

T H E S I S
on
THE RESPONSE OF MECHANICAL TISSUE TO
TENSION IN THE PEDICEL OF APPLE

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THE RESPONSE OF MECHANICAL TISSUE TO
TENSION IN THE PEDICEL OF APPLE.

INTRODUCTION

Whether or not the question, "What force holds the apple when it does not fall?", also occurred to Sir Isaac Newton's mind when he was day-dreaming as a truant beneath the apple tree, is a matter of conjecture. Be that as it may, the question is interesting. And if one were in the habit of day-dreaming periodically for a season under the same apple tree, the question might arise, "Does the apple stem or pedicel grow stronger as the apple grows heavier, and if so, in what way?" Here we have a pendant organ, like any pendant fruit stalk, which is subjected not only to a continued strain but an increasing strain of tension under natural conditions. The apple's own increase in weight brings about a gradual change in one of the forces affecting the pedicel, that is, one of its environmental factors. Does it respond to this change, and how? In order to discover this it is necessary to study the structure and anatomy of the pedicel at various stages of growth and also find some means of measuring any response to increasing weight which may be found. This has constituted the chief object of the investigations reported in this paper.

Before undertaking this investigational work, a study of botanical literature was made to ascertain the present state of scientific information regarding the occurrence and arrangement of strain-bearing tissues in plants and the adjustment of such tissues to meet conditions imposed by nature or experimentally. The results of this search of the literature, continued up to the present, are summarized briefly in the following pages.

In the history of botanical research, the study of plant anatomy is old. It is not dependent upon the advances of chemistry, of taxonomy, or the development of fine cytological technique. In modern form it arose out of the field of morphology by the advent of the microscope. But before the microscope lent its aid the eye could observe the form of plant bodies and the arrangement of its organs. So anatomy which deals with internal structure and tissues is as old as morphology, which was first established in its descriptive form by Theophrastus.

Theophrastus was a pupil and friend of Aristotle and wrote his discussions about the third century B.C. Eames and MacDaniels in their Introduction to Plant Anatomy (2, p. 322) state that Theophrastus in extending his studies to gross internal feature says: "Plants are made up of bark (phloios), wood (zylon), and pith (metra),

when pith is present." He discusses the nature of annual rings also, and describes the stem in more detail, as "a fabric of veins, nerves, and flesh"--the nerves being the minute fiber-like parts; the veins the larger strands, (apparently the vascular bundles) which are characterized by the fact that they can be split, but not otherwise readily separated; whereas flesh can be readily divided in all planes like a "lump of earth." (p. 323).

Eames and MacDaniels continue: "Nothing of moment was accomplished to break the long interval of nearly nineteen hundred years from Theophrastus to the sudden awakening of anatomy in 1671." It was then that Robert Hooke, an English mathematician and architect in playing with a magnifying lens, "the new toy" discovered that these tissues were "perforated and porous like a honeycomb." (2, p. 324)

Since then newer fields have opened or older fields have broadened, by the advance of technique and resulting discoveries until it was found that living things are not just structures per se as dissected, but are creatures of response and modification and a plant in this respect is no less a living thing than an animal.

In the continuous development of plant anatomy after the discovery of protoplasm and the establishment of the cell theory various attempts at classification of tissues were made, based chiefly on ontogeny. These

proved of little value and a new basis was sought and found in function by Julius von Sachs (1832-1897) who made the first physiological tissue classification. (1, p. 336)

This physiological viewpoint of plant anatomy has reached a high development in the work of Gottlieb Haberlandt, now professor of plant physiology at the University of Berlin, as presented in his Physiologische Pflanzenanatomie which has come out in five editions between 1884-1918. Haberlandt groups tissues into great systems according to function, as for example the dermal, mechanical, absorbing, photosynthetic, conducting, storage, ventilating, secretory, motor, sensory systems. In this classification a tissue is not necessarily structurally continuous. For example, the bast fibers and wood fibers are not distinguishable by any tangible morphological character; their difference lies in their location which is no sound basis of distinction from a mechanical standpoint. (3, p. 155)

Although this functional view of plant anatomy may not be of value to the plant anatomist who is interested in the phylogenetic origin of a tissue or the nature of a cell type, it is of value to the physiologist who is interested in functions and to the ecologist who is interested in responses. It is in this responsive or adaptive point of view that Haberlandt's work is especially useful in the present paper.

