AN ECOLOGICAL STUDY OF THE GENUS RUBUS WITH REFERENCE TO DROUGHT RESISTANCE

THESIS FOR THE DEGREE OF PH. D.

Charles H. Mahoney

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Horticulture Fruit culture

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by

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TABLE OF CONTENTS

INTRODUCTION

The genesis of this study was the desirability of promoting small fruit culture and production in the Southern Great Plains Area of the State of Texas. Existing knowledge of the severity of the growth season climate in that section and of the general failure of previous attempts to succeed there with small fruit culture made it evident that a difficult problem must be undertaken, a problem centering in the question of drought resistance.

The locality mentioned is exceedingly xerophytic. Though drought resistance in some types of plants, particularly the cereals, has been widely investigated and much scientific and practical information gained thereby, little has been attempted with the so called small fruit plants. By way of a beginning, it was possible to take a purely genetic viewpoint and proceed accordingly. This would have led to elaborate trials with numerous species and varieties, selection of the most promising ones, followed by hybridizations and then further selections, and so on. Eventually, this type of attack might have given the desired success.

It seemed, however, that the more strictly genetic phase of the problem might better come last than first. Both logic and expediency dictated that it was necessary as a preliminary measure to make studies which would yield quantitative data that would give 1) a summary of the environal factors to which plants are exposed in that locality, 2) a knowledge of the structure and behavior of small fruit species and varieties in habitats where they do thrive, 3) information on the modifications which these same types undergo when transplanted to more xerophytic localities, including the one in Texas, and 4) a knowledge of which existing forms are the most plastic as regards the inherent capacity to undergo the required xeromorphic changes and thus become more drought resistant and better adapted to the habitat under consideration. Upon the completion of such studies, it becomes possible, if desirable, to proceed with the genetic phase of the problem more intelligently and with greater confidence. It should help greatly to know not only the characteristics of the various plant forms as they are, but also the potential ability of these same forms to adapt themselves in those respects which increase the probability of their survival under severely xerophytic conditions.

Accordingly, this study took the aspect of an investigation of the ecological adaptation of small fruit plants with reference to drought resistance. Efforts were concentrated on certain species of the genus Rubus. Are some of these varieties more capable of the required xeromorphism than others, and, if so how much farther do they go in the proper directions than those which are less capable?

HABITATS

Three habitats were selected which show a very marked difference of climate. The northern site is the Michigan Experiment Station substation located at South Haven on Lake Michigan in the southwest part of the state and in the heart of one of its most important fruit sections. The elevation is 582 feet above sea level; the temperature and relative humidity are fairly uniform because of the influence of Lake Michigan. None of the climatic factors shows any marked variability here and the growing season is fairly cool, moist and uniform in average years. The important fruit crops produced in this section are the apple, peach, pear, cherry, strawberry, raspberry, and blueberry. The average annual rainfall is 33.2 inches.

The intermediate habitat is the Government Field Station at Woodward, Oklahoma. This site is in the western part of the state and east of the southern great plains section. The elevation is 2,002 feet above sea level, and the average annual rainfall 24.15 inches. This site is characterized by much drier atmospheric conditions than the Michigan habitat and the evaporating power of the air is much greater. There is much more wind, which combined with higher temperatures and lower relative humidity, makes the water relations of the plant a very important consideration. The climate is much more variable than that of Michigan. The most important crops grown in western Oklahoma are cotton, grain sorghums, and corn.

The third habitat is at the southern end of the Great Plains on the grounds of the Texas Technological College at Lubbock, Texas. This habitat approaches closely a rather marked xerophytic condition for most of the cultivated perennial fruit crops. Quoting Shantz (23), "....a short grass region adapted to short season annual crops." As a habitat it is much more severe with respect to transpiration and water loss than the Oklahoma site. The extremely high winds, dust storms, and flying sand combined with the extremely low relative humidity from January to June create such an enormous evaporating power of the air that only those types of cultivated perennial plants which possess the ability to withstand drought survive. The relative humidity often drops below 10 per cent for three to five hours during the middle of the day in the spring months. The elevation is 3,205 feet above sea level; the annual rainfall is 19.52

inches, but for the years included in the study it has been less. The windrun averages about 8,000 miles per month in the spring and most of it is during the day. Cotton and grain sorghums are the principal crops grown. Gramma grass (Bouteloua gracilis), Buffalo grass (Bulbilis dactyloides), Bear grass (Yucca glauca), and low growing composites are the native plants found in this section.

Some material was secured from the government gardens at Washington, D.C. in 1929. This locality is only 100 feet above sea level, and the average annual precipitation 42.24 inches. The relative humidity is high and, though the temperatures are high, this station can be classed as mesophytic.

The habitats afford a wide range of plant environment and are such as to serve effectively in the subjection of any species or variety to distinctly different degrees of xerophyty. The following tables (1 and 2), give the meteorological data in detail for the several stations in the two seasons (1928 and 1929) during which the plants were grown in the different localities and the materials for study obtained.

Meteorological data for the Texas habitat were obtained from instruments in a standard shelter 12 inches above the ground among the plants. Temperature and relative humidity records were obtained by taking two hour interval readings from the weekly charts of a hygro-thermograph which was checked twice a day with a standardized thermometer and sling-psychrometer. Soil temperatures at 12 inches depth were recorded by a soil thermograph. Livingston porous cup atmometers were used, both the white bulb and the black radio-atmometer. The latter was not entirely satisfactory, due to the dust and sand which caused the loss of the collodion coating in the repeated washing off of the sand. The atmometers were not used in the other two habitats, which is unfortunate, as there can be only an approximate comparison of the evaporating power of the air in the three sites. The meteorological data for the Oklahoma, Michigan, and Washington, D.C., habitats were secured from the monthly reports issued by the government meteorologists and from data supplied by the Michigan Experiment Station substation at South Haven, and the Government Field Station at Woodward, Oklahoma.

The season of 1928 (table 1).

Table 1 shows that the rainfall for this growing season was almost identical for the Michigan and Oklahome habitats, but the rainfall at the Texas station was 40 per cent less than in the other habitats. However, the most important consideration is not rainfall alone but rainfall in conjunction with the evaporating power of the air, which, in the Texas habitat at least, is responsible for atmospheric drought. The

Table 1. Meteorological data for the three habitats in which Rubus was grown during the season of 1928.

	South Haven, Michigan - 1928								Woodward, Oklahoma - 1928						
	Temperature			Relative humidity					Temperature			Relative humidity			
	Mean min.	Mean max.	Mean	Mean A.M.	Mean P.M.	Mean	Rain in inches	Wind-* run in miles	Mean min.	Mean max.	Mean	Abso. min.	Mean	Rain in inches	Wind-run in miles
March	26.2	43.4	34.8	83	71	77.0	1.53	8945	36.5	64.7	50.6	-	-	1.21	6839
April	33.4	51.7	42.6	78	70	74.0	2.28	8568	41.8	70.7	56.2	14.0	53.9	1.88	7494
May	44.6	63.9	54.2	71	59	65.0	1.76	6523	54.0	82.2	68.1	28.0	62.4	6.57	4535
June	51.0	70.5	60.8	81	71	76.0	6.75	6502	61.4	85.0	73.2	34.0	70.1	6.60	4508
July	61.8	79.5	70.6	83	71	77.0	2.18	6140	68.9	93.5	81.2	32.0	59.7	1.96	5516
Aug.	60.3	80.5	70.4	83	73	78.0	2.92	5797	63.1	93.7	79.9	34.5	57.3	0.51	5055
Sept.	50.6	70.6	60.6	80	73	76.5	4.37	6877	56.2	88.6	72.4	24.0	55.2	0.95	5650
Oct.	47.5	64.8	56.2	83	77	80.0	4.01	7959	49.9	76.9	63.4	-	-	5.42	-
Season							25.80							25.10	

*Records from Grand Haven, Michigan

Table 1. Continued.

Lubbock, Texas - 1928						
Temperature			Relative humidity			
Mean min.	Mean max.	Mean day	Abso. min.	Mean day	Rain in inches	Wind-run in miles
46.1	65.9	58.9	3	40.4	.015	8400
51.4	74.7	64.1	4	33.1	.100	9539
63.6	81.8	70.7	4	56.2	2.740	6706
66.0	90.0	75.0	5	53.0	1.060	8988
66.6	91.6	79.1	12	59.0	6.780	4901
67.5	85.9	76.0	4	60.9	4.870	4482
58.6	84.8	72.0	3	43.6	.040	4423
56.5	77.4	65.0	2	44.9	2.040	5972
					17.740	

difference in relative humidity between Michigan and Oklahoma is extremely large in April and again from midsummer to September. The total windrun on the shore of Lake Michigan is higher than in Oklahoma but at the latter station, combined with much lower relative humidity, much higher temperature, and more sunlight, the evaporating power of the air is much greater. Compared with the Oklahoma habitat, the Texas habitat shows a difference in average monthly relative humidity as great as that between Michigan and Oklahoma. This difference in relative humidity is very marked in the spring months, as are the differences in total windrun, mean monthly temperatures, and mean maximum temperatures. The South Plains site represents more or less xerophytic conditions as one extreme, and the shore of Lake Michigan the mesophytic conditions as the other extreme, with Oklahoma more or less intermediate.

The season of 1929 (table 2).

In general the 1929 season does not show the differences in relative humidity between Michigan and Oklahoma that prevailed in 1928. This is true in the earlier part of the growing season when shoot growth is most active. The difference in temperatures is not as pronounced as it was in 1928. The difference in relative humidity between Oklahoma and Texas was very great in 1929. In 1928 and 1929 the mean monthly temperatures of the Texas station were slightly higher

Table 2. Meteorological data for the four habitats in which Rubus was grown during the season of 1929.

	South Haven, Michigan - 1929								Woodward, Oklahoma - 1929						
	Temperature			Relative humidity					Temperature			Relative humidity			
	Mean min.	Mean max.	Mean	Mean A.M.	Mean P.M.	Mean	Rain in inches	Wind-run in miles	Mean min.	Mean max.	Mean	Abso. min.	Mean	Rain in inches	Wind-run in miles
March	31.6	48.2	39.9	85	79	82.0	2.62	9073	36.0	66.0	51.0	-	-	2.61	5670
April	38.5	56.5	47.5	83	68	75.5	6.68	8798	48.5	75.7	62.1	21.5	58.9	0.61	7635
May	44.0	63.9	54.0	76	67	71.5	3.37	7694	55.5	75.9	65.7	34.0	72.1	3.75	5599
June	52.2	72.8	62.5	-	-	71.0	3.02	-	64.6	91.1	77.9	26.0	57.5	0.84	5713
July	60.2	79.9	70.0	74	63	68.5	0.81	6141	59.5	94.5	82.0	28.0	57.2	3.30	5238
Aug.	56.2	77.5	66.8	79	61	70.0	2.20	6145	69.1	97.8	83.4	26.0	52.5	1.83	4368
Sept.	52.4	74.5	63.4	81	66	73.5	1.73	6486	59.2	84.0	71.6	38.5	64.1	5.52	5517
Oct.	41.6	57.8	49.7	86	74	80.0	4.08	8148	48.5	73.0	60.8	-	-	1.95	-
Season							24.51							20.41	

Table 2. Continued.

Lubbock, Texas - 1929							Washington, D. C. - 1929							
Temperature			Relative humidity				Temperature			Relative humidity				
Mean Min.	Mean Max.	Mean day	Abso. Min.	Mean	Rain in inches	Wind-run in miles	Mean min.	Mean max.	Mean	Mean A.M.	Mean P.M.	Mean	Rain in inches	Wind-run in miles
42.8	66.1	55.0	2.0	39.8	2.03	7349	40.1	60.4	50.2	67	54	60.5	2.64	5422
56.8	77.9	65.0	1.0	39.8	0.08	8187	46.6	68.7	57.6	73	56	64.5	6.10	5307
60.0	87.0	71.2	4.0	47.4	6.91	5972	54.1	74.9	64.5	73	63	68.0	2.29	3968
60.0	101.0	85.2	2.0	30.3	0.91	6016	62.0	82.5	72.2	74	64	69.0	7.41	3186
62.5	99.0	86.0	6.0	36.4	0.20	4815	66.8	87.0	76.9	72	63	67.5	1.29	3063
62.0	100.0	88.7	8.0	34.6	1.68	3260	65.0	83.9	74.4	75	60	67.5	1.30	3138
55.0	94.2	76.0	11.0	52.2	1.36	4489	59.7	80.6	70.2	81	68	74.5	4.32	2989
43.5	81.5	68.0	10.0	50.4	3.56	3142	45.8	65.5	55.6	81	65	73.0	4.82	4397
					16.73								30.17	

than those of Oklahoma.

Climatological data for Washington D.C. are given in table 2. The temperatures are slightly lower, the humidity much higher, the windrun much less, and the precipitation about twice as much in this habitat, as compared with the Texas habitat.

There were no great differences between 1928 and 1929 in the Michigan habitat. The 1928 season had higher temperatures, more clear days, and less rainfall during the earlier part of the growing season. The 1929 season, however, had higher relative humidity and higher windrun during the same part of the season.

The Oklahoma habitat had much more severe atmospheric drought conditions in 1929 than in 1928. The temperatures were higher, relative humidity lower, rainfall lower, and windrun higher.

The Texas habitat also experienced a higher evaporating power of the air in 1929. The temperatures were higher, relative humidity lower, and rainfall lower during the late spring and early summer months. The windrun, however, was slightly less in 1929.

PLANT MATERIALS AND METHODS

The genus Rubus, which includes the red raspberry, black raspberry, blackberry, dewberry and the many hybrids, was used in this work. As many similar varieties as possible from each habitat were selected for comparison but only a few varieties of some of the species were grown in all the habitats. Rubus strigosus, occidentalis, strigosus x occidentalis, are the species of raspberries which are found mainly in the Michigan habitat. Rubus strigosus x Rubus innominatus was grown in the Texas habitat and vegetatively was quite adaptable. The dewberry is represented by Rubus flagellaris roribaccus Bail. variety Lucretia, which was grown in all three habitats, and Rubus flagellaris geophilus Bail. was grown in the Oklahoma habitat. Many species of blackberries and blackberry-dewberry hybrids were used. Rubus allegheniensis Bail., laudatus Bail., titanus Bail., and several varieties of Rubus velox Bail. give a range of blackberry and blackberry-dewberry species.

All varieties were planted at Lubbock in the spring of 1927, with the exception of McDonald which was planted in 1928. Two hundred plants each of Cuthbert, Viking, and Columbian were planted in 1927 with no success. All plants were watered every week by the flooding method until the summer rains started in June. Two hundred plants each of Cuthbert, Viking, and Columbian were cut back to six inches and again planted in 1928, and the soil moisture during this season was kept at the field optimum for these three varieties. None survived except one shoot of Columbian which suckered up during the midsummer rains and was killed by the first frost. All plants were in one block, subject to the same climatic changes, and no protective windbreaks were used. The sectioning material from Texas was taken from all plants which had been established for at least one year, with the exception of McDonald planted in 1928. The material from the other habitats was taken from plants which had been established for some time, with exception of the 1928 samples from Plum Farmer in Oklahoma, which had been transplanted that spring.

Stem material was taken from all the varieties in all the habitats for histological study approximately one week before the average date of the first killing frost in the fall. The stem material was taken from the third or fourth internode from the ground of shoots of the current season. During the first year this material was put up in a formalin-alcohol preserving solution containing some glycerine, but in the second season the material was cut fresh. The latter method is much more satisfactory as the formalin-alcohol solution hardens the material making cutting of complete thin cross sections difficult. During the first year the sections were stained by the ordinary safranine-haematoxylin method advocated by Chamberlain (6) for freehand sections. In the second year, the order of the safranine and haematoxylin was reversed, and other minor changes made.

