	<i>Gm.</i>	<i>Gm.</i>	
3.	2.68	12.14	8.2	2.10	1.802	1.462	1.23
	2.39	11.2	7.6	1.80	1.387	1.117	1.24
	2.50	9.4	6.0	1.70	1.070	.753	1.41
	2.62	9.1	5.9	1.60	1.026	.649	1.57
	2.68	9.0	5.4	2.30	.942	.615	1.46
	2.44	8.4	5.1	1.65	.871	.600	1.45
	2.44	8.3	5.5	1.40	.831	.567	1.47
	2.48	7.8	4.7	1.85	.710	.446	1.57
	2.55	7.7	4.3	1.70	.677	.409	1.65

HEIGHT OF PLANT, 16 INCHES; WEIGHT, 819 GRAMS

4.	2.07	10.4	6.1	2.15	1.334	0.956	1.39
	2.40	9.5	5.7	1.90	1.058	.767	1.38
	2.19	9.0	6.0	1.70	.966	.695	1.37
	2.54	8.8	4.9	1.95	.819	.514	1.59
	2.66	8.7	5.0	1.85	.865	.551	1.57
	2.59	8.7	5.0	1.85	.829	.532	1.51
	2.71	8.6	5.1	1.25	.681	.686	1.43
	2.65	8.3	5.1	1.70	.769	.512	1.52
	2.77	7.1	4.9	1.10	.724	.416	1.74
	2.40	6.4	4.3	1.05	.605	.352	1.72

There is progressive sclerenchymatization of the peripheral phloem, which now involves some phloem formed during the current year. One or two new resin canals are formed during the entire growing season. Where only one canal is formed, the radial extent of the phloem bundles from the last canal to the cambium is very large (fig. 4, C).

Although particles of rubber form in the new phloem ray, even during early growth, appreciable quantities are not found until the latter part of July. Rubber appears first in the vicinity of the last-formed canal (fig. 4, B), whence it extends upward until it meets the heavy deposit in the basal part of the old ray. The xylem ray of the new increment contains no rubber until toward the end of the growing season.

EFFECT OF IRRIGATIONS ON GROWTH AND TISSUE DIFFERENTIATION

The effect of variation in water supply on the general growth of guayule plants is apparent even to the casual observer. Plants from the biweekly irrigated plot are taller and much heavier than those from the control plot, which was irrigated only once a month (tables 3 and 4). Plants from plot 4 were the smallest; their stems were thin, and they weighed less than half as much as plants from plot 0. Plants from plot 2 were not quite so heavy as those from plot 1, even though plot 1 was kept dry a month longer. The explanation may be found in the greater fertility of plot 1, as shown by the performance of previous crops. Plants from plot 3 were somewhat heavier than those from plot 4, although the two plots had been kept dry for an identical period, except that water was withheld a month earlier from plot 3 and irrigation was resumed a month earlier.

Increment measurements of transverse dimensions of bark and wood were made on fresh material whenever cambial activity, however slight, permitted a clean separation of these tissues along the cambium line. The same pieces of stem, weighed before and after decortication, gave a comparison of ratios of bark to wood by weight. Together, these two methods provided a fairly reliable index of quantitative growth in relation to water supply, provided care was taken

TABLE 4.—Average green weight, dry weight, percentage of rubber, grams of rubber per plant, and pounds of rubber per acre, Nov. 30, 1943, and Feb. 15, 1944, at State College, N. Mex.

Plot No.	Green weight per plant		Dry weight per plant		Rubber per plant				Rubber per acre	
	Nov. 30	Feb. 15	Nov. 30	Feb. 15	Nov. 30	Feb. 15	Nov. 30	Feb. 15	Nov. 30	Feb. 15
	Grams	Grams	Grams	Grams	Percent	Percent	Grams	Grams	Pounds	Pounds
Control	1,158	1,186	444	556	4.68	5.63	20.55	31.30	237	262
0	1,861	1,651	723	686	4.15	4.81	30.00	33.82	347	391
1	1,374	1,525	506	652	4.67	5.21	23.03	33.71	273	390
2	1,328	1,299	492	557	6.00	5.35	29.50	29.05	341	336
3	885	960	326	369	5.48	5.78	18.41	23.14	213	267
4	817	734	276	201	6.00	6.05	16.56	19.61	191	227

to use fresh material, preferably collected in the morning and measured and weighed before there was a loss of water from the tissues.