With all due recognition of the work of such men as Grew and Malpighi, Nageli and von Mohl, De Bary and Van Tieghem and others (also discussed by Eames and MacDaniels) whose works were not outlined, it may be said that compared with other fields of botanical research, the field of plant anatomy as a field has not developed far. It remains today an almost neglected branch of plant science. Its attention (~~interests~~) has been diverted into other fields such as physiology, taxonomy, cytology, genetics, ecology which are constantly demanding more knowledge concerning structure. It is in meeting these requirements that anatomy is of service. (2, p. 341). Thus as in the present studies it serves ecology. If we attempt to study responses as expressions in structure, and its modifications as the result in part of the interaction of their environment upon their own potentialities, we can more logically interpret both adaptation and structure.

Mechanical Tissues in Plants.

The importance of supporting structures.---One of the most outstanding and interesting tissue systems in the plant body is the supporting structure. Haberlandt very effectively discusses its importance. The maintenance of stability is as essential in the plant body as in a bridge; it is as special a function as the transport of

water or the manufacture of food. No plant with any degree of complexity can thrive or even maintain its own existence unless its plant body is firmly interwoven as a whole and each of its organs possesses the required amount of mechanical strength safeguarding it against all possible forms of injury or strains and stresses to which it is constantly subjected. An organ, insufficiently strengthened may at any time be broken across, torn apart, bruised, crushed, pulled out, or whipped to shreds according to the circumstances of the environment. It must, therefore, be so constructed or reinforced as to withstand such injuries. This resistance and stability a plant has achieved throughout the course of evolution, once more by the operation of the principle of the division of labor expressed in the development of mechanical tissue and its distribution.

Principal types of cells in mechanical tissue.--The chief types of cells constituting mechanical tissues as recognised by present day text books are, briefly, collenchyma, sclerenchyma, and fibrous xylem elements. Collenchyma are parenchyma cells; living and still meristematic, whose walls are thickened at the corners or points adjacent other cells. They serve generally as a preliminary support in young growing organs. Sclerenchyma includes two kinds of cells--stone cells, which are most usually very thick walled parenchyma cells, the walls

being so thick that the pits are canals and truly they are stony; and bast fibers which are stone cells, narrower, much elongated and tapering. These serve as additional support in an organ more advanced in growth. Xylem fibrous elements are tracheids as in Gymnosperms, and wood fibers which are like bast fibers, as in Angiosperms. Xylem, although primarily the water conducting tissue, constitutes the chief element of strength because of its fibers (except in organs or parts where it is little developed), and it is its fibers that makes wood woody. All of these principal types of cells are encountered in eating a pear. The resistance offered in biting into it is due to collenchyma just beneath the skin. The grit in your teeth when eating the bite is due to stone cells. The strong tough strings in the core which will hardly break when pulling out the stem are bundles of bast fibers and wood fibers.

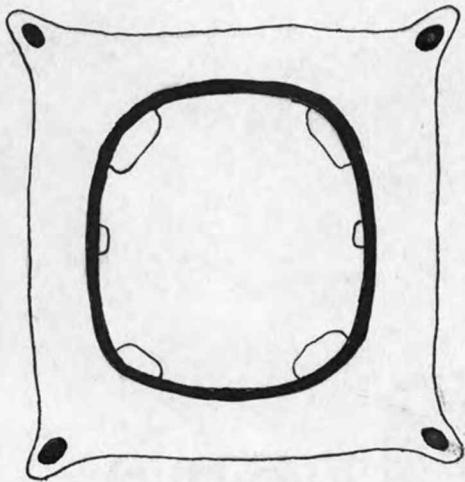
The arrangement of mechanical tissues.--A comprehensive study of these strengthening elements as mechanical tissue scattered amidst other tissue systems in the plant reveals the fact that there is an accurate correspondence between the occurrence of them as the mechanical system and the need for it. The result of this harmony is beauty of design. It expresses the same principles which govern the architect's or engineer's plan of construction. Perhaps it is just a coincidence, but to me it is a point of

great interest in this connection that it was an architect (see p. 3) and not a botanist who first, in his interested examined all sorts of things to see what they were like, found that plant tissues are "perforated and porous, much like a honey comb." Haberlandt analyzes this expression of engineering principles in the arrangement of these tissues. The following summarized discussion is based upon his treatise. The drawings are original.

He writes: "The very same mechanical principles that are embodied in a modern railway bridge of bold and elegant design, were expressed perhaps with even greater perfection hundreds and thousands of years ago in the skeletal systems of the plants of former geological periods." The first principle is the attainment of maximum strength with the minimum of material. The plant accomplishes this by the patterns of arrangement as seen in cross sections. The second fundamental principle, is an arrangement of material so as to offer resistance to the forces of bending, compression, and tension.