The leaf material was taken from the main leaflet through the midrib at approximately the same height on the stem in all three habitats. In the alcohol-xylol method of parafin imbedding used the first year the alcohol made cutting of thin sections difficult, and the N-butyl alcohol method, as given by Zirkle (29), was used for dehydration the second year with much better results. The sections cut more readily and without the loss of hairs on the lower epidermis.

REVIEW OF LITERATURE

Stem Modifications Due to Physical Factors.

The amount of literature dealing with histological studies of stem anatomy as influenced by environment, if that which deals with descriptions of typical xerophytic and mesophytic types is eliminated, is very limited. Casual mention is made of internode length, diameter and other gross characters by many of those who worked on leaf modifications, such as Dufour (8), Krüger (14), Schimper (22), McLean (20), Starr (25), and Cannon (5).

Eberhardt (11), who grew various woody, as well as herbaceous, plants in dry and in moist air, found that dry air caused an increase in the number of xylem vessels and that their walls were much thicker, the number of vascular bundles in the leaf was larger, and the cells of the epidermis, cortex, and pith were smaller. He states that dry air promotes the development of tissues whereas humid air prevents it, and that moist air inhibits the development of cork.

Zoltkewich (30) showed the great significance of the conducting system in the determination of drought resistance. He found that drought-resistant alfalfa possesses a much better developed conducting system in the stem than the less resistant clover. In alfalfa the xylem is a broad compact ring, whereas in the clover the greater portion of the transverse section is composed of pith.

Duliot (9) found that the height of Rubus idaeus grown at 2400 metres in the Pyrenees was only 40 per cent; the internodes 50 per cent in length; and the leaf surface only 40 per cent that of plants grown near Paris.

One of the most complete pieces of work on the ecological anatomy of stems is that of McDougall and Penfound (19). Stem material of woody plants taken from position of maximum and minimum light on the same plant was studied. They report in summary of their results: "The data shows that sun stems show the following modifications from shade stems in woody plants: (a) a slight reduction in the percentage of cork in the shrubs, but a small increase in the trees; (b) a slight decrease in the percentage of cortex, Benzoin mellissafolium being an exception; (c) a marked increase in sclerenchyma; (d) a large increase in the percentage of xylem with an accompanying diminution of pith." The stems of the lower strata have a smaller amount of conducting tissue and an increase in percentage of parenchyma.

Leaf Modifications Due to Physical Factors.

Mrs. Clements (7) has reviewed very thoroughly the literature on leaf modifications. In general her conclusions agree fairly closely with those of earlier investigators. Some of her conclusions are presented here:

(1) A typical hydrophyll consists entirely of sponge cells and air spaces.

(2) A typical xerophyll consists entirely of palisade cells with few air-spaces and with

or without water-storage tissue.

(3) A typical mesophyll consists of equal amounts of palisade and sponge tissue, and moderate air-spaces.

(4) Decreased light and increased water both cause an increase in leaf surface and a decrease in thickness.

(5) The lateral tension in the cells which causes a thinning of the leaf is due to the sensitiveness of chlorophyll to light.

(6) In weak light the chloroplasts arrange themselves in the most favorable position for the absorption of the light.

(7) Increased light and decreased water both cause a reduction in leaf surface and increase in thickness.

(8) Strong light causes a closer arrangement of the chlorenchym cells, and especially of the palisade.

(9) Decreased water causes a decrease in transpiring surface and hence closer arrangement of the cells, especially of the sponge, and prolateness in the sponge cells.

(10) Humidity is closely connected with water content, but is also directly efficient in changing the cuticle.

(11) Temperature acts indirectly upon the plant through water and humidity.

Hanson (12) has worked out the modifications of leaves taken from the periphery and the center of the same tree for some of the most important shade trees. He has reviewed fully the literature appearing since the time of the publication of Mrs. Clements' paper. He found that the atmometer evaporation was 1½ to 2 1/3 times as great at the south periphery as within the crown of the tree. The humidity was also slightly higher. The periphery leaves of Fraxinus pennsylvanica lost from 3 to 6 times as much water as the leaves from the center of the tree, and of Ulmus americana about 12 times as much. He reports even greater thickness of south periphery leaves as compared to center leaves, than had heretofore been reported.

Boodle (3) reported hypoderm in leaves grown in dry and exposed situations.

Bergen (2) reports greater transpiration in sun leaves due to greater activity, which he attributes to the larger stems and bundles which can transfer more water to the greater evaporating surface of the thicker leaves.

Renner (21) states that the transpiration rate of small mature leaves is increased to much greater extent than that of large leaves.

The study of crop ecology made by Bruner and

Weaver (4) on Manchuria barley, Marquis spring wheat, and White Kherson oats at Lincoln in eastern Nebraska, at Phillipsburg in north central Kansas, and at Burlington in eastern Colorado, merits presentation of some of their conclusions. These three stations present a wide range of environmental conditions, chiefly in air and soil moisture, which become more xerophytic westward. They report that "Histological studies showed for plants at the progressively more xerophytic station, more stomata per unit area, thicker epidermal cell walls, smaller epidermal cells, shorter guard cells, less intercellular space, more compact chlorenchyma, and fewer vascular bundles in the cross section of the leaf, and also a smaller size of the leaf. The latter is due to the fact that the cells of the leaf are both fewer in number as well as smaller."

The work of Cannon (5) on the histology and morphology of the vegetation of the more arid portions of South Africe is very complete and gives quantitative measurements of structures as found in that environment. He found that epidermal cells vary greatly in size; in one case, Grewia cana, the epidermal cells of the dorsal side were 7.6 times larger than the cells directly opposite on the ventral side, and he brings out the fact that there is little uniformity among xerophytes in this connection, that the most striking single anatomical character common to perennials of an arid region is the heavy outer epidermal wall, and that this holds in most cases except in those where the leaf has a permanent cover of trichomes. He found that in some species the epidermis consists of more than one cell layer, while some had a hypoderm of one cell layer and in others it was several cells thick. He found much variation in the position of the guard-cells; in some cases they are above the surface of the leaf, some below and some flush, and he believes that the depth of the guard-cells depends chiefly upon the thickness of the outer epidermal wall. Trichomes were found in 12 of the 27 species whose leaves were studied, but their presence is not regarded as a characteristic particularly associated with an arid habitat.

Eames and MacDaniels (10) in their chapter on ecological anatomy, state that in structural adaptation to xerophytic conditions the most common modification is heavy cuticularization and extreme cutinization of epidermal and even subepidermal cells, and that many xerophytic plants may possess a hypoderm which may be cutinized in some cases but more often is lignified; sclerenchyma tissue is usually more pronounced in zerophytes as masses of fibres or stone cells usually arranged as layers between the mesophyll and the epidermis or hypodermis.

McDougall and Penfound (19) state, "....leaves in successively lower strata in a deciduous forest have larger cells, more intercellular space, less cuticle, a relatively poorer conducting system, and larger chloroplasts. The leaves of the lower strata are not necessarily thinner than those higher up."

Maximov (18) summarizes very thoroughly the important work of Zalenski (28) whose results run counter to many of the generally accepted theories. Zalenski's work deals with that phase of leaf modification which may have an important bearing on drought resistance. He found that the higher the attachment of the leaf to the stem, the stronger is the relative development of its venation, the greater the total length of vascular bundles, including the finest branches, per unit area of the leaf surface; the thicker the outer wall of both upper and lower epidermal cells, and the smaller the dimensions of all mesophyll cells. Maximov states that Zalenski's Law is, "that the anatomical structure of the individual leaves of one and the same shoot is, so to speak, a function of their distance from the root system". Maximov also found a higher transpiration rate from the higher leaves, and he sums up on the basis of his work and that of other workers: "all influences which result in a greatly increased loss of water by the plant, or a restricted supply of water to the developing leaves, lead to essentially similar changes of leaf

structure".
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structure". He states that xeromorphic plants are distinguished not by a lower but by a higher rate of transpiration and assimilation.

Alexandrov (1) described as an adaptation to xerophytic conditions, the parenchymatous conducting sheath which surrounds the veins of the leaf.

That plants do respond anatomically to xerophytic conditions is brought out by the investigators mentioned above. The general trend of xeromorphic stem modifications, as given by several investigators, appears to be an increase in development of periderm, sclerenchyma, phloem and xylem, and a decrease in pith in the drier habitats. The leaf responses appear to be an increase in percentage of palisade tissue with a corresponding decrease of spongy tissue, an increase in thickness of the cutin layer, increase in thickness of leaf, increase in venation, increase in number of stomata, and under extreme conditions a large increase in amount of conducting parenchyma, and lignification of epidermal walls. Practically no work has been done on the anatomical modifications of Rubus. These modifications may follow the general trend mentioned above, but differ in many particulars which should be known.

LEGEND FOR SYMBOLS USED IN TABLES 3 TO 8

The figures given in tables 3 to 8 represent an average of ten readings from five to ten sections. The abbreviations used in all the tables for histological measurement of stem material are: Cu., thickness of cutin; Col., number of rows of collenchyma in cortex; Ph., width of phloem; P. Per., width pericycle periderm; Rows P. Per., number of layers of pericycle periderm including the layers of endodermis; R. En., number of rows of endodermis; P. F., width of pericycle fibres; L. P. F., length of pericycle fibre groups tangentially; Cor., width of cortex excluding pericycle periderm measured opposite fibres; X., width of xylem; V., size of vessels; D., diameter of shoot; I. P. Per., the distance between the pericycle fibre groups; S. Ck., width of superficial cork; D. Cor., width of collenchyma and small thick-walled dense parenchyma of outer cortex.

Table 3*. Histological stem measurements of Rubus occidentalis L.

	Texas				Oklahoma			
	Plum Farmer				Plum Farmer			
	1928		1929		1928		1929	
	Microns	% of radius	Microns	% of radius	Microns	% of radius	Microns	% of radius
Cu.	3.7	0.08	6.5	0.14	2.5	0.08	6.0	0.16
Col.	-	-	9.0	-	4.0	-	4.3	-
Ph.	228.4	4.96	184.5	3.90	125.4	4.25	140.0	3.75
P. Per.	164.9	3.58	53.9	1.14	32.1	1.09	80.0	2.14
Rows P. Per.	18.0	-	6.0	-	4.0	-	9.2	-
R. En.	4.0	-	2.0	-	1.0	-	2.0	-
P. F.	28.7	0.62	53.7	1.14	39.1	1.32	43.2	1.16
L. P. F.	105.6	-	200.0	-	168.9	-	158.3	-
Cor.	162.4	3.53	192.5	4.08	139.9	4.74	124.5	3.33
X.	2696.3	58.60	1201.2	25.40	522.0	17.70	1444.3	38.70
V.	51.7	-	46.5	-	40.0	-	35.9	-
D.	9200.0	-	9440.0	-	5900.0	-	7470.0	-
I. P. Per.	-	-	61.2	-	76.8	-	185.6	-
Pith.	-	28.73	-	64.00	-	70.80	-	50.76
S. Ck.	0	-	0	-	-	-	0	-

*For explanation of symbols see legend on page 24.

Table 3. Continued.

Oklahoma				Michigan			
Cumberland				Cumberland			
1928		1929		1928		1929	
Microns	% of radius	Microns	% of radius	Microns	% of radius	Microns	% of radius
5.0	0.12	7.5	0.28	2.5	0.04	0.75	0.02
6.0	-	3.3	-	4.4	-	4.30	-
81.2	1.89	89.3	3.32	201.5	3.53	119.00	3.22
50.0	1.16	103.9	3.86	69.2	1.21	33.70	0.91
5.6	-	13.1	-	8.6	-	4.50	-
1.0	-	3.0	-	2.0	-	1.00	-
87.7	2.04	48.6	1.81	77.6	1.36	49.40	1.34
175.4	-	180.0	-	179.8	-	175.00	-
128.3	2.98	113.0	4.20	145.0	2.54	95.00	2.57
850.4	19.80	1000.3	37.20	1740.0	30.50	654.90	17.70
60.6	-	49.4	-	50.2	-	40.10	-
8600.0	-	5380.0	-	11,400.0	-	7390.00	-
80.5	-	119.4	-	118.9	-	65.60	-
-	72.01	-	45.13	-	60.80	-	74.24
0	0	113.0	4.20	-	0	-	0

Table 4*. Histological stem measurements of Rubus strigosus x Rubus innominatus

	Texas				Washington, D. C.	
	Van Fleet				Van Fleet	
	1928		1929		1929	
	Microns	% of radius	Microns	% of radius	Microns	% of radius
Cu.	S.Ck.	-	2.5	0.03	3.7	0.14
Ph.	284.2	4.06	307.7	4.30	170.2	6.25
Col.	S.Ck.	-	3.3	-	3.5	-
P. Per.	208.2	2.97	93.1	1.30	65.5	2.40
Rows P. Per.	25.3	-	10.4	-	6.2	-
R. En.	4.0	-	3.0	-	2.0	-
P. F.	60.2	0.86	85.0	1.19	55.9	2.64
L. P. F.	240.0	-	220.9	-	193.1	-
Cor.	397.3	5.67	334.5	4.69	197.9	7.27
X.	2876.8	41.10	3200.9	44.80	653.9	24.00
V.	60.0	-	79.7	-	53.6	-
D.	14,000.0	-	14,300.0	-	5440.0	-
I. P. Per.	274.8	-	171.9	-	78.1	-
S. Ck.	211.0	3.01	-	-	-	-
Pith	-	42.30	-	43.70	-	57.30

* For explanation of symbols see legend on page 24.

Table 5*. Histological stem measurements of the prostrate dewberries.

Rubus flagellaris var roribaccus Bail.

	Texas				Oklahoma			
	Lucretia				Lucretia			
	1928		1929		1928		1929	
	Microns	% of radius	Microns	% of radius	Microns	% of radius	Microns	% of radius
Cu.	5.0	0.14	2.5	0.07	5.0	0.18	5.0	0.22
Ph.	225.5	6.35	175.1	5.00	136.3	4.90	111.2	4.83
P. Per.	57.2	1.61	62.5	1.78	38.6	1.38	31.7	1.38
Rows P. Per.	5.5	-	5.4	-	3.6	-	3.5	-
R. En.	1.0	-	1.0	-	1.0	-	1.0	-
P. F.	75.1	2.11	77.5	2.21	77.2	2.76	71.9	3.13
Cor.	292.2	8.23	320.4	9.15	261.7	9.35	208.8	9.08
X.	1196.2	33.70	816.3	23.30	706.1	25.22	612.6	26.60
V.	86.5	-	96.4	-	72.6	-	78.2	-
D.	7100.0	-	7000.0	-	5600.0	-	4600.0	-
I. P. Per.	-	-	-	-	-	-	-	-
D. Cor.	164.6	-	-	-	131.9	-	-	-
S. Ck.	23.7	-	168.2	-	0	-	0	-
Pith	-	47.90	-	53.70	-	56.20	-	55.20

* For explanation of symbols see legend on page 24.

Table 5. Continued.

Rubus flagellaris geophilus Bail.

Michigan		Oklahoma			
Lucretia		Mayes			
1929		1928		1929	
Microns	% of radius	Microns	% of radius	Microns	% of radius
3.7	0.19	2.5	0.10	4.5	0.16
125.1	6.32	141.4	5.54	141.4	5.07
31.5	1.59	36.2	1.42	100.2	3.59
3.4	-	3.8	-	9.2	-
1.0	-	1.0	-	2.0	-
72.4	3.66	96.4	3.78	71.6	2.57
192.8	9.74	236.3	9.27	200.8	7.20
607.5	30.68	506.8	19.90	688.0	24.70
84.5	-	82.0	-	91.0	-
3960.0	-	5100.0	-	5580.0	-
73.7	-	-	-	-	-
-	-	105.8	-	162.4	-
0	-	-	-	-	-
-	47.80	-	60.00	-	56.70

Table 6*. Histological stem measurements of Rubus allegheniensis Bail.