A summary of increment measurements of transverse dimensions and weight determinations of bark and wood is given in table 5. The ratios of the radius of the wood to the bark are directly related to plant weight and water supply (table 5), the biweekly irrigated plot producing proportionately the largest quantity of wood and plot 4 the smallest. Concomitantly, the ratio of bark to wood by weight is smallest for the biweekly irrigated plot. Somewhat incongruous is the performance of plots 3 and 4, which received the same volume of irrigation water, except that in plot 3 the dry period was begun and terminated 1 month earlier.

TABLE 5.—Relative quantity of bark and wood, Oct. 18, 1943¹

Plot No.	Radius of wood	Thickness of bark	Ratio of radius of wood to bark	Ratio of bark to wood by weight
	Mm.	Mm.		
Control	2.95	1.45	2.03	1.24
0	3.60	1.59	2.26	.88
1	3.30	1.75	1.89	1.17
2	2.70	1.44	1.87	1.42
3	2.95	1.75	1.77	1.43
4	2.65	1.62	1.63	1.52

¹ For details see table 2.

Seasonal growth increment of wood and bark was determined by measuring the transverse dimensions under the microscope. For the bark these measurements are reliable only so long as there is little or no rubber in the newly formed part of the ray. The demarcation line between the old and the new growth becomes indistinct as rubber increases abundantly in the new ray tissue, until finally it is difficult to separate old and new growth. The seasonal wood increment is more easily shown, because little rubber is deposited in the new wood rays before the end of the growing season. The common eccentricity of growth in the branches of guayule must also be taken into account, with the accompanying variation in the width of the bark; in the wood the variation in length of the different radii is even more pronounced. Thus, while the figures on increment measurement do not lend themselves to statistical treatment, they do represent reliable tendencies if care is taken to select material of uniform growth.

SEASONAL DEVELOPMENT OF SECONDARY PHLOEM AND
APPEARANCE OF RUBBER

Long before there is any outward manifestation of growth, the cambium is activated and forms new tissues, the rate of differentiation increasing as outside influences become more favorable.

Relatively little is known about the developmental history of secondary tissues in general and of the phloem in particular. According to Strasburger (8), phloem production begins later and continues longer than that of xylem, and the transition from cambium to phloem is abrupt during the growing season. Russow (7) also found the demarcation between cambium and phloem to be very sharp in summer and obscure during the dormant season, indicating that during the growing season developmental stages were passed very rapidly. The concept that in both gymnosperms and angiosperms some phloem cells remain in an immature state through the winter and resume differentiation in spring (3) has been supported by the recent study of Abbe and Crafts (1) on the phloem of white pine and other coniferous species.

In guayule, priority of tissue differentiation belongs definitely to the xylem. It is late in April, when the weather has become warm and flower stalks begin to appear, that the cambium forms phloem cells by reciprocal division. By that time the new xylem increment is already a half millimeter broad—as broad as the band of secondary phloem that will develop during the entire vegetative period. There is no carry-over of undifferentiated phloem cells into the new season, since the tissues in winter condition show fully matured sieve tubes adjacent to the cambium.

The appearance of rubber has been mentioned previously in connection with increment measurements. No rubber in detectable quantity is seen during the early months of the vegetative season, partly because phloem tissue formation is initiated much later than xylem and partly because rubber synthesis is synchronized with a slowing up or cessation of the growth processes because of water deficiency. Rubber deposits in the phloem rays of the new increment were first observed early in July in plants of plots 1 and 3 and a little later in plants from plots 2 and 4. These plots had been without irrigation water since the end of April and of May, respectively. At the end of July particles of rubber were also seen in the new phloem rays of plants from the control plot. Early in August the rubber content of the new phloem rays of plants from plots 1 to 4 had increased considerably; a medium heavy deposit was also evident in the control plot, but there was only a small quantity in plants from the heavily irrigated plot. In September the phloem rays of plants from plots 1 to 4 were so filled with rubber that the demarcation line between old and new growth was no longer distinguishable.