The first, resistance to bending or inflexibility, is affected in the plant by the operation of the I-girder principle. Maximum strength with the use of minimum material is attained by building the flanges (the top and bottom of the girder) of solid material, whereas the web is made of less material as in the rails of railway tracks, or of less or inferior material as in the lattice work of

bridge girders. In plants similar flanges are mechanical cells, whereas the web may consist of vascular tissue or of parenchyma. The simple I-girder is the simplest device for resistance to bending. It renders inflexibility in a single plane. The compound girders render inflexibility in several planes. This is widespread in the vegetative kingdom, found most commonly in stems. The simplest example is in the mint family--two girders crossing each other.



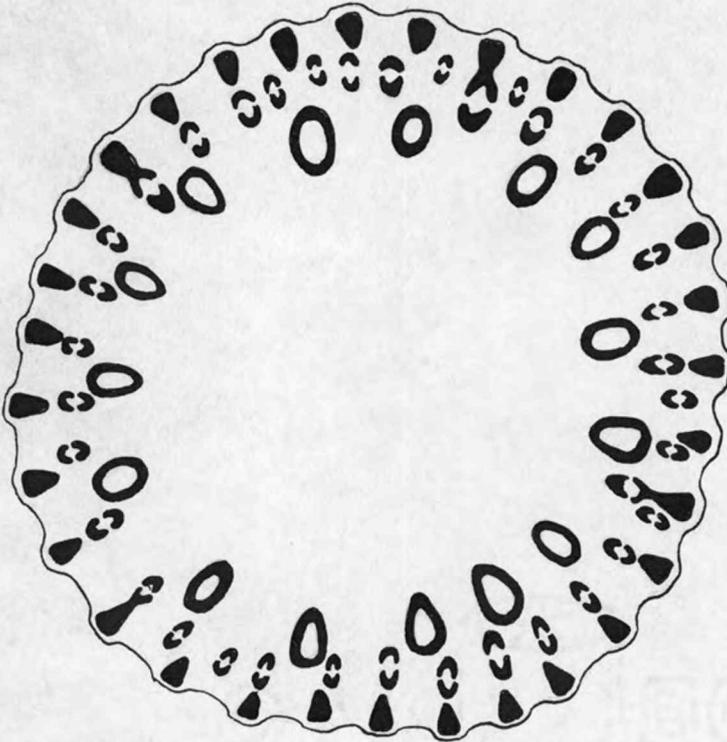
Cross section diagram of Coleus sp.--a mint. The mechanical tissues are in black.

The corners form two diagonal I-girders. In the center is a hollow cylinder.

When many girders or flanges are so closely crowded that they undergo lateral fusion, they become a hollow cylinder or tube. This is also a very prevalent type of mechanical construction among plants, and is much more effective than the same amount of material in a solid cylinder, providing the supporting cylinder equals one seventh to one eighth of the total diameter. Grasses are good examples.

The composite I-girder is also common in the plant kingdom. Here the girders instead of the flanges are com-

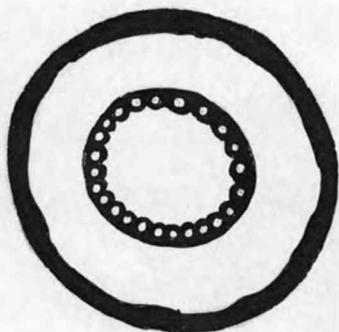
poundly arranged--the radially opposite girders acting as flanges. Each flange may be exposed alternately to tension and compression and therefore the individual flanges look like I-girders. These do not warp or buckle before the elastic limit of the tissue is reached.



Juncus effusus-
a sedge.

An
illustration
of the above
discussion.

When these composite girders undergo lateral fusion, the flanges form two hollow cylinders one within the other. This is well shown in the prop roots of corn. Their need for resistance to bending and compression is terrific. The wind causes them to be alternately stretched and compressed, and their structure corresponds exactly with this requirement.