	Michigan		Texas				Texas			
	Eldorado		Eldorado		Eldorado		Snyder		Snyder	
	1929		1928		1929		1928		1929	
	Microns	% of radius	Microns	% of radius	Microns	% of radius	Microns	% of radius	Microns	% of radius
Cu.	5.0	.12	3.7	0.13	6.2	0.13	8.7	0.25	6.2	0.13
Ph.	398.5	9.38	306.7	10.40	443.7	9.54	253.1	7.23	279.1	5.94
P. Per.	21.5	.50	53.6	1.81	49.6	1.07	44.0	1.26	44.1	.94
Rows P. Per.	3.0	-	5.2	-	4.2	-	5.1	-	5.5	-
R. En.	1.0	-	1.0	-	1.2	-	1.0	-	1.0	-
P. F.	77.6	1.82	38.6	1.31	173.3	3.73	90.0	2.57	131.2	2.79
Cor.	144.3	3.39	240.0	8.13	202.6	4.36	339.3	9.69	170.4	3.62
X.	1371.7	32.30	1613.1	54.70	2117.0	45.50	941.0	26.90	1534.1	32.60
V.	87.1	-	71.2	-	99.9	-	89.7	-	87.9	-
D.	8500.0	-	5900.0	-	9300.0	-	7000.0	-	9400.0	-
S. Ck.	0	-	0	-	0	-	0	-	0	-
D. Cor.	-	-	179.1	-	-	-	151.5	-	122.5	-
I. P. Per.	249.4	-	-	-	-	-	-	-	-	-
Pith.	-	52.50	-	23.50	-	35.60	-	52.10	-	54.00

* For explanation of symbols see legend on page 24.

Table 7**. Histological stem measurements of blackberry-dewberry hybrids

Rubus velox Bail.

	Texas				Oklahoma			
	McDonald				McDonald			
	1928*		1929		1928		1929	
	Microns	% of radius	Microns	% of radius	Microns	% of radius	Microns	% of radius
Cu.	3.7	0.17	3.75	0.08	2.5	.06	3.1	0.10
Ph.	245.0	11.40	268.50	9.20	321.2	7.83	173.2	5.77
P. Per.	20.1	.93	33.50	1.15	48.0	1.17	25.6	.85
Rows P. Per.	3.1	-	3.70	-	5.5	-	3.3	-
R. En.	1.0	-	1.00	-	1.0	-	1.0	-
P. F.	56.5	2.63	79.70	2.74	108.7	2.65	102.2	3.41
Cor.	138.5	6.44	132.60	4.56	303.8	7.41	202.3	6.74
X.	938.9	43.70	1180.30	40.60	1243.4	30.30	762.7	25.40
V.	47.9	-	75.10	-	92.9	-	81.4	-
D.	4300.0	-	5820.00	-	8200.0	-	6000.0	-
D. Cor.	100.5	-	100.00	-	145.7	-	100.0	-
S. Ck.	-	-	-	-	-	-	-	-
Pith	-	34.80	-	41.80	-	50.50	-	57.70

* Note: Just planted this year.

** For explanation of symbols see legend on page 24.

Table 7. Continued.

Rubus titanus Bail.

Oklahoma				Oklahoma			
Early Wonder				Mammoth			
1928		1929		1928		1929	
Microns	% of radius	Microns	% of radius	Microns	% of radius	Microns	% of radius
3.7	.09	2.5	0.06	2.5	0.07	3.75	0.11
256.9	6.19	173.3	3.98	247.2	6.96	267.50	7.87
35.1	.84	28.0	.64	28.9	.81	29.00	.85
4.0	-	3.8	-	3.0	-	3.90	-
1.0	-	1.0	-	1.0	-	1.00	-
118.9	2.86	116.0	2.67	89.9	2.53	84.80	2.49
195.7	4.71	266.1	6.12	275.5	7.76	192.00	5.65
1125.9	27.10	891.0	20.50	812.7	22.90	906.20	26.60
97.4	-	93.7	-	71.0	-	72.90	-
8300.0	-	8700.0	-	7100.0	-	6800.00	-
118.9	-	108.7	-	144.3	-	66.00	-
0	-	45.9	-	0	-	98.40	-
-	58.20	-	66.10	-	60.00	-	57.30

Table 8**. Histological stem measurements of red raspberries.

	Rubus strigosus				R. strigosus x R. idaeus			
	Michigan				Michigan			
	Cuthbert				Viking			
	1928		1929		1928		1929	
	Microns	% of radius	Microns	% of radius	Microns	% of radius	Microns	% of radius
Cu.	-	-	2.5	0.08	3.7	0.06	3.7	0.07
Ph.	186.5	3.39	189.9	5.84	280.6	4.38	189.9	3.76
Col.	-	-	-	-	5.0	-	3.0	-
P. Per.	141.9	2.58	61.6	1.89	92.5	1.44	63.1	1.25
Rows P. Per.	17.6	-	7.1	-	11.6	-	9.1	-
R. En.	5.0	-	3.0	-	2.0	-	3.0	-
P. F.	60.0	1.09	63.3	1.95	100.8	1.57	73.9	1.46
L. P. F.	202.3	-	297.2	-	200.8	-	211.7	-
Cor.	-	-	233.4	7.18	145.0	2.26	116.7	2.31
X.	1962.6	35.70	1306.4	40.20	1787.1	27.90	1429.0	28.30
V.	52.0	-	61.9	-	57.2	-	59.7	-
D.	11,000.0	-	6500.0	-	12,800.0	-	10,100.0	-
D. Cor.	-	-	102.2	-	120.3	-	41.3	-
I. P. Per.	208.1	-	190.7	-	124.0	-	232.7	-
S. Ck.	0	-	0	-	0	-	0	-
Pith.	-	-	-	42.90	-	62.40	-	62.80

** For explanation of symbols see legend on page 24.

Table 8. Continued

Rubus strigosus

Oklahoma		Michigan	
St. Regis*		Latham	
1929		1929	
Microns	% of radius	Microns	% of radius
1.2	0.05	5.0	0.12
101.5	3.79	167.5	4.04
3.0	-	-	-
101.4	3.79	79.7	1.92
10.2	0	9.0	-
3.0	-	3.0	-
33.4	1.25	50.7	1.22
-	-	217.5	-
189.2	7.07	168.9	4.07
776.5	29.00	1404.3	33.80
48.9	-	67.1	-
5350.0	-	8300.0	-
118.2	-	121.8	-
Cont.	-	142.1	-
0	55.00	-	54.80

* Planted in the spring of this year.

Part I. PRESENTATION OF STEM DATA

The data on the histological measurements of the one year shoots of the different species of Rubus are given in tables three to eight inclusive. The data for each tissue will be presented separately to compare the degree of xeromorphic modification of this tissue in the different species in each habitat and for the two different seasons in the same habitat. These tables will be found at the beginning of this section, hence, further reference to tables will not be given in the following discussion.

CUTIN

The data show no consistent increase in thickness of the cutin layer on Rubus occidentalis L. in the progressively drier habitats; however, there is a considerable increase in thickness during the drier season of 1929 in the same habitats for the Oklahoma and Texas varieties. Likewise, there was no consistent development of a thicker cutin layer on the prostrate dewberries (Rubus flagellaris), the semi-prostrate blackberry-dewberry hybrids (Rubus velox Bail., Rubus titanus Bail.), or the blackberries (Rubus allegheniensis Bail.), in the drier habitats because of the tendency to form superficial periderm in the more xerophytic habitats.

CORTEX

The histological data show that there is a tendency for Rubus flagellaris Bail. and Rubus occidentalis L. to form a greater width of cortex, both in actual width and on the basis of the percentage of the stem's radius, in the progressively drier habitats. Rubus occidentalis L. shows a more consistent increase of cortex when compared on the percentage of radius basis, whereas Rubus flagellaris Bail. shows a more consistent increase in actual width. Rubus occidentalis L. and Rubus flagellaris Bail., grown in the more xerophytic habitats, developed more layers of collenchyma which had heavier walls than those grown in the more mesophytic habitats. The stem stomata of the prostrate Lucretia dewberry (Rubus flagellaris roribaccus Bail.), show some noticeable modifications. In the Michigan habitat the stomata appeared at regular intervals around the stem opposite the vascular rays, and no thick walled collenchyma had formed beneath them. The Oklahoma stems during the same season had fewer stem stomata with a heavier cutin deposit on them and the vascular rays beneath them had become lignified, indicating that the stomata ceased to function much earlier in Oklahoma than in Michigan. The stomata were evident only on the lower side of the Texas stems as superficial periderm had formed on the upper exposed side. Below these stomata the vascular ray cells were heavily lignified and there had been one to three extra layers of pericycle periderm laid down. These stomata evidently ceased to function very early in the season. One to two layers of collenchyma had formed under the stomata in Texas, one row in Oklahoma, and none in Michigan.

The Van Fleet (Rubus innominatus x Rubus strigosus), developed a smaller percentage of cortex in Texas than at Washington D.C., although the actual width in the latter habitat was less. The actual width and percentage were less in the drier year of 1929 in the Texas habitat. The number of rows of collenchyma remained fairly constant although the walls were much thicker in the more xerophytic habitats. Rubus allegheniensis Bail., Rubus velox Bail., and Rubus titanus Bail., likewise formed less cortex both in actual width and on the percentage of the stem's radius during the drier years in the same habitat. However, Eldorado, an upright blackberry, formed less cortex in Michigan than in Texas but in the latter habitat there was a great deal less formed in the drier year. Another exception was Mammoth (Rubus titanus Bail.), a western dewberry hybrid, which formed less cortex during the drier year in the Oklahoma habitat. The blackberries and blackberry-dewberry hybrids tended to form more rows of collenchyma with heavier walls in the drier season and in the more xerophytic habitats. The cortical cells of the McDonald hybrid (Rubus velox Bail.), were filled with countless minute droplets of a brownish tannin-like substance which appeared to be similar to the deposits in the secondary and tertiary endodermis of the pericycle periderm. The blackberries and blackberry-dewberry hybrids tended to form fewer stem stomata in the more xerophytic habitats. There were usually three to four rows of thick walled collenchyma developed under these stomata in Texas, one to two in Oklahome, and none or one in the Michigan habitat.

PERICYCLE PERIDERM

Environment does not appear to have had any appreciable effect on the development of pericycle periderm in Rubus occidentalis. In the Plum Farmer shoots there was more pericycle periderm laid down during the less severe year in Texas but considerably more during the drier year in Oklahoma. Cumberland developed more during the drier year of 1929 in Oklahoma, but in 1928 there was less developed than during the same season in Michigan. Van Fleet (Rubus innominatus x Rubus strigosus), did develop considerably more pericycle periderm in the Texas habitat than at Washington D.C., and there was a layer of tertiary endodermis formed in the Texas stems. At this point the significance ends because there was twice as much pericycle periderm laid down in the Texas habitat during the year of less severe atmospheric drought.

There was considerably more pericycle periderm laid down in the stems of the Texas Lucretia (Rubus flagellaris roribaccus Bail.), than in the Oklahoma stems, but no appreciable difference between that developed in Oklahoma and Michigan. Likewise, there was no consistency in the differences in the amounts developed during the different seasons in the same habitat. Mayes (Rubus flagellaris geophilus Bail.), did develop considerably more pericycle periderm during the drier year in Oklahoma and there was a layer of secondary endodermis formed, the only member of Eubati in which this occurred.

Although there was a considerably greater development of pericycle periderm in the shoots of the high bush blackberry (Rubus allegheniensis Bail.), in the more xerophytic habitat, the lack of consistency of greater development in the drier years in the same habitat would indicate that atmospheric drought conditions do not influence the development of this tissue in this particular species. Likewise, there were no significant differences in the development of pericycle periderm in the blackberry-dewberry hybrids (Rubus velox Bail., and Rubus titanus Bail.), due to environmental conditions.

PERICYCLE FIBRE GROUPS AND THE TYPE OF INTERVENING TISSUE

The data show that there is a slight increase in the size of pericycle fibre groups both transversely and longitudinally in the progressively drier habitats for the varieties of Rubus occidentalis L. The Plum Farmer variety showed much more consistency in this respect than Cumberland since the latter variety developed wider groups in the less severe of the two years in Oklahoma. There are noticeable differences in the continuity of the fibre ring as shown by an average of eight rows of intervening vascular ray cells between the groups in the Oklahoma stems, whereas, there were only four rows present between the groups in the Texas stems. Van Fleet (Rubus innominatus x Rubus strigosus), likewise, formed wider groups in the Texas as compared to the Washington habitat, but these groups were further apart at the former station with a great deal more vascular ray tissue between them;

hence a less continuous ring was formed.

Whereas there were no significant differences in the width of the pericycle fibre groups in either year for Lucretia (Rubus flagellaris roribaccus), in any of the habitats, there were some marked differences in the type of tissue between the fibre groups. In 1929 the fibre groups did not tend to form a continuous ring in the Michigan stems. The vascular ray cells were normal, even though the walls had thickened somewhat, but in the Oklahoma stems small groups of new fibres had formed in the vascular ray region and only one or two rows of vascular ray cells extended outward between them. The amount of vascular ray tissue in the Oklahoma stems was only a small fraction of that in the Michigan. In the Texas stems the fibre groups formed a continuous ring. In most cases the main fibre groups had been connected by a single layer of fibres, in other cases the vascular ray cells had changed over into stone cells (plage 2), and in rare cases where fibres or stone cells had not connected the fibre groups the vascular ray cells had become thick-walled and heavily lignified. This condition was found in the Texas stems under the superficial cork, which indicated that this condition arose early before superficial cork was formed. This same condition held somewhat for the 1928 season, although in the Oklahoma habitat only a few stone cells were developed. However, there were present a large number of the intermediate stage between vascular ray cells and stone cells. More stone cells were formed in the Texas material but there seems to have been a greater tendency in the dewberry to throw new fibres across this region in 1928. The vascular ray cells inside this region in the Texas stems were full of crystals.

The upright blackberry Eldorado (Rubus alleg-heniensis Bail.), formed larger pericycle fibre groups in the xerophytic habitat and Snyder formed larger groups in the drier of the two seasons in the same habitat. The most significant difference be-tween the Michigan and the Texas Eldorado, in relation to the fibre groups, was that the vascular ray cells in the Texas stems were changed into stone cells al-most entirely and formed a continuous sclerenchyma ring. There were no stone cells formed in the Michigan Eldorado. Snyder developed stone cells between the groups as well as new fibres in both seasons. The remarkable thing about the fibres in Snyder is that in many cases new pericycle fibres almost replaced the phloem, leaving only a narrow strip of seive tubes on each side. This latter case was found in both 1928 and 1929. On the other hand, the blackberry-dewberry hybrids (Rubus velox Bail., Rubus titanus Bail.), showed no appreciable increase in size of fibre groups in the drier habitats or seasons, but the type of tissue between the pericycle fibre groups showed some interesting differences. During the 1929 season the vascular ray region of the Texas McDonald between the pericycle fibre groups was changed into stone cells in most cases. In the other cases the intermediate stage was reached which consisted of very thick walled lignified cells which were not as yet pitted. In the same variety in Oklahoma no stone cells were found in this region, but one to two rows of partly lignified cells were formed through the vascular tissue. In Early Wonder during the same season in Oklahoma the vascular ray cells in this region were very much larger than in the McDonald but were not lignified, although they were thicker walled than the vascular ray cells beneath them. During the 1928 season more or less the same condition observed in the 1929 material was found with a few variations. The McDonald in Oklahoma in 1928 developed no stone cells but thick walled partly lignified cells were formed and in addition a layer of one to two rows of new fibres were laid down across this region. The Texas McDonald formed stone cells but in addition new rows of fibres were laid down across the vascular region which, with the stone cells, formed a continuous sclerenchyma ring.