The point of initial rubber deposit in the new phloem ray is not uniformly localized. Often rubber appears first in that part of the ray that is tangentially in line with the last-formed resin canal, whence it extends outward and central, or the first noticeable deposit may appear near the upper part of the ray. If so, the demarcation line between the old and the new increment is eliminated earlier.

Rubber appears in the xylem rays much later. As early as the middle of July it may be seen in minute quantities in plants from plots 1 to 4. The deposits never become heavy enough at any time during

the growing season to obliterate the dividing line between the old and the new increment.

While staining reactions indicate a heavy deposit of rubber in the phloem rays by the end of the growing season, additional deposits are made throughout the winter months, as shown by a comparison of the rubber analyses (table 4).

The nature of rubber synthesis in winter from photosynthetic reserves presumably is still a moot question. The only visible food reserve in guayule is starch localized in the cells of the endodermis and around the secondary resin canals. The limited supply of this starch, which disappears in winter, does not argue in favor of its being a potential source of rubber. On the other hand, inulin⁴ is found in an appreciable quantity and could be closely connected with rubber synthesis, except that both the inulin and the rubber content of the tissues increase at the same periods.

Late in fall the rubber content of heavily irrigated plants is lower than that of plants grown under restricted water economy (table 4). Since the former possess ample storage facilities, however, an analysis made in midwinter should show an appreciable increase in the percentage of rubber, provided the demands made on photosynthetic products during vegetative growth do not prevent the accumulation of reserves, in one form or another, from which rubber could be synthesized. This expectation was only partly realized, however, during the 10-week interval between the two analyses (table 4).

On the subject of winter synthesis of rubber, Dr. A. C. Hildreth⁵ has the following to say:

Winter synthesis of rubber does not necessarily have to be from photosynthetic reserves previously stored. The plants carry foliage ordinarily, and temperature and light conditions are often favorable for photosynthesis. Consequently, rubber could be synthesized from current products of photosynthesis without drawing on reserves. In fact, we have no evidence at all that carbohydrate reserves can be transformed into rubber. The only experiments conducted that have a bearing on this point indicate that rubber formation does not take place in winter if the plants are defoliated.

This view has much to recommend it; also it would help to explain the relatively small increase shown during December and January (1943-44), when abnormally low temperatures prevailed. The accumulation of prerubber reserves, although not as yet demonstrated, remains a possibility, since, especially in young plants, the sudden filling of the storage tissues early in the fall could hardly be accounted for by current synthesis alone, even when the decrease in cambial activity, which would release more building material for rubber formation, is taken into account.

RETROGRESSIVE CHANGES IN SECONDARY PHLOEM

A characteristic feature of the bark of guayule is the sclerenchyma, which progressively displaces all old conducting-phloem elements. The sclerenchyma appears in a cross section of the bark as discrete bundles of given depth and width, as determined by the spacing of the medullary rays and the resin canals.

⁴ CURTIS, O. F., JR., MCRAVY, W. L., SLATTERY, M. C. REGIONAL AND SEASONAL DISTRIBUTION OF RUBBER, CARBOHYDRATES, AND NITROGEN IN GUAYULE. Paper presented at the Winter Research Progress and Plans Conference, Guayule Project, Salinas, Calif., 1944. [Processed.]

⁵ From a letter, dated May 9, 1944, by A. C. Hildreth, project leader, Special Guayule Research Project, Bureau of Plant Industry, Soils, and Agricultural Engineering.

The most peripheral sclerenchymal groups (fig. 1, A) may be irregular, conforming to the mode of growth of the first secondary phloem as a whole. Sclerosis proceeds radially, centrad from without, flattening and crushing the walls of the sieve tubes and at times overtaking some of the neighboring ray cells. The initial stages of sclerenchymatization of the old active phloem are evident before new phloem cells are formed by the cambium, but on the whole the two processes are synchronized so that the quantity of active phloem tissue remains fairly constant. During most active growth, new cell development temporarily exceeds sclerosis, so that the band of active phloem is at times quite broad. Since the ray tissue of the new secondary phloem contains no rubber, progressive sclerosis can be followed easily by noting the position of the apex of the rubber-free ray in relation to the fibers. When the two levels are on the same tangent, all of the 1942 season's active phloem in a given bundle has become sclerotic. Quite often the flanges of the active phloem groups mature fibers in advance of the center (fig. 4, B) and meet the apex of the rubber-free ray at an earlier date.