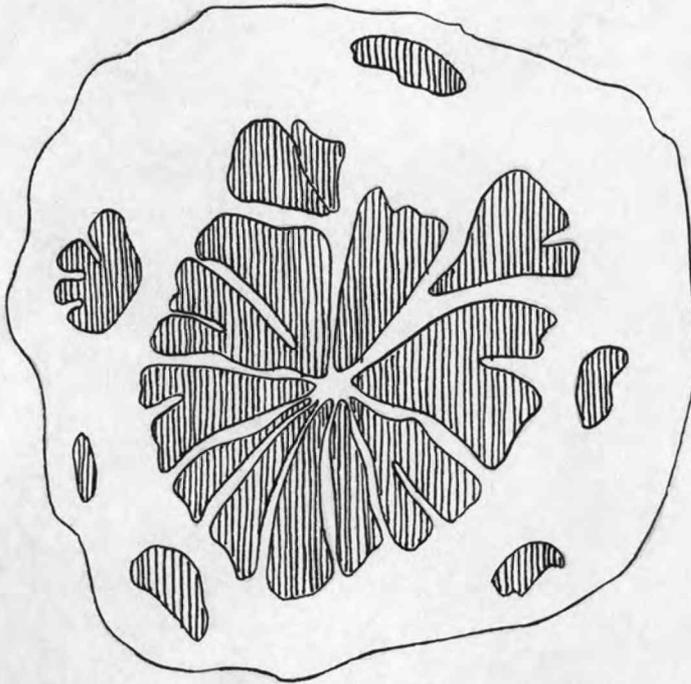
Cross section diagram of
Sorghum prop-root.

Two concentric hollow cylinders.
Resistance to bending produced
the outer cylinder.
Resistance to pulling produced
by inner cylinder.

Resistance to compression--the second of the three great forces mentioned, which supportive structures must endure--is achieved by the same arrangements which make for flexibility. This is advantageous since often the same structures are called upon to resist both bending and compression. However, incompressibility is most effectively achieved by the solid cylinder or pillar. In plants, ideal examples are tree trunks. The greater the spread and weight of branching the greater becomes the diameter.

Tension is the third force requiring resistance in supportive structures. This is achieved by the quality of inextensibility. In the organs of plants which must have inextensibility combined with inflexibility, the strength depends upon the cross sectional area or the total combination of mechanical elements. The disposition of these elements is a matter of indifference. The more closely aggregated the resistant elements are, however, the more uniform the distribution of tension is likely to be; hence the aggregation of mechanical cells

into a single compact and solid mass is the most advantageous arrangement. A good example is found in the tree where in bending there is an alternate compression and tension on the root. Of the flexible, inextensible organs, the stems of lianas or climbers are good examples. Here instead of having a solid mass or concentric hollow cylinders of material, the mechanical elements are broken up into strands embedded in soft tissues.



IPOMAEA SP.--
morning glory, a
liana.

Here xylem is the only mechanical tissue in practically a solid center resisting tension or stretching, and additional solid strands making it flexible and rope-like.

Often these softer tissues die away leaving separate strands like ropes. In the vascular system of certain lianas the cambium occurs in concentric layers. In others cambium rings develop outside of the regular central one. Each one then, becomes a separate stem which twists about the others in a rope-like manner, and a rope is the ideal structure, for the combination of flexibility with

resistance to tension.

Leaf petioles also belong to this class. An interesting anatomical study of the long slender, vertically flattened petioles of three species of *Populus* is presented by Leach (11). A consecutive series of transverse sections cut at equal intervals from the base to the apex show how peculiarly like a liana the mechanical elements are arranged. Near the base the cross section is cylindrical, with the rope-like strands grouped throughout the center. This makes for flexibility in any plane. At the base they are arranged horizontally. This makes for flexibility up and down. In the center and toward the apex the rope-like bunches are arranged in a verticle row. This makes for bending sidewise with little resistance to torsional (twisting) strains.

Another group of flexible organs which offer resistance to tension are pendant fruit stalks. It is here that the interest of this piece of research lies since it is with the mechanical elements which enable the apple pedicel to withstand the weight of the fruit that this study is concerned. Search of the literature reveals but little light upon this particular phase of plant anatomy.

Factors Influencing Change in Mechanical Tissues.

Studies and research show that the factors influencing change in mechanical tissue are heredity, water relations, and a change in the quality or quantity of a strain or

stress. The first two factors lie outside the scope of the present studies. The third factor is of interest here since a change produced by an intensification of a stimulus, as the increasing weight of a growing apple, is evidence of a response or adjustment. Haberlandt says: "- =

- -a certain amount of direct accommodation to external conditions on the part of the mechanical system may take place during the life of the individual, or in the course of development of some of its organs. In this connection special stress must be laid upon the relation between the qualitative development of the mechanical system and the action of those mechanical forces which are ultimately responsible for the presence of the entire skeletal system. It is probable that the forces in question act as stimuli that tend to accentuate the qualitative and quantitative development of the stereome (mechanical system)." (3, p. 194)

Very little work has been done by way of investigation bearing out a response to change in quality of a mechanical force. In 1803, Knight recorded an investigation in which an increase in wood growth resulted in seedling apple trees from motion due to wind. The lower parts of the stems which were rendered as rigid as possible increased very little in size in comparison to the parts kept in motion by the wind. (3, p. 194-5. Note 107 p. 723)

Unpublished observations made by Dr. W. S. Cooper in 1922 on Monterey cypress indicate that branches swaying to and fro in one plane increased exceedingly on both sides of the center in that plane, like plates. Those branches on which the wind acted constantly from one direction increased abnormally on the leeward side.