PHLOEM

The Plum Farmer variety of Rubus occidentalis L. developed slightly more phloem in Texas than in Oklahoma, both in actual width and on the percentage basis. Cumberland, belonging to the same species, actually developed less phloem in the Oklahoma habitat than in Michigan. It is quite evident that the inexplicable variations from season to season in the same habitat, and in one case those found in two different habitats (Oklahoma and Michigan), would indicate lack of any uniform xeromorphic modification of this tissue in the black raspberries studied. On the other hand, the purple raspberry (Rubus innominatus x Rubus strigosus), developed considerably more phloem, in actual width, in the Texas as compared to the Washington habitat, and slightly more in the Lubbock habitat during the drier season, (plate 3). The percentage of the stem's radius which was made up of phloem was slightly larger in the Washington stems, probably because of the much smaller stem diameter.

The Lucretia dewberry (Rubus flagellaris roribaccus Bail.) grown in all three habitats showed a consistent increase in actual amount of phloem in the progressively drier habitats, but more phloem was developed during the less severe year in both Texas and Oklahoma, (plate 2). Mayes, belonging to the same species, developed practically the same amount during both seasons in the single habitat in which it was grown. These inexplicable seasonal variations within the same habitat indicate that atmospheric conditions do not seriously affect the formation of phloem in the prostrate dewberries.

Rubus allegheniensis Bail., the high bush blackberry, was the only species which showed consistent increase of phloem tissue in the progressively drier habitats and during the drier season in the same habitat. The blackberries developed from two to three times more phloem than the black raspberries in the same habitat. The blackberry-dewberry hybrids (Rubus velox Bail.) developed considerably less phloem during the drier season in Oklahoma but the percentages were notably higher. McDonald developed more phloem in Texas than in Oklahoma during 1929. This variety was planted in the spring of 1928 in Texas, and it is interesting to note that it developed twice as much phloem during its first season as was developed by Plum Farmer (Rubus occidentalis L.) during its first season in Oklahoma. Rubus titanus Bail. developed more phloem in Oklahoma during the season of greater atmospheric drought.

XYLEM

The amount of xylem developed in the black raspberries (Rubus occidentalis L.) did not appear to depend solely upon climatic conditions. There was a considerable increase in the amount of xylem developed in the Texas Plum Farmer stems as compared to those of this variety grown in Oklahoma. Cumberland, grown in Oklahoma and Michigan, did not show an appreciable increase of xylem development in 1928 in Oklahoma, but there was a considerable increase of this tissue during 1929 in this habitat. There was a slight increase in size of vessels in the progressively drier habitats, but there was a slight decrease in the size of vessels during the drier year in the same habitat. There was, however, a uniform increase in number of vessels per unit area in the progressively drier habitats. However, the purple raspberry Van Fleet (Rubus innominatus x Rubus strigosus) showed a considerable increase in the amount of xylem developed in Texas as compared to Washington with a significant increase in number of vessels per unit area, (plate 3). There was a slight increase in the percentage development and in actual amount during the more xerophytic season in Texas. The xylem tissue of this vigorously growing variety appeared to be influenced by its environmental conditions much more than the black raspberries. In the dewberries (Rubus

flagellaris Bail.) there was a slight increase in the actual width of xylem in the progressively drier habitats during 1929, (plate 2). However, there was a slight decrease in the actual amount during the drier year in the same habitat for the Oklahoma and Texas stations. Mayes, belonging to the same species, did develop a larger amount of xylem, both in actual width and on the percentage basis, during the drier year in the one habitat in which it was grown.

In the upright exposed shoots of the Eldorado and Snyder blackberries (Rubus allegheniensis Bail.) there was a very significant increase in the amount of xylem developed, both in actual microns and on the basis of the percentage of the stem's radius, in the progressively drier habitats and during the most severe season in the same habitat. Along with this increase in xylem development there was a slight increase in size of vessels and a very significant increase in number of vessels per unit area.

The semi-upright blackberry-dewberry hybrids (Rubus velox Bail. and Rubus titanus Bail.) did not show the degree of xylem modification that was found in the high bush blackberries. There was a small increase of xylem development in the Texas McDonald over that of Oklahoma in 1929. This increase is not apparent in 1928 as this was the first growing season for McDonald. There was, nevertheless, a slight decrease in xylem development in the Oklahoma habitat during the drier year for McDonald and Early Wonder. Mammoth (Rubus titanus Bail.), however, showed a slight increase during the drier year in the same habitat. The size of vessels in these hybrids does not show any uniform variations. All members of the sub-species Eubati developed more xylem vessels in the progressively drier habitats and during the drier season of the same habitat, (plate 3).

SUPERFICIAL PERIDERM

Plum Farmer did not develop superficial cork in either Texas or Oklahoma. Cumberland, however, which belongs to the same species, developed a layer of superficial cork in the Oklahoma habitat in 1929 which covered about 20 per cent of the stem's circumference and averaged 113 microns in width. No superficial cork was found on the stems in the latter habitat in 1928 nor in Michigan in either year. There was no superficial cork developed on Van Fleet (Rubus strigosus x Rubus innominatus) as a layer in either the Texas or Washington habitat in 1929. There were occasional sections of the stem that had been split in the Texas habitat and these had been covered over with superficial cork. In one case of the latter type a group of fibres was present surrounded by cork. In 1928 the Van Fleet in Texas developed a very heavy layer of superficial cork entirely around the stem, and it averaged 211 microns in width.

The most outstanding anatomical modification for the Lucretia dewberry (Rubus flagellaris Bail.) was in the superficial cork which was developed on the upper exposed surface of the stems in Texas (plate 2), and which did not occur in either of the other two habitats. It is also significant that the amount developed in the less severe year of 1928 was only 36 per cent as thick as that developed in 1929. The Mayes dewberry which belongs to the same species did not develop superficial cork in Oklahoma during either year.

The blackberries Eldorado and Snyder which belong to Rubus allegheniensis did not develop superficial cork in any of the habitats during either season. McDonald and Early Wonder blackberries (Rubus velox Bail., and Rubus titanus Bail.) gave some very striking modifications during 1929. The Texas McDonald showed the periderm deposits all through the cortex which has been described under cortex. This same variety in Oklahoma did not show this condition nor was there any regular layer of superficial periderm formed. Early Wonder in Oklahoma did show some superficial cork on about 25 per cent of the stem's circumference. It was spotted, however, and not a regular continuous layer. These spots averaged 46 microns in width. Mammoth in Oklahome developed a layer of superficial cork during the 1929 season that averaged 98.4 microns in width. There was no superficial cork developed during 1928.

PITH AND STEM DIAMETER

There appeared to be no consistent modifications of the percentage of pith due to climatic conditions in the stems of the two varieties of Rubus occidentalis which were grown. Plum Farmer in Texas developed a higher percentage in 1929 but a lower percentage in 1928 than that developed in Oklahoma. Cumberland in Oklahoma developed a lower percentage in 1929 but a higher percentage in 1928 than that developed in Michigan. There was a considerable increase in the diameter of the Plum Farmer shoots in the Texas as compared to the Oklahoma habitat in both seasons and a slight increase during the drier year in the same habitat. This was not the case with Cumberland which developed larger stems in the Michigan as compared to the Oklahoma habitat during both seasons. Likewise, there was a decrease in diameter during the drier year in the Oklahoma habitat for this variety. The stems of Van Fleet (Rubus innominatus x Rubus strigosus) developed a higher percentage of pith in the Washington than in the Texas habitat, and the percentage of the latter station remained fairly constant during both seasons. The diameter of the Texas shoots was nearly three times that developed at Washington D.C.

The differences in the amount of pith developed in the stems of the dewberries (Rubus flagellaris) in the three habitats were no greater than would be expected, due to the probable error in sampling. There was a considerable increase in the diameter of the shoots in the progressively drier habitats. There was a slight decrease in the diameter during the drier year in Oklahoma for Lucretia but a slight increase for Mayes. The blackberries (Rubus allegheniensis Bail.) and blackberry-dewberry hybrids (Rubus velox Bail.) do show a significant decrease in percentage of pith in the more xerophytic habitats. Although there was a decrease in the drier habitats, there was a uniform increase in percentage during the drier year in the same habitat. The upright blackberries (Rubus allegheniensis Bail.) consistently developed larger stems during the same year in the drier habitats and during the drier season in the same habitat. This was not the case with the blackberry-dewberry hybrids (Rubus velox Bail., and Rubus titanus Bail.). These showed inexplicable variations in stem diameter during the two seasons in the same habit, and in the different habitats.

The data for the red raspberries (Rubus strigosus Michx.) are given in table 8, and with one exception they were all grown in the Michigan habitat. The two seasons in Michigan were quite comparable and therefore the tissue modifications can hardly be attributed entirely to environmental conditions. Latham was the only variety of the red raspberries that developed stem stomata. Ranere or St. Regis, grown in Oklahoma during 1929, was the only red variety grown in either of the two southern habitats. A comparison of the stem data of St. Regis with that of Cuthbert brings out some very interesting differences. The width of the pericycle periderm of Viking and Cuthbert in Michigan was only three-fifths that laid down in the newly planted St. Regis in Oklahoma. The primary and secondary endodermis were completely filled with heavy deposits and the size of the cells was greater than in varieties of the same species in Michigan. The cells of the tertiary endodermis of the St. Regis were extremely large, as compared to those of Cuthbert in Michigan, and the walls were covered with very heavy deposits of some substance which appeared to be suberin. The cortex outside the pericycle periderm layer appeared to be dead, as though the periderm had cut off moisture and plant foods before the end of the first season.

LEGEND FOR SYMBOLS USED IN TABLES 9 TO 12

The interpretations of the symbols which are used in tables 9 to 12 are as follows: W. Pal., the depth of the palisade tissue in the cross section of the leaf measured in microns; % Pal., the percentage of palisade; W. Sp., the depth of the spongy tissue in the cross sections of the leaf measured in microns; % Sp., the percentage of spongy tissue; T. Ep., the transverse diameter of the upper epidermal cells in the cross section of the leaf measured in microns; L. Ep., the transverse diameter of the lower epidermal cells in the cross section of the leaf measured in microns; T. Lf., the thickness of leaf measured in microns.

Table 9*. Histological leaf data of black and purple raspberries grown in different habitats.

Rubus occidentalis L.

	Cumberland		Cumberland		Plum Farmer		Plum Farmer		Unknown	
	1928	1928	1929	1929	1928	1928	1929	1929	1928	1929
	Mich.	Okla.	Mich.	Okla.	Okla.	Tex.	Okla.	Tex.	Tex.	Tex.
W. Pal.	58.6	38.7	54.7	36.2	57.2	77.2	61.9	81.5	45.6	52.9
% Pal.	49.4	45.5	49.4	52.5	49.5	53.7	47.1	60.4	46.2	46.8
W. Sp.	36.5	21.1	34.2	10.1	31.1	37.5	40.9	29.9	28.0	30.4
% Sp.	30.7	24.8	31.1	14.6	26.9	26.1	31.1	22.2	28.4	26.9
T. Ep.	15.9	15.9	13.6	13.1	17.7	15.5	17.4	13.9	16.1	18.7
L. Ep.	7.7	9.4	7.9	9.5	9.5	13.6	11.1	9.5	8.9	11.1
T. Lf.	118.7	85.1	110.6	68.9	115.5	143.8	131.3	134.8	98.6	113.1

* For explanation of symbols see legend on page 53.

Table 9. Continued.

Rubus strigosus x
R. innominatus

New Logan		Van Fleet		Van Fleet	
1928	1929	1928		1929	1929
Mich.	Mich.	Tex.		Tex.	Wash.
42.9	42.1	52.9		60.9	41.5
47.3	53.1	44.4		50.7	40.4
27.1	19.1	41.1		31.6	38.0
30.0	24.1	34.5		26.3	37.0
13.0	11.0	16.6		16.7	14.9
7.7	7.1	8.4		10.9	8.2
90.7	79.3	119.0		120.1	102.6

Table 10*. Histological leaf data of dewberries and blackberries.

	Rubus flagellaris roribaccus Bail.					var. geophillus Bail.		Rubus allegheniensis Bail.				
	Lucretia		Lucretia			Mayes		Eldorado			Snyder	
	1928	1928	1929	1929	1929	1928	1929	1928	1929	1929	1928	1929
	Okla.	Tex.	Mich.	Okla.	Tex.	Okla.	Okla.	Tex.	Tex.	Mich.	Tex.	Tex.
W. Pal.	43.5	54.2	37.9	85.7	95.5	80.2	67.2	102.4	101.9	71.7	78.6	81.7
% Pal.	34.4	38.7	33.3	46.1	48.9	50.7	48.3	47.8	57.1	49.5	42.8	47.9
W. Sp.	47.6	43.4	50.6	53.9	53.5	37.7	31.5	74.2	41.1	38.0	62.7	52.2
% Sp.	37.6	31.0	44.5	29.0	27.4	23.9	22.7	34.6	23.0	26.2	34.2	30.6
T. Ep.	22.0	28.7	13.6	28.9	30.1	25.6	26.2	25.6	24.1	23.2	28.4	24.7
L. Ep.	13.5	13.7	11.7	17.2	16.2	14.5	14.1	12.1	11.4	11.9	13.7	11.9
T. Lf.	126.6	140.0	113.8	185.7	195.3	158.0	139.0	214.3	178.5	144.8	183.4	170.5

* For explanation of symbols see legend on page 53.

Table 11*. Histological leaf data for the blackberry-dewberry hybrids.

	Rubus velox Bail.						Rubus titanus Bail.			
	McDonald				Early Wonder		Mammoth		Jordan	
	1928	1928	1929	1929	1928	1929	1928	1929	1928	1929
	Okla.	Tex.	Okla.	Tex.	Okla.	Okla.	Okla.	Okla.	Okla.	Okla.
W. Pal.	67.7	78.9	83.5	85.1	81.9	99.5		89.9	71.6	88.0
% Pal.	45.2	50.0	50.7	52.1	47.4	55.3		53.8	43.3	56.1
W. Sp.	48.9	43.2	45.0	36.6	51.0	36.5		40.7	54.2	32.2
% Sp.	32.6	27.4	27.3	22.4	29.5	20.3		24.3	32.7	20.5
T. Ep.	22.6	23.1	23.6	27.4	26.9	29.7		24.5	26.9	24.5
L. Ep.	10.6	12.4	12.6	14.2	12.9	14.1		12.1	12.7	12.0
T. Lf.	149.8	157.6	164.7	163.3	172.7	179.8		167.2	165.4	156.7

* For explanation of symbols see legend on page 53.

Table 12*. Histological leaf data for red raspberries.

Rubus strigosus Michx.

	Cuthbert		Viking		St. Regis	Latham
	1928	1929	1928	1929	1929	1929
	Mich.	Mich.	Mich.	Mich.	Okla.	Mich.
W. Pal.	54.5	60.5	57.0	60.2	38.6	69.2
% Pal.	50.4	51.3	45.1	50.5	44.5	52.3
W. Sp.	28.6	32.1	38.6	36.4	24.4	40.4
% Sp.	26.4	27.2	30.6	30.5	28.1	30.5
T. Ep.	14.7	16.1	20.2	13.6	15.6	14.6
L. Ep.	10.4	9.2	10.4	9.1	8.2	8.2
T. Lf.	108.2	117.9	126.2	119.3	86.8	132.4

* For explanation of symbols see legend on page 53.

Part II. PRESENTATION OF LEAF DATA

Histological leaf data are presented in tables 9 to 12 inclusive and represent an average of 10 measurements taken from at least five slides. These tables will be found at the beginning of this section, hence further reference to tables will not be given in the following discussion.