In plants from the control plot, all of last season's active phloem became sclerotic early in July, at a time when the rate of xylem formation was subsiding and phloem differentiation was at its height. In plots that had been kept dry during May and June, the levels of the fibers and rubber-free ray tissues did not meet until 3 weeks later.

Sclerosis imperceptibly involves the first-formed phloem of the current season. This process may come to an apparent halt above the last-formed resin canal. But gradually the flanges of the phloem below the canal become involved and by the end of the season, depending on the time of initiation of the last canal, a complete tangential band of fibers is formed.

To what extent sclerosis involves the phloem of the current increment is not easily determined, since the accumulation of rubber in the new phloem sector erases the demarcation line between old and new growth. In plants from the dry plots this may happen before midsummer. In the ash (*Fraxinus excelsior* L.) Giff (5) found the summer phloem crushed before winter, whereas the fall phloem survived the winter and was crushed in spring. Although no distinction between summer and fall phloem can be made in guayule, an analogous relation exists.

THICKNESS AND COMPOSITION OF BARK IN RELATION TO PERFORMANCE

The volume of rubber-bearing tissue in the stem varies with thickness of bark and total stem diameter and with the percentage composition of ray tissue, sclerenchyma, and active phloem.⁶ In rapidly growing plants xylem development is favored, but the new phloem increment is not necessarily small, so that the quantity of bark tissue produced by cambial activity and expansion in the old cortex is considerable. According to Lloyd (6), the quantity of rubber-bearing tissue formed in a branch of an irrigated plant may be $5\frac{1}{2}$ times that produced by a dry-land plant of similar age.

⁶ WHITING, A. G., and MITCHELL, J. W. MEASUREMENT OF RUBBER-PRODUCING TISSUES IN GUAYULE STEMS. Paper presented at the Winter Research Progress and Plans Conference, Guayule Project, Salinas, Calif., 1944. [Processed.]

The effect of differential irrigation on the development of bark and wood is indicated in table 5. The measurements, whether made externally with calipers or on cross sections with a microscope, are not too dependable, because of eccentricity of growth. For this reason the figures on ratios of bark to wood by weight are more significant. Also, different plants, while having a similar gross weight, may show a preponderance of either thick or thin branches, a fact that may help explain the small xylem and phloem radius for plot 2 as compared with plot 3. The ratios of bark to wood by weight are conspicuously large for all dry plots with the exception of plot 1. The ratio for the heavily irrigated plot 0, while negative in this particular sample, is usually slightly positive.

Thus, maximum performance in terms of pounds of rubber per acre is the resultant of a large annual increment in which the bark-wood ratio favors the bark, provided its structural composition and the rate of rubber synthesis remain unaffected.

The most important structural variation that adversely affects bark-storage capacity is an overdevelopment of sclerenchyma. The form and size of the groups of sclerenchyma depend on the mode of growth of the differentiating phloem elements. The broader the tangential dimensions of the groups of phloem of a given radius, the more ample is the translocation system and concomitantly the more favorable are the chances for rapid growth; conversely, the effect of sequacious sclerenchyma is more depressing on available storage space. To obtain the maximum performance in terms of pounds of rubber per acre, effort should be made to balance the beneficial effect of a large phloem and small ray complement on growth against a small phloem but large ray complement with its less effective translocation system but its greater storage accommodation for rubber.