PALISADE AND SPONGY TISSUE

The four varieties of Rubus occidentalis L. show distinct xeromorphic modifications of mesophyll in the progressively drier habitats and during the drier season in the same habitat. The variations among the varieties are not in the type but in the degree of modification. In Cumberland, however, the actual amount and percentage of palisade tissue was slightly higher in the 1928 Michigan leaves, but the decrease in percentage of spongy tissue in the Oklahoma leaves was considerable. The percentages are much better compartive values as the Oklahoma leaves of Cumberland were much thinner in both seasons than those of Michigan. The Plum Farmer leaves developed uniformly higher percentages of palisade tissue in the Texas habitat than they did in Oklahoma with a correspondingly greater decrease of spongy tissue, and in the 1929 Texas leaves a layer of hypodermis was formed (plate 4). All varieties of Rubus occidentalis L. developed more layers of shorter and more compact palisade cells, and the chloroplasts were smaller and more numerous in the leaves grown in the more xerophytic habitats (plate 4). Van Fleet (Rubus innominatus x Rubus strigosus), during 1929, likewise, developed a great deal more palisade tissue in Texas, both in actual amount and on the percentage basis, than it did at Washington D.C. The layers of palisade cells and chloroplasts were more numerous, and the sponge cells were much more compact in the 1929 Texas leaves than in those of Washington (plate 4) or the 1928 Texas leaves.

The Lucretia dewberry (Rubus flagellaris roribaccus Bail.) not only developed a higher percentage of palisade tissue, but also a greater actual width, in the progressively drier habitats and drier seasons in the same habitat. There was a corresponding decrease in percentage of spongy tissue and the latter was much more compact (plate 5). There was a slight increase in percentage of palisade but no significant difference in percentage of spongy tissue in the 1929 as compared to the 1928 Mayes (Rubus flagellaris geophilus Bail.) grown only in Oklahoma. There was one row of palisade cells and very loose spongy tissue in the 1929 Michigan Lucretia leaves, and the palisade was not perpendicular to the epidermis (plate 5). There were two fairly uniform rows in the Oklahoma and two very compact uniform rows in the

Texas leaves. The sponge cells were much denser in the Texas than in the Oklahoma or Michigan leaves (plate 5).

The high bush blackberries (Rubus allegheniensis Bail.) developed a uniformly higher percentage of palisade tissue in the drier habitats and during the drier years. The palisade cells, chloroplasts and sponge cells were much more compact in the drier habitat and during the drier season in the same habitat (plate 6). The Texas Eldorado leaves had three and often four rows of palisade as compared to two for the Michigan leaves (plate 6).

All of the blackberry-dewberry hybrids (Rubus velox Bail. and Rubus titanus Bail.) showed a slight increase in actual amount, and in percentage, of palisade tissue and slight decrease in percentage of spongy tissue in the drier habitats and during the drier season in the same habitat. It is of interest to note that there were no significant differences between the percentages of palisade or spongy tissue of any of the semi or upright species of Rubus in the same habitat during the same season. The drought resistant blackberry-dewberry hybrids did not show the extreme xeromorphic modifications of mesophyll that were found in some of the stem tissues where these species were compared to other less drought resistant species in the same habitat.

There were no significant differences in the type or amount of mesophyll in the leaves of the varieties of Rubus strigosus grown in Michigan or of the one variety

(St. Regis) grown in Oklahoma. The two seasons in Michigan showed no appreciable differences in climatic factors and therefore no significant anatomical differences should be expected.

EPIDERMAL CELLS

There were no significant differences in the transverse diameter of the top epidermal cells, in the leaf cross section, that could be attributed to climatic influences for the leaves of Rubus occidentalis L. The cells did, however, appear to be slightly shorter in the drier habitats,(plate 4). There appeared to be a slight increase in the diameter of the lower epidermal cells in the drier habitats but the size of these cells remained fairly constant in the same habitat during both seasons. There was a thin layer of cutin on the top epidermis of the Michigan Cumberland, whereas, this variety in Oklahoma developed fairly heavy layers of cutin on both epidermises. There was a uniform increase in the thickness of cutin layer on the upper and the development of a cutin layer on the lower epidermis in the drier habitats and also during the drier season. The walls of the upper epidermis were much thicker and were lignified in the xerophytic habitat, (plate 4). The upper epidermal cells of Van Fleet (Rubus innominatus x Rubus strigosus), however, were slightly larger in the

Texas leaves than in those from Washington, but were approximately the same size in the Texas leaves during both seasons, (plate 4). The lower epidermal cells were slightly larger in the drier habitat and during the drier season. There were no cutin layers developed on either epidermis in the Washington habitat, whereas, in Texas a very heavy cutin layer was developed on the upper epidermis and the cells themselves had heavy, lignified walls, (plate 4). There was no cutin layer on the lower epidermis of the Texas leaves in either year due, perhaps, to the heavy coating of hairs.

The size of the upper epidermal cells of the prostrate dewberries (Rubus flagellaris Bail.) was uniformly larger in the progressively drier habitat and slightly larger during the drier season in the same habitat, (plate 5). The size of the lower epidermal cells, however, showed no appreciable differences that could be attributed to climatic influences. There was a uniform increase in thickness of the cutin layer on the upper epidermis in the progressively drier habitats with lignification of the walls in the Texas habitat, (plate 5). The walls were much thicker and more heavily lignified during the drier season in the Texas habitat. There was no cutin layer on the lower epidermis of the Michigan leaves, a thin layer on the Oklahoma, and a fairly thick layer on the Texas leaves during 1929. There was no cutin deposited on the lower epidermis of the Texas or Oklahoma leaves in 1928.

There were no appreciable differences in the size of either the upper or lower epidermal cells of the blackberries (Rubus allegheniensis Bail.) or the blackberry-dewberry hybrids (Rubus velox Bail. and Rubus titanus Bail.), that could be attributed to climatic differences. There was a uniform increase in thickness of the cutin on the upper and lower epidermis in the drier habitats and during the drier season in the same habitat, (plate 6). There was a uniform increase in the wall thickenings of the upper epidermal cells and an increase in the amount of lignification which is a characteristic xeromorphic modifications.

St. Regis, the only variety of Rubus strigosus Michx. grown in Oklahoma, did not develop epidermal cells any larger than other varieties of the same species in Michigan. A fairly heavy cutin layer was developed on both epidermises of St. Regis in Oklahoma, whereas, Cuthbert in Michigan developed none. Latham was the only red raspberry that developed cutin on both epidermises in Michigan, and Viking developed a thin layer on the upper epidermis.

BUNDLES AND CONDUCTING PARENCHYMA

The bundles and conducting parenchyma of Rubus occidentalis showed some interesting xeromorphic modifications, (plate 6). The number of bundles in the cross section of the leaf developed during 1928 was 30 per cent greater in the Oklahoma Cumberland than in Michigan. The Michigan bundles had a conducting sheath of a single layer around the bundles, whereas, in the Oklahoma leaves the conducting parenchyma not only extended around the bundles but also extended from the upper to the lower epidermis. In 1929 there was about the same percentage difference in the number of bundles between Oklahoma and Michigan and in the amount of conducting parenchyma. There were about 25 per cent more bundles in the Oklahoma leaves in 1929 than in 1928, although the difference in amount and type of conducting parenchyma was not significant. The leaves of Plum Farmer developed about 20 per cent more bundles in Texas during 1928 than in Oklahoma. There was a single layer of conducting tissue around the bundles in Oklahoma, whereas, in Texas the cells were much larger and two to three layers surrounded the bundles and extended from upper to lower epidermis. The same relationship of bundles and conducting tissue was found in 1929 between the two habitats as was the case in 1928. There was a slight increase in number of bundles and size of conducting parenchyma in 1929. Approximately the same type and number of bundles were found in the 1929 and 1928 Oklahoma leaves, although the bundles themselves were slightly larger in 1929.

In Texas the 1929 conducting tissue was approximately the same as in 1928. However, in 1929 the conducting tissue appeared to be connected with the hypoderm. There was a slight increase in size and number of bundles in 1929.

In Texas the conducting parenchyma around the bundles was larger and more numerous in the leaves of the Unknown variety (Rubus occidentalis L.) during 1929 than in 1928. The number of bundles was about 35 per cent greater in 1929. The conducting tissue extended from upper to lower epidermis in the leaves of both seasons.

Van Fleet (Rubus innominatus x Rubus strigosus) in Texas during 1929 developed about 35 per cent more bundles and they were larger than those developed in Washington D.C. the same season. The bundles in the Washington leaves were surrounded by a single layer of conducting parenchyma and a single row extended to the upper epidermis. In the Texas leaves there were two or three layers of conducting parenchyma around the bundles and two rows extended to the upper epidermis. In most cases all the cells between the bundles and the lower epidermis were conducting parenchyma cells. The number of bundles developed in the 1928 Texas leaves was only 40 per cent of that developed in 1929. The bundles were also slightly smaller in 1928.

During the 1929 season the bundles of Lucretia (Rubus flagellaris roribaccus Bail.) in Michigan were small and they were located towards the bottom of the leaf. In Oklahoma the bundles were much more numerous but only slightly larger and they were also located near the lower epidermis. In Texas the bundles were very large, often taking up a great proportion of the leaf's thickness, and they were also more numerous than in Oklahoma. The amount of conducting parenchyma in the Michigan leaves was insignificant. There was a single row of small parenchyma cells around the small bundles in Oklahoma, whereas, in Texas there were two rows of large cells around the bundles and these cells extended to both the upper and lower epidermis. In 1928 there were 30 per cent more bundles and they were larger in the Texas than the Oklahoma leaves. The conducting tissue was more pronounced in the Texas leaves, extending from upper to lower epidermis. The number of bundles developed in the 1928 Oklahoma leaves was 30 per cent less and the number in the Texas leaves was almost 50 per cent less in 1928 than in 1929. The number of bundles in the 1929 Mayes (Rubus flagellaris geophilus Bail.) in Oklahoma was nearly twice as large as that of 1928. There was a much greater development of conducting tissue in the 1929 leaves and in longitudinal section there appeared to be storage cells. The conducting tissue did not extend from upper to lower epidermis in 1928 as it did in 1929.

In the high bush blackberries (Rubus allegheniensis Bail.) the number of bundles in the Michigan Eldorado was only one-third that of the Texas variety. The conducting tissue in the Michigan variety showed a much greater development than the black-raspberries in the same habitat, but the cells were not as large nor did they extend the entire width of the leaf as they did in the Texas leaves. The bundles were 20 per cent more numerous in the 1929 Texas leaves and the conducting cells larger and more numerous than in the 1928 leaves grown in the same habitat. Although Snyder in Texas developed a large number of bundles in the 1928 leaves they were much more numerous in 1929. The conducting tissue around the bundles in the 1929 leaves consisted of two to three layers to the lower epidermis and two layers to the upper epidermis. In 1928 there was a single layer of cells around the bundles and one layer extended to the upper and two layers to the lower epidermis.

The drought resistant blackberry-dewberry hybrids (Rubus velox Bail. and Rubus titanus Bail.) developed characteristic xeromorphic modifications of conducting tissue. The development of bundles in McDonald during 1928 was a great deal more pronounced in the Texas leaves than in Oklahoma. There was only a single row of conducting parenchyma around the Oklahoma bundles, whereas, in Texas the cells were much larger and one row extended to the upper and one row to the lower epidermis. In 1929 the number of bundles and the amount of conducting parenchyma was a great deal more in the Texas than in the Oklahoma leaves. In Oklahoma there was only a slightly greater development of bundles and conducting tissue in 1929 than in 1928, but in Texas there was about 40 per cent greater development of bundles and conducting tissue in 1929. The number of bundles in the 1929 Oklahoma Early Wonder was much larger than in 1928. The conducting parenchyma cells were larger and one row extended to the upper and one row to the lower epidermis on the larger bundles in 1929. In 1928 only a single layer of cells formed a sheath around the bundles and the cells did not extend to either epidermis. Jordan in Oklahoma had a much larger number of bundles in 1929 and larger and more extensive conducting tissue than in 1928. In 1929 there were two rows of large cells which made up the conducting sheath and one layer extended to the upper and one layer to the lower epidermis. In 1928 there was only a single layer of parenchyma cells around the bundles.

The one variety of Rubus strigosus grown in Oklahoma did not develop the modification of conducting tissue that was characteristic of the drought resistant

Eubati. The bundles in St. Regis were small but were very numerous, and they had a single row of large parenchyma cells surrounding them. Latham, probably the most drought resistant variety of red raspberries included in this study, developed exceedingly large bundles, as compared to Cuthbert, in Michigan during 1929, and they were almost twice as numerous as well. Whereas, Cuthbert developed a few small parenchyma cells around its small bundles, Latham developed two rows of large cells which extended to the top epidermis.

THICKNESS OF LEAF

There were no consistent increases in thickness of leaf, due to more xerophytic conditions, for the black raspberries (Rubus occidentalis L.). In fact, Cumberland developed thinner leaves in Oklahoma than in Michigan during both seasons. Plum Farmer leaves were slightly thicker in Texas than in Oklahoma, but the difference in 1929 could hardly be called significant. The Van Fleet raspberry, however, had thicker leaves in Texas than in Washington D.C., but the Texas leaves were approximately the same thickness in both seasons. St. Regis (Rubus strigosus) developed thinner leaves in Oklahoma than other varieties of the same species in Michigan.

On the other hand, the prostrate Lucretia dewberry (Rubus flagellaris roribaccus Bail.), developed slightly

thicker leaves in the progressively drier habitats and during the drier season in the same habitats, (plate 5). Mayes, however, belonging to the same species, developed slightly thicker leaves during the least severe season in Oklahoma.

The upright blackberry Eldorado (Rubus allegheniensis Bail.), developed thicker leaves in Texas than in Michigan in 1929, (plate 6), but the thicker leaves were developed in the least severe season in the Texas habitat. Snyder likewise developed thinner leaves during the drier season in the same habitat. There were no appreciable increases in leaf thickness in the more xerophytic habitats or seasons in the blackberry-dewberry hybrids (Rubus velox Bail., and Rubus titanus Bail.).

It appears then that leaf thickness in Rubus depends far less upon environmental than upon inherited factors and, indeed, is distinctly less influenced by environal factors than are many other anatomical characters.

GENERAL DISCUSSION AND CONCLUSIONS

From an examination of the climatological data it is evident that any xeromorphic modifications are due more to atmospheric than to soil drought. This has been brought out clearly in the Texas habitat where in the course of four years approximately four hundred red raspberry plants were planted, none of which lived even though the soil moisture was kept at the field optimum during the first two months after planting. This would indicate that no one of the factors, such as temperature, relative humidity, or extreme sunlight, per se, is the cause of the failure of red raspberry plants in the Southwest, but the fact that the rate of water loss is greater than the rate of absorption. Why then do certain species of the blackberries and dewberries succeed? Is it because the absorption rate exceeds the rate of water loss and hence creates a surplus of water in the plant? Or is it due to the fact that through certain xeromorphic changes in stem and leaf structure the water loss is reduced? Or is it that the modifications of conductive elements favor a greater translocation rate?

Maximov (18) and his co-workers have shown, however, that xeromorphic plants are distinguished by a higher and not by a lower rate of transpiration and assimilation.

The anatomy of the shoots of the drought resistant species of Rubus in the Texas habitat at an early stage of growth, during the period of greatest atmospheric drought, when compared to the same species in other habitats and to other less drought resistant species, shows definite modifications for greater water conduction. The young stems of the drought resistant blackberries and dewberries have stem stomata which very early in the season when the leaves are pushing out insure a rapid rise of water through the quickly enlarging xylem. When the leaf area is large enough to insure a strong enough pull by virtue of its increased number of stomata, number of bundles and conducting parenchyma, certain xeromorphic changes occur in the stem which prevent water loss through the stem's surface. These changes are cutinization of the stomatal openings, formation of thick walled collenchyma under the stomata and a modification which practically isolates the cortex from the conduction elements. This latter modification is the development of a ring of pericycle fibre groups which has been made continuous by the formation of pericycle fibres and stone cells across the vascular ray tissue. Moreover, under extreme conditions of atmospheric drought, superficial cork is formed. These latter changes, combined with a greater development of xylem, containing a greater number of vessels and a greater development of phloem, provide the drought resistant species with a conductive system in the stem which is isolated from outside atmospheric variations. The degree of the modification of the above tissues is much smaller in the less resistant species and in the moister habitats.

In addition to the stem modifications there are certain correlated leaf modifications. The conducting system is greatly increased in the leaves of the drought resistant sub-genus Eubatus. The degree of modification in the Texas habitat depends upon the habits of growth. The prostrate dewberries do not exhibit the degree of modification shown by the semi-prostrate blackberry-dewberry hybrids or by the upright blackberries. They all, however, show a greater xeromorphic structure in the more xerophytic habitats. Zalenski (28) showed that the higher the attachment of the leaf on the stem or the greater its distance from the root system, the greater was its venation and its xeromorphic structure. He did not show the degree of difference in xeromorphic structure between leaves the same distance from their respective root systems when one was upright and the other prostrate. The prostrate type of Rubus, i.e., Lucretia, developed superficial cork on the upper exposed surface of the stem but not on the lower side in the Texas habitat. This was not true in the other habitats and its leaves did not show quite the same degree of xeromorphic structure as the more upright species.

All of the drought resistant species of Eubatus in the Texas habitat exhibited certain xeromorphic leaf modifications, in addition to those of the stem, which seems to prove that these plants had a much greater potential absorption power than the less resistant Ideobatus. First was the development of a greater number of bundles which were much larger and contained more vessels than the less drought resistant species. This is in accordance with the findings of Zalenski (28), Maximov (18), McDougall and Penfound (19), Bergen (2), and others. Second, there was a much greater development of conducting parenchyma which formed a sheath two to three layers wide around the bundles and in most cases two to three rows of these cells connected the bundles to the upper and lower epidermises. This has been described by Alexandrov (1) as an adaptation to xerophytic conditions to provide rapid conduction to the mesophyll during periods of atmospheric drought. In addition to the changes mentioned above there were more layers of palisade cells. The individual palisade cells were more compact, and contained a much larger number of smaller chloroplasts. The decrease in the spongy tissue is even more marked than this increase in palisade. These latter changes would indicate a greater assimilation rate as has been noted for other plants by many American and European investigators.

The number of stomata on the leaves in the different habitats was not determined because of the thinness of the leaf which made peeling of the lower epidermis difficult and also because of the large number of hairs covering the lower epidermis. However, the works of Bruner and Weaver (4), Dufour (8), Wagner (26), Eberhardt (11), and Bergen (2), Kiesselbach and Keim (13), and others, have shown conclusively that the more xerophytic the habitat the greater the number of stomata per square unit of area. The data in this paper do not show that the number of stomata and that the water loss is greater in more xerophytic habitats. However, the evidence given on stomata by the above workers, combined with the evidence given by Maximov (18) and his Russian co-workers on the increased transpiration rate under xerophytic conditions make plausible these assumptions for the genus Rubus. Although the works of Lloyd (16), Loftfield (17), Livingston, and Brown (15), and Edith Shreve (24), show that the stomata are not the sole regulators of transpiration, they undoubtedly are the apertures through which most of the water vapor is lost from Rubus leaves in Texas as there is a layer of cutin on both epidermal surfaces. The outer walls of the epidermal cells are also thickened and lignified. These latter modifications would indicate that as soon as the stomata had closed, when the water loss greatly exceeded absorption, further loss of water would be negligible.

The evidence presented in this paper shows that there are certain xeromorphic modifications which are associated with drought resistance. There is a much greater degree of modification in the sub-genus Eubatus which includes the dewberries, blackberry-dewberry hybrids and various species of blackberries. The question then arises whether or not these anatomical characteristics are the factors which determine drought resistance. There is undoubtedly a strong correlation as the degree of modification is an indication of the ability to withstand atmospheric drought. This is brought out in the non-adaptability of the red raspberries and the intermediate position of the black and so-called purple raspberries. The type of root system undoubtedly has an important bearing on soil drought as is brought out clearly in the work of Weaver and Bruner (27) on vegetable crops. Drought resistance is probably also due to physiological processes. The fact that certain plants reach the wilting point when the water content of the leaf has been reduced 10 or 12 per cent whereas others do not wilt when the reduction reaches 30 to 40 per cent would indicate that there must be some colloidal water which is held by the protoplasm that enables it to withstand prolonged wilting. As Maximov (18) states, "....The internal physico-chemical properties of the protoplasm would appear to play the principal role in drought resistance, rather than the more superficial morphological or anatomical peculiarities of the plant." The latter statement is undoubtedly true but in the selection of plants to breed for drought resistance it is logical to assume that those species, which have the inherent plasticity, as regards xeromorphic adaptation of tissues, to withstand water loss must necessarily be capable of drought resistance. Furthermore, if a plant did not have the inherent xeromorphic characteristics which would give it a great absorption rate and decrease unnecessary water loss through atmospheric drought, it would hardly seem possible that a high percentage of colloidal water would make up for the lack of these characteristics if the plant had a mesophytic stem and leaf structure.

In Rubus it appears that resistance to atmospheric drought is brought about by the prevention of tissue water loss. The sub-species Eubatus is much more plastic in anatomical modification and drought resistance than Ideobatus. Within Eubatus and prostrate dewberries

(Rubus flagellaris) are the most drought resistant, followed by the blackberry-dewberry hybrids (Rubus velox Bail. and Rubus titanus Bail.), then Rubus laudatus Bail., and Rubus allegheniensis Bail. The differences in the degree of resistance might possibly be in the degree of exposure, and if the shoots of Rubus flagellaris were trained upright they might not be as resistant to atmospheric drought as Rubus laudatus or allegheniensis.

As a result of this study it appears that the production of small fruits on the Plains of Texas, on a small scale, would be practical. After drought resistant varieties were found, it would then be possible to improve the quality of the fruit by further hybridization and selection. Dense evergreen windbreaks and possibly overhead irrigation would prove of great assistance in producing a good quality of well filled out fruits of blackberries and dewberries.

SUMMARY

1. There was no consistent increase in thickness of the cutin layer on the stems of the black and purple raspberries, blackberries, blackberry-dewberry hybrids, or dewberries, in the progressively drier habitats or during the drier season in the same habitat.
2. The black raspberries and dewberries developed a wider cortex along with more rows of thick walled collenchyma in the drier habitats.
3. The blackberries and blackberry-dewberry hybrids formed less cortex in the stems grown during the drier season and in the drier habitat. There were also more layers of collenchyma formed which had heavier walls.
4. The Van Fleet formed less cortex in the Texas habitat but the amount of collenchyma remained fairly constant.
5. The Eubati had stem stomata, and in the xerophytic habitats and drier season, thick walled collenchyma extended across under them early in the season.
6. The cortical cells of McDonald (Rubus velox Bail.), grown in the xerophytic Texas habitat, were filled with minute droplets of a brownish tannin-like substance which gave the color reactions of cork.

7. Climatic conditions had no appreciable effect on the amount of pericycle periderm laid down in the stems of any of the species studied.
8. The black raspberries grown in the progressively drier habitats developed slightly longer and wider pericycle fibre groups, which tended to form a more continuous ring, measured by the amount of intervening vascular ray tissue.
9. The dewberries formed a continuous sclerenchyma ring in the xerophytic habitat by the formation of new fibres across the vascular ray tissue.
10. The blackberries and blackberry-dewberry hybrids formed a continuous sclerenchyma ring by the formation of stone cells across the vascular ray tissue in the xerophytic habitat.
11. There were no consistent xeromorphic modifications of phloem in the progressively drier habitats for the black or purple raspberries.
12. The prostrate dewberries developed more phloem in the progressively drier habitats but less in the drier season in the same habitat.
13. The high bush blackberries (Rubus allegheniensis Bail.) developed more phloem in the drier habitats and season. This species developed twice as much phloem as the black raspberries in the same habitat.

14. The black raspberries showed no appreciable increase of xylem in the drier habitats and season.

15. Van Fleet developed a great deal more xylem in the xerophytic habitat and slightly more in the drier season in the same habitat.

16. There was a greater xylem development in the progressively drier habitats for all members of Eubati, with a slight increase for the blackberries, and a slight decrease for the dewberries and hybrids, in the drier season.

17. There was a tendency to form superficial periderm under extreme xerophytic conditions in the dewberry and blackberry-dewberry hybrids.

18. There were no stem stomata formed on the black, purple, or red raspberries, with the exception of Latham.

19. Environment did not appear to have any effect upon the percentage of pith formed.

20. The xeromorphic modifications found in the leaves of Rubus plants, with the exception of Rubus strigosus Michx., in the more xerophytic stations and seasons of greater atmospheric drought are as follows:

    a. A significant increase in the percentage of palisade tissue.

b. A significantly greater decrease in the percentage of spongy tissue.

c. Heavier outer wall of top epidermal cells with thicker layer of cutin.

d. A very definite increase in the number and size of leaf bundles.

e. An increased development of conducting parenchyma around the bundles, especially in the Texas habitat.

f. The extension of several rows of conducting cells from bundles to both epidermises.

g. The development of a cutin layer on the lower epidermis under xerophytic conditions.

h. The development of more layers of shorter, wider, and more compact palisade cells.

i. A decrease in the size of sponge cells with much greater compactness and fewer intercellular spaces.

j. A thickening of the walls of the upper epidermal cells which were lignified in the Texas habitat.

k. A greater density of chloroplasts in the palisade and sponge cells.

21. The thickness of the leaves of Rubus is not solely dependent upon environmental factors.

22. There was a layer of hypodermis developed in one variety of Rubus occidentalis L. in the Texas habitat.

23. There were no appreciable modifications of the diameter of leaf epidermal cells which could be attributed to environment.

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The author wishes to express his appreciation for the helpful guidance and criticisms of Professors J. W. Crist, V. R. Gardner, F. C. Bradford, and E. W. Woodcock. Professor W. C. Dutton assisted in taking the photomicrographs. Mr. Stanley Johnson, of the South Haven Station; Mr. L. C. Locke, of the Government field Station at Woodward, Oklahoma; and Mr. George F. Waldo, of the Bureau of Plant Industry, have supplied stem and leaf material each year from their respective stations, without which this piece of work would not have been possible.

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DESCRIPTION OF PLATES

Plate 1.

Photomicrographs of cross-sections of one year shoots. Same magnification.

Fig. 1. Cumberland black raspberry (Rubus occidentalis L.) grown in Michigan during 1929. Compare with Fig. 2. Col., collenchyma; p. per., pericycle periderm; s. ck., superficial cork; p.f., pericycle fibre groups; ph., phloem; xy., xylem.

Fig. 2. Cumberland grown in Oklahoma during 1929. Note the presence of superficial cork, the width of pericycle periderm, the width of phloem, increase in number of vessels, increase in size of vascular rays, and very large increase in xylem. Compare with fig. 1.

Fig. 3. Plum Farmer (Rubus occidentalis L.) grown in Oklahoma during 1929. Compare with fig. 4.

Fig. 4. Plum Farmer grown in Texas during 1929. Compare with fig. 3. Note the greater amount of collenchyma, phloem, and greater continuity of pericycle fibre groups, and increase in number of vessels.

Plate 2.

Photomicrographs of cross-sections of Dewberry shoots. Same magnification.

Fig. 1. Lucretia (Rubus flagellaris roribaccus Bail.) shoot grown in Michigan during 1929. Compare with fig. 2 and fig. 3.

Fig. 2. Lucretia shoot grown in Oklahoma during 1929. Note the continuity of pericycle fibre ring as compared to that in fig. 1. Note how the collenchyma have formed under the stomata as compared to that of Michigan (fig. 1).

Fig. 3. Lucretia grown in Texas during 1929. Note the large deposit of superficial periderm, wide cortex with larger seive tubes, and almost solid ring of pericyle fibres as compared to those of figs. 1 and 2.

Fig. 4. Mayes (Rubus flagellaris geophilus Bail.) grown in Oklahoma during 1929. Compare with fig. 2.

Plate 3.

Photomicrographs of stem cross-sections. Same magnification.

Fig. 1. McDonald (Rubus velox Bail.) grown in Oklahoma during 1929.

Fig. 2. McDonald grown in Texas during 1929. Note the larger amount of phloem with more seive tubes, and larger number of vessels as compared to McDonald in fig. 1.

Fig. 3. Van Fleet (Rubus strigosus x Rubus innominatus) grown at Washington, D.C., during 1929. Compare with fig. 4.

Fig. 4. Van Fleet grown in Texas during 1929. Compare with fig. 3. Note the enormous number of pericycle fibres, the amount of phloem, xylem, and pericycle periderm as compared to that of fig. 3.

Plate 4.

Camera lucida drawings of leaf cross-sections.

Fig. 1. Van Fleet grown at Washington, D. C., during 1929. X 650.

Fig. 2. Van Fleet grown in Texas during 1929. X 650.

Fig. 3. Plum Farmer (Rubus occidentalis L.) grown in Oklahoma during 1929. X 640.

Fig. 4. Plum Farmer grown in Texas during 1929. X 640. Note the layer of hypodermis under the upper epidermis.

Plate 5.

Camera lucida drawings of leaf cross-sections of Lucretia dewberry (Rubus flagellaris rori-

baccus Bail.) X 700.

Fig. 1. Lucretia grown in Michigan during 1929.

Fig. 2. Lucretia grown in Oklahoma during 1929.

Fig. 3. Lucretia grown in Texas during 1929.

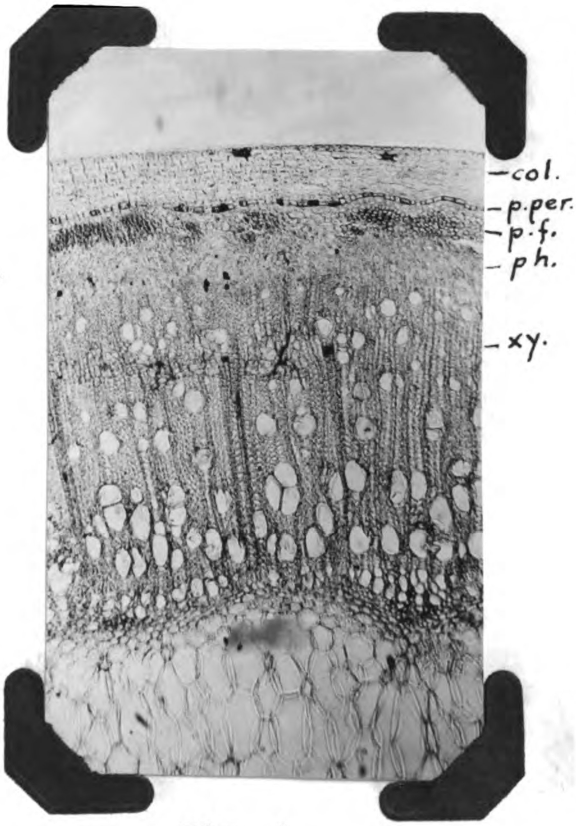
Plate 6.

Camera lucida drawings of leaf cross-sections.

Fig. 1. The Eldorado blackberry (Rubus allegheniensis Bail.) grown in Michigan during 1929. X 640.

Fig. 2. Eldorado leaf grown in Texas during 1929. X 640.

Fig. 3. Cross-section through bundle and conducting parenchyma of blackberry leaf grown in Texas. T. ep., top epidermis; pal., palisade cell; c. par., conducting parenchyma cell; bu., bundle; sp., spongy tissue cell; and l. ep., lower epidermis. X 700.