With due allowance for regional variation in stem cross sections, plants of a given variety show little difference in sclerenchyma development under varying soil-moisture stress (fig. 5). In plots 0 and 2, there is a fairly broad band of sclerenchyma below the last canal except that tangentially two of the groups of active phloem are broader in plot 0. In both plots nascent resin canals may be seen near the cambium. In plants from plots 1 and 3 there is as yet little sclerenchyma below the last canal. For some reason, stems from plots 0 and 1 were harder to cut on the microtome than stems from plots 3 and 4, which would argue in favor of thinner walls or weaker lignification for the latter, although observations by Addicott and Bornhurst¹ on guayule nursery seedlings indicate higher lignin deposits for plants growing under greater soil-moisture stresses.

No correlations seem to exist between percentage of rubber and relative development of sclerenchyma in plants of the same type but grown in different localities (fig. 6). The available storage space for rubber appears to be about the same in the different types of material, but since the rubber content differs widely, the storage space is only partly utilized in plants that are low in rubber.

¹ADDICOTT, F. T., and BORNHURST, J. PRELIMINARY NOTE ON THE ANATOMICAL EFFECTS OF MOISTURE STRESS IN NURSERY SEEDLINGS OF GUAYULE. Paper presented at the Winter Research Progress and Plans Conference, Guayule Project, Salinas, Calif. 1944. [Processed.]

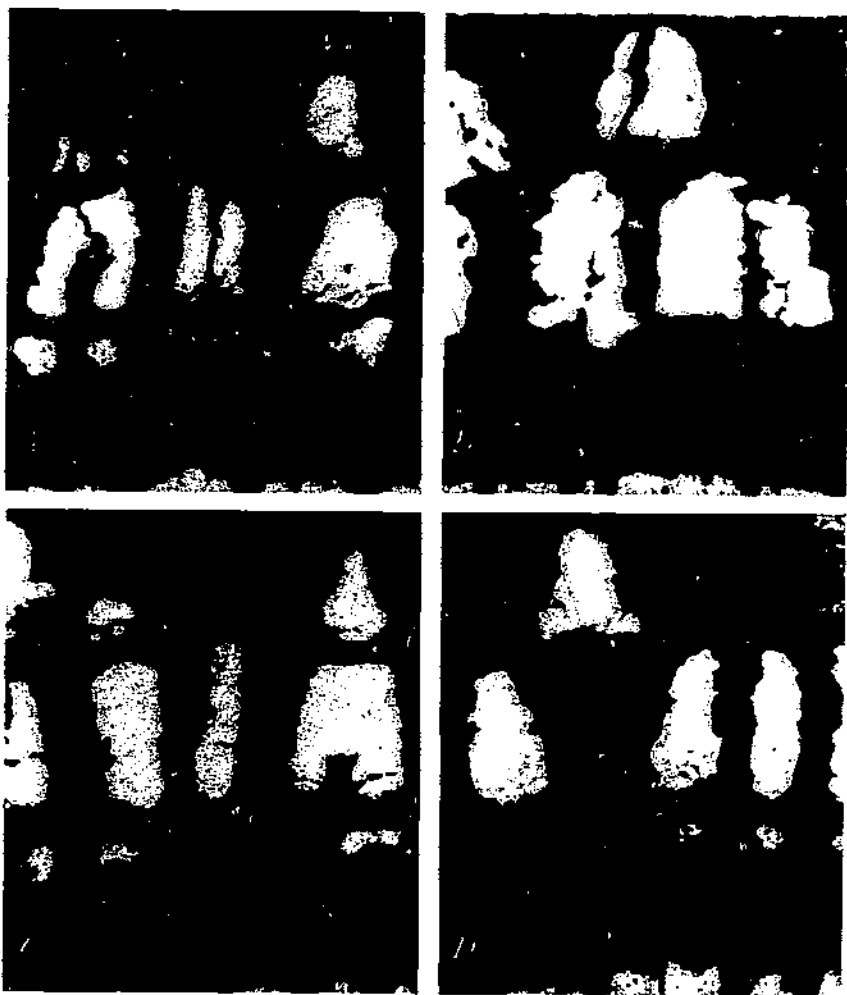


FIGURE 5.—*A* (from plot 0), Nascent resin canals next to cambium. *B* (from plot 1), Slight quantity of irregular sclerosis below last row of resin canals. *C* (from plot 2), Nascent resin canals close to cambium; sclerosis more advanced than in *B*. *D* (from plot 3), Nascent resin canals close to cambium; sclerosis intermediate between *B* and *C*. All $\times 42.7$. All material taken October 1