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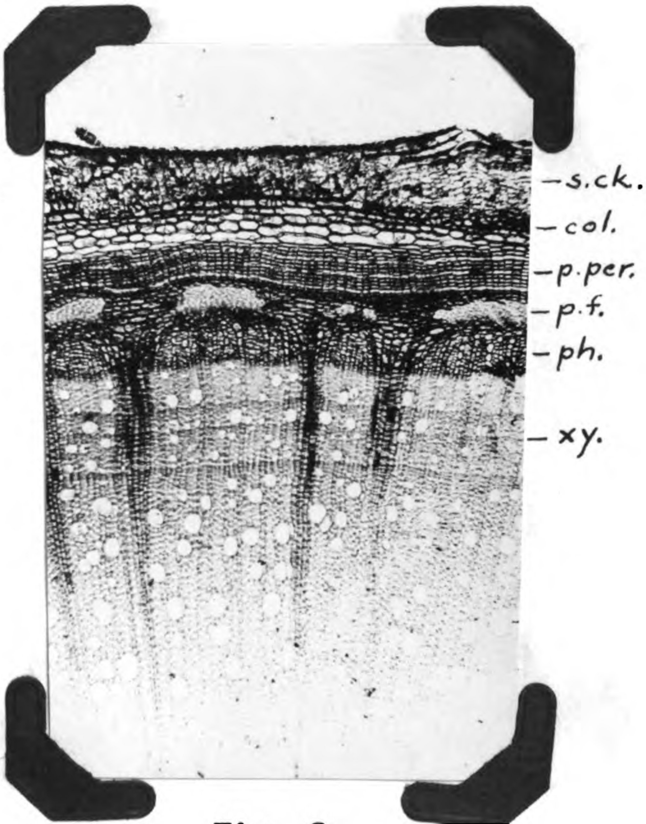

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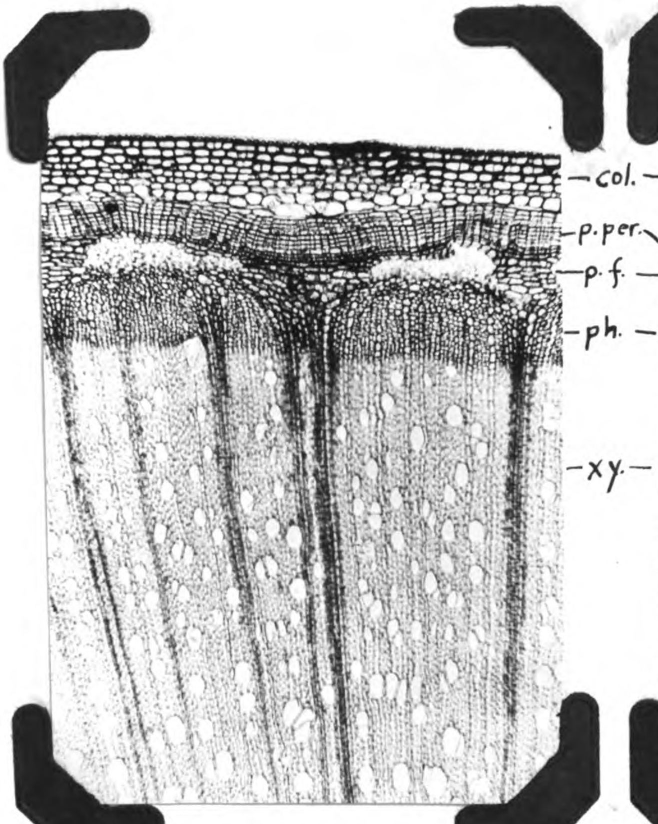

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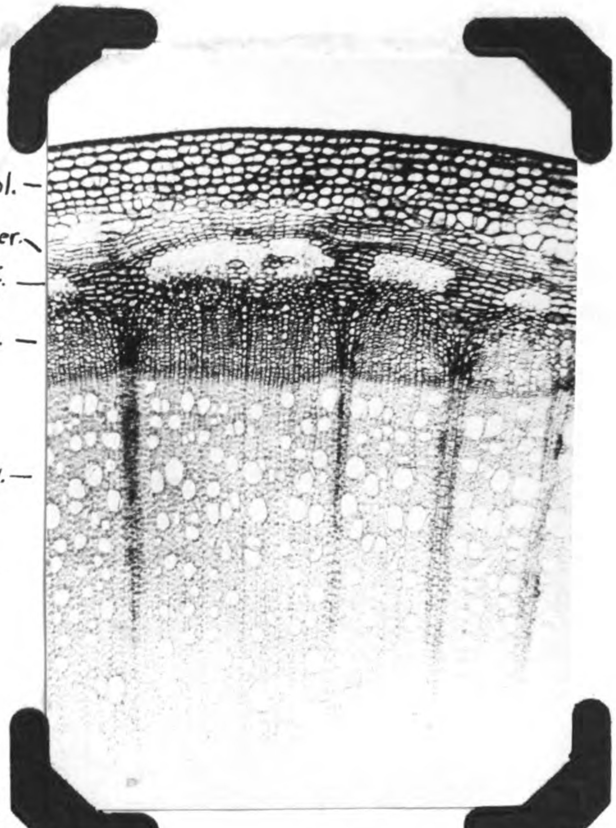

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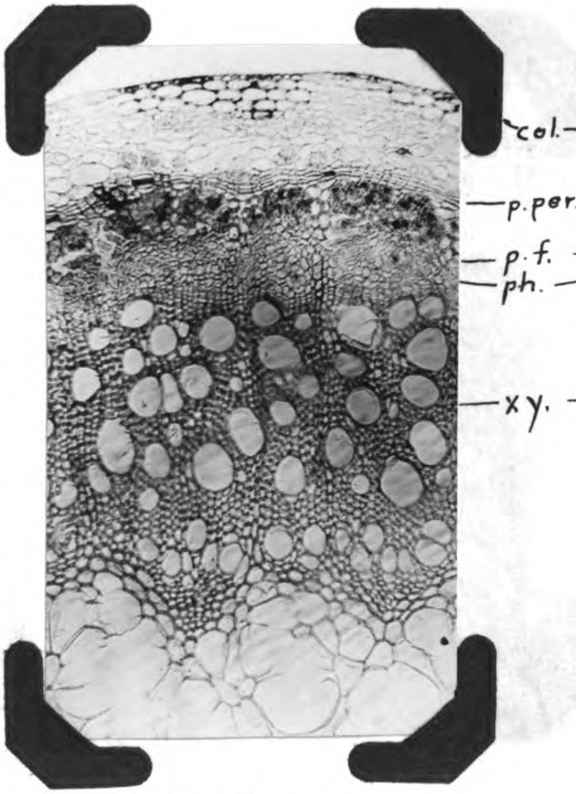

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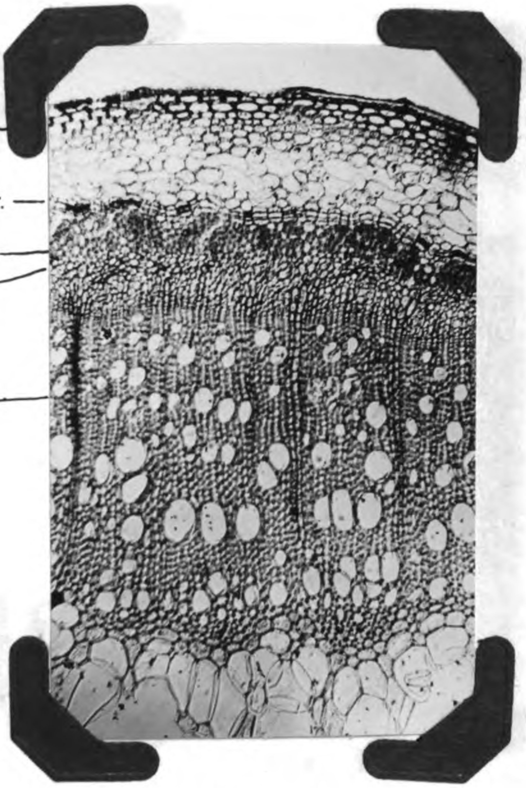

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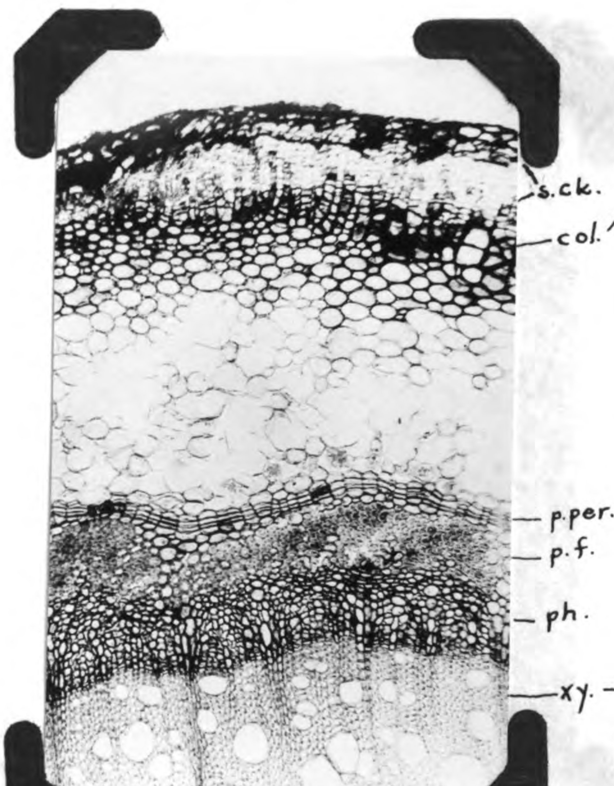

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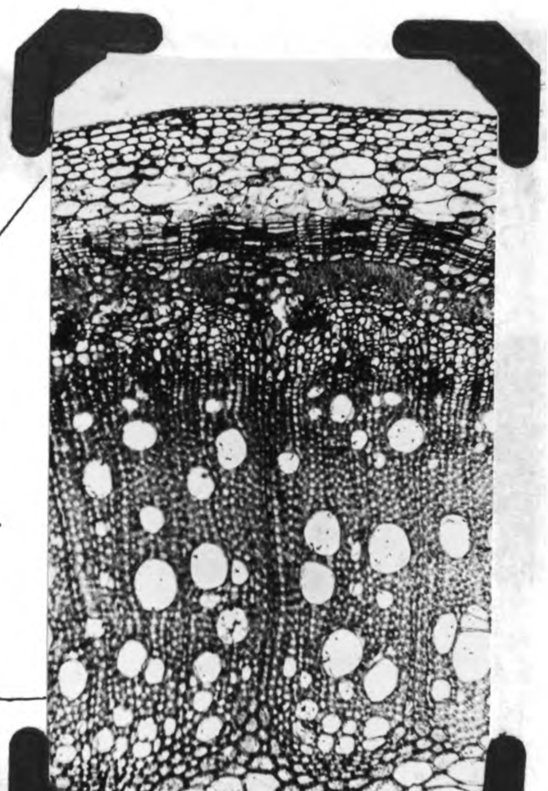

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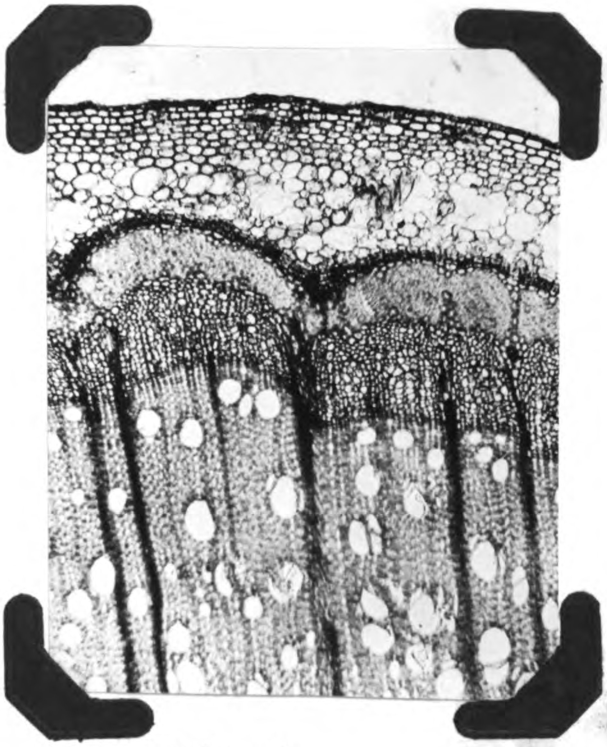

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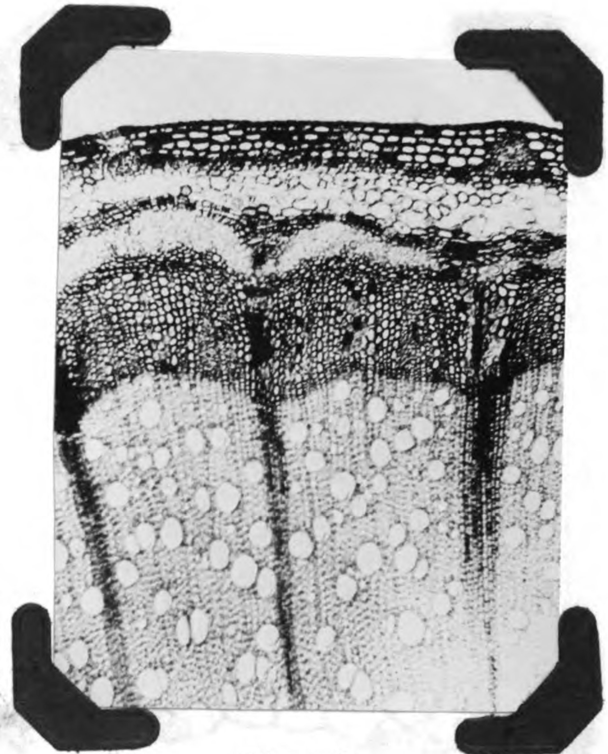

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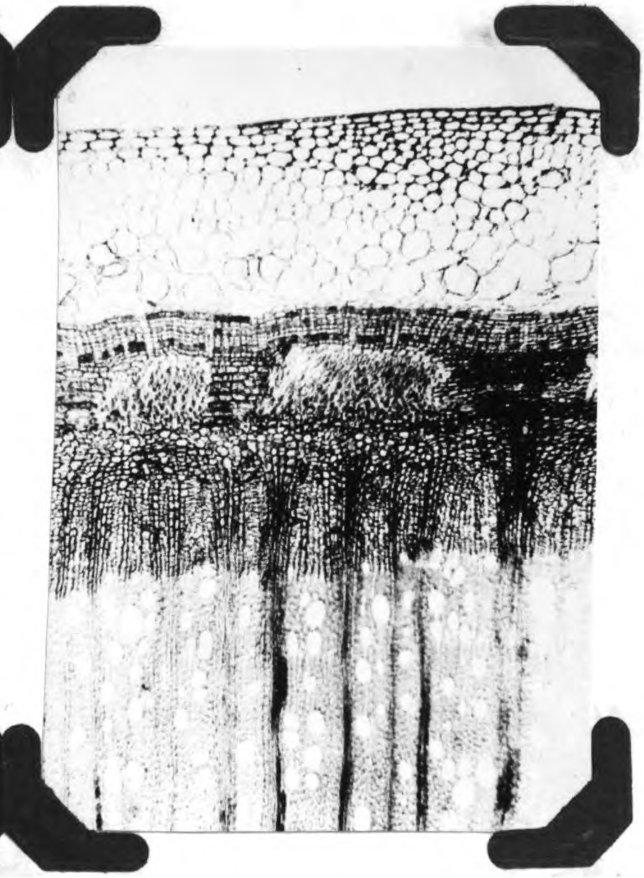

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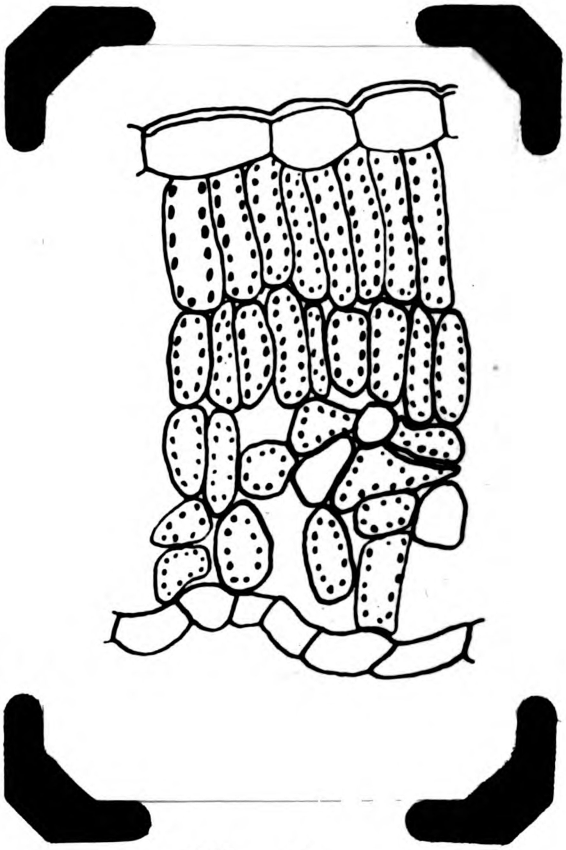

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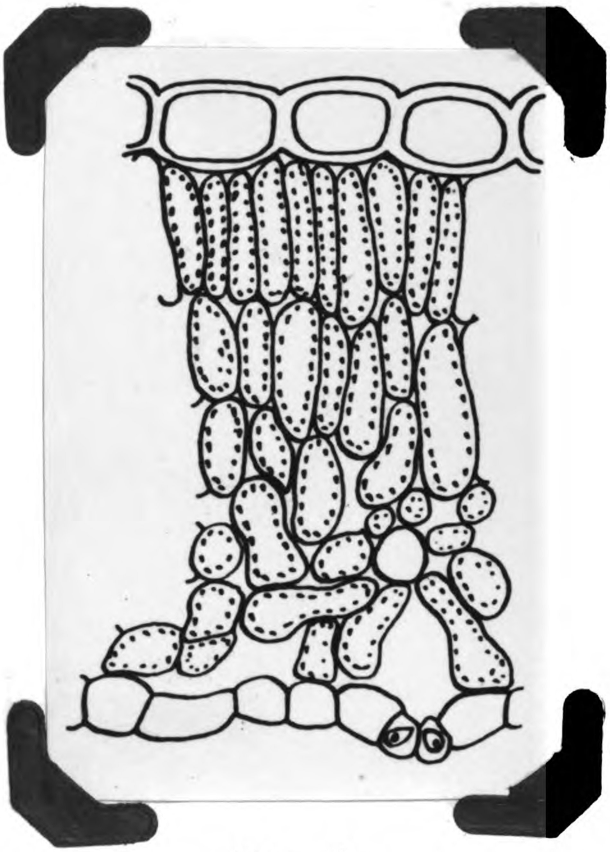

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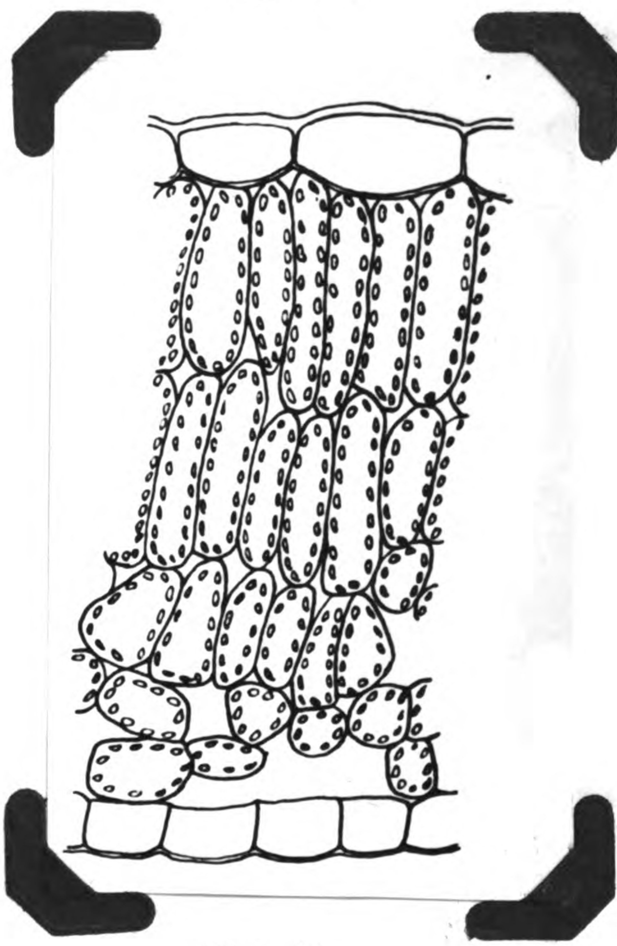

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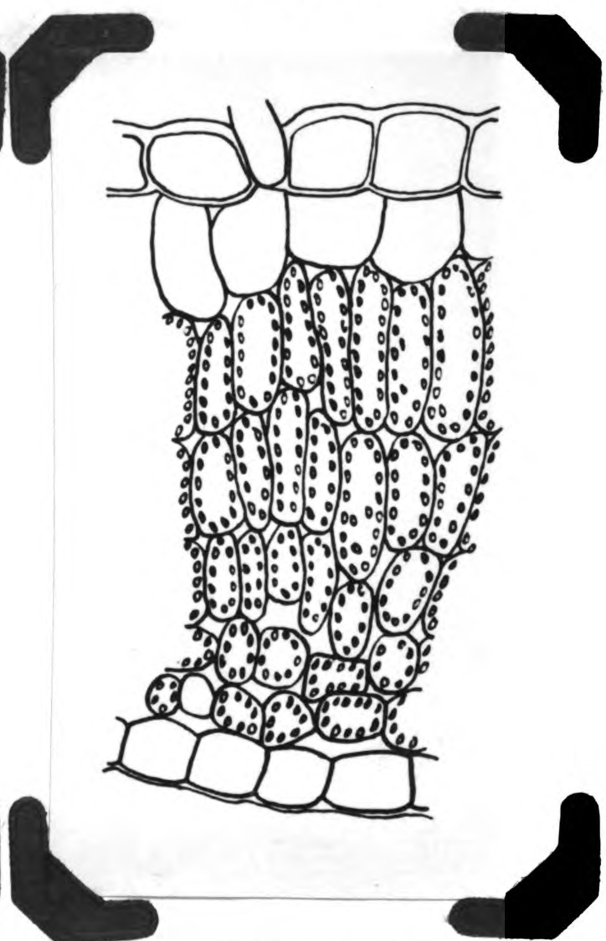

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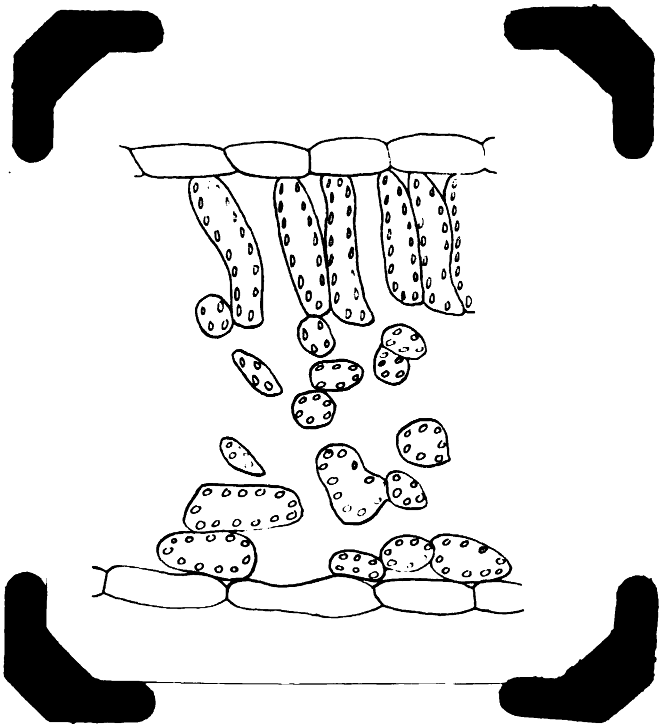

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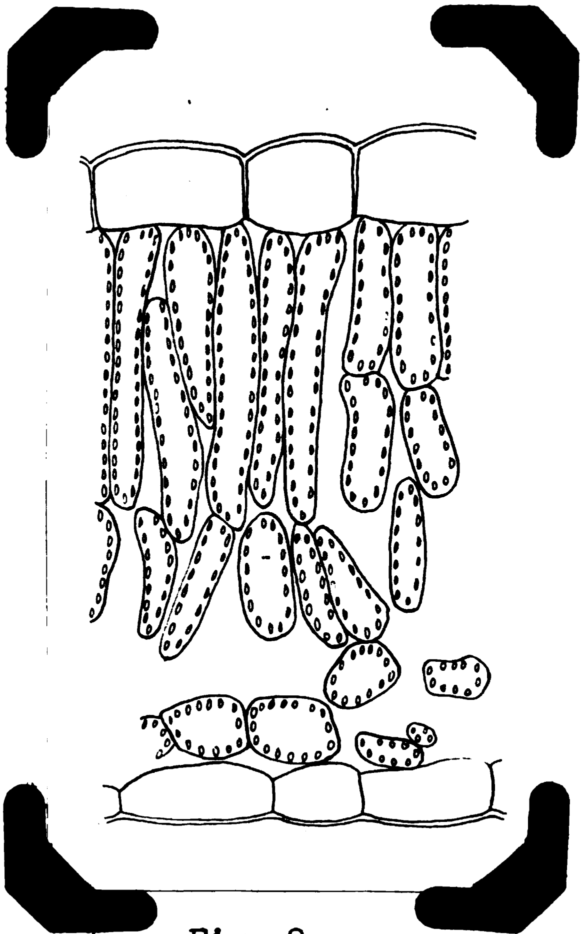

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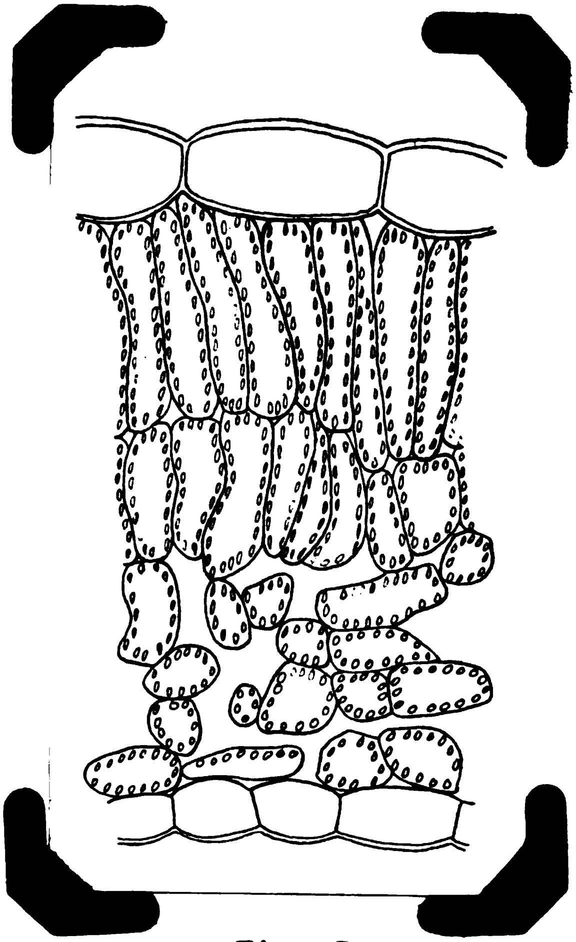
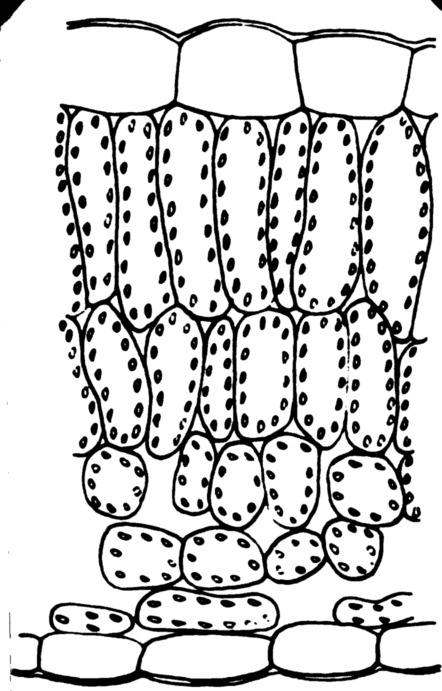


Fig. 3.

Plate 6.



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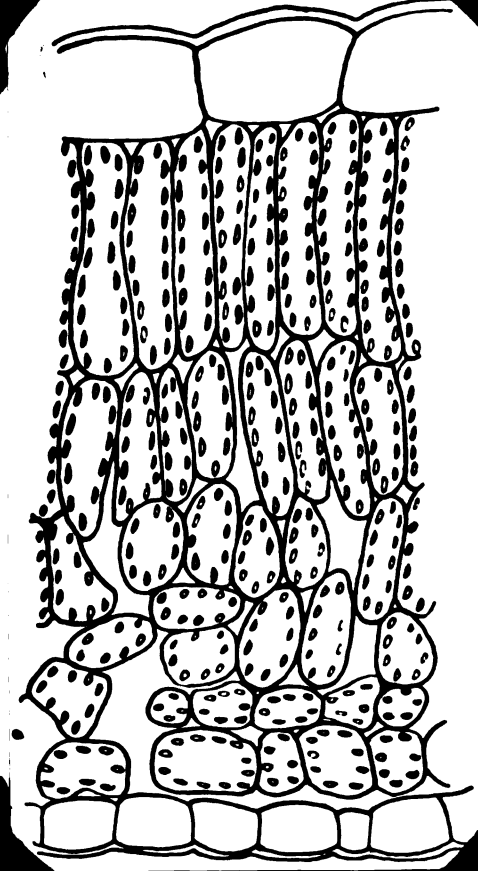

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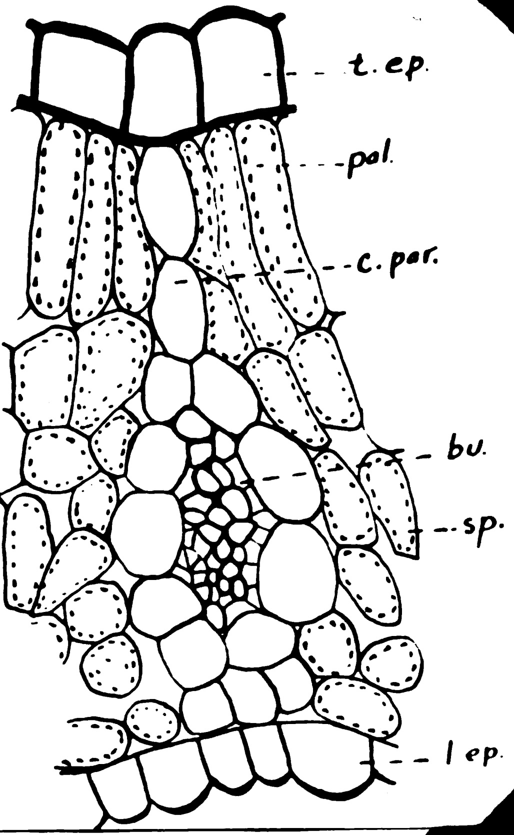

Fig. 3.

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