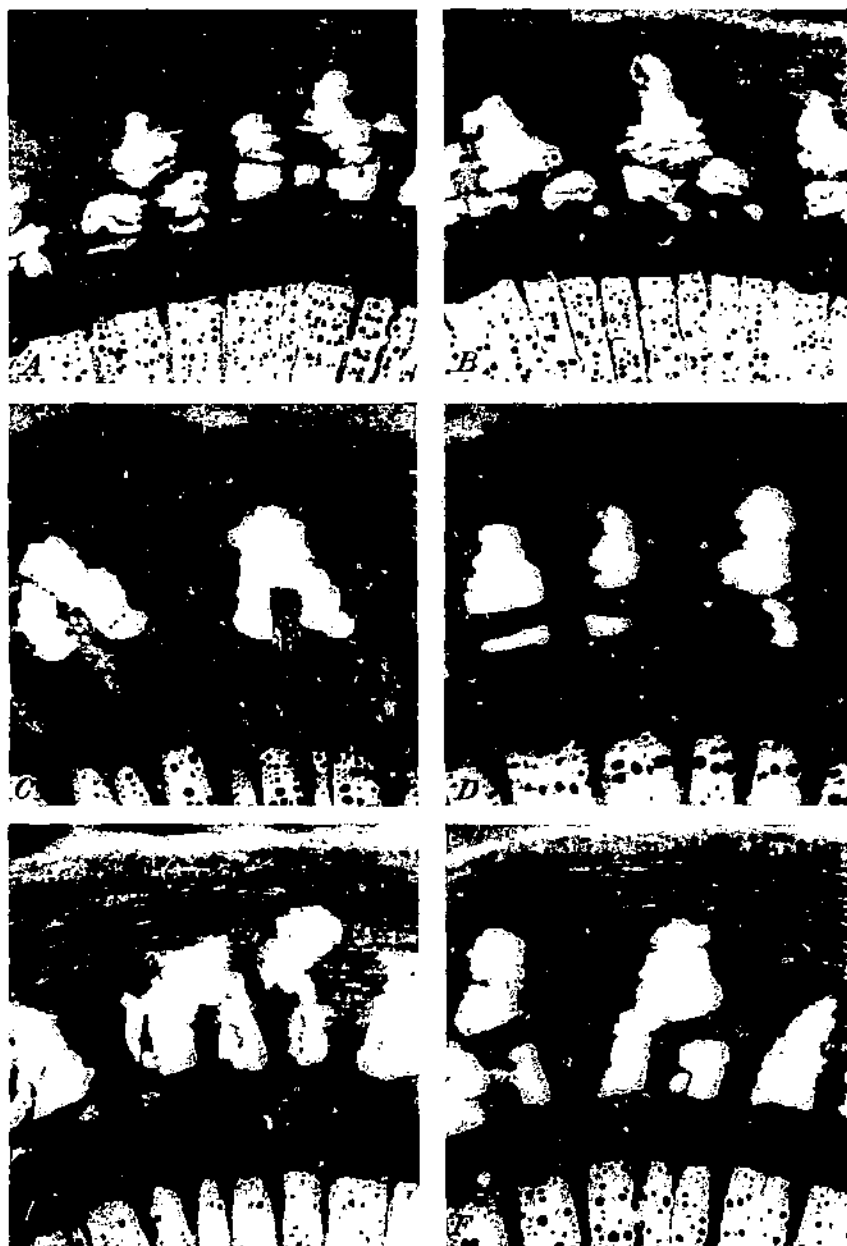


FIGURE 6.—A, Stem sections of material low in rubber. \times 21.5. B, Stem section of another branch of same material. \times 21.5. C, Variety 406 from Rio Grande City, Tex., high in rubber. \times 43. D, Variety 593 from Rio Grande City, high in rubber. \times 43. E, Variety 406 (control plot, State College). \times 43. F, Variety 593 (control plot, State College). \times 43.

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