Studies made by Boning (8) in 1922 on about 47 species of shrubs and herbaceous plants revealed an unequal wood growth on the upper and lower sides of bent shoots due to mechanical stretching on the upper side and pressure on the lower side. A few showed no difference.

In her studies on the effect of external compression on the structure of roots and stalks, Mme. Bloch¹ (7) in 1920 found that in the effects of artificial compression, simulating that produced by stony ground or rock fissures, some tissue elements are suppressed or altered depending on the conditions to which subjected, while others continue to develop almost normally.

Pieters, (15) in 1896 published a study on the influence of the strain of fruit bearing on the permanent mechanical tissue of the tree. He found that any weakness in fruit bearing shoots, compared with vegetative shoots of the same age, size and apparent vigor, indicated by a decreased xylem development was compensated for by supplementary mechanical tissues--hard bast and liquified cortex and pith cells--which did not occur in the leafy shoots.

In Haberlandt's 1914 edition, he cites, as the most important contribution up to that time on the effects of artificial tension, the work of Vochting. Vochting found

1. Since I could obtain an account of this work only in an abstract of it in the Science Monthly 1:262, 1920, I could not tell whether the effects were due to radial compression of tube or to imprisonment.

that in stems of curly kale placed in a horizontal position with weights attached to the end, the secondary woody cylinder grew more actively on the upper and lower sides where the tension was greatest. This agrees with the preceding observations mentioned. In other experiments of his, pumpkins were allowed to ripen, not as is the usual case, while resting on the ground, but while hanging freely in the air by their stalks, so that they were continuously subjected to considerable longitudinal tension. A general increase in the thickness of the cell-walls was observed, not only in the case of the mechanical tissues but also in that of the parenchymatous ground-tissue; the secondary wood was likewise found to contain an unusually large proportion of mechanical elements. (3, p. 196-7).

PRESENT INVESTIGATIONS

Since so little light has been shed on the subject, the present investigations were undertaken to discover, if possible, by the study of appropriate material what sort of response may take place in mechanical tissue to the strain of tension. A pendant fruit pedicel appeared to afford a good field for this kind of study because it is subjected to a continued and increasing strain of tension. Furthermore, it is a small complete unit, immediately concerned and maturing in a single season. The selection of the apple pedicel as an object of study for the present work was the result of its added advantage of availability, comparative ease in handling, and the possibility of measurement, both of the pedicel and its fruit.

Preliminary Studies at Minnesota

In the summer of 1923 I collected some apple pedicels with their apples from a Patton Greening tree in the horticultural orchard of the University of Minnesota farm, every week between June 6, and August 22, and measured and weighed them. I found that the pedicels did not increase perceptibly in either diameter (the cross sectional area is elliptical) nor in length, nor in weight. (see table 1). The slight increase in diameter at the end of the season was due to a slight fleshening of the cortex as cross sections revealed later. The shortening of the pedicel at

Average Measurements of Twelve Patton Greening Pedicels
Picked at Intervals During the Summer of 1923.

Date picked	Short diameter mm.	Long diameter mm.	Length mm.	Weight gr.	Weight of apples gr.
June 6	1.90	2.33	18.67	0.0778	2.1910
" 13	1.79	2.09	18.00	0.0794	6.3021
" 20	1.99	2.50	17.38	0.0913	10.6729
" 27	2.28	2.76	16.20	0.1034	17.3145
July 6	2.00	2.49	18.67	0.0974	25.2443
" 11	2.18	2.62	16.70	0.0944	35.1548
" 18	2.16	2.74	14.75	0.0780	37.9388
" 25	2.17	2.59	13.96	0.0683	50.3780
Aug. 1	2.04	2.47	16.12	0.0866	64.1613
" 8	1.91	2.34	18.70	0.0956	57.4266
" 15	2.06	2.50	17.50	0.0882	63.0205
" 22	2.10	2.60	17.20	0.1106	75.0254
Sept 26	2.72	3.06	13.60	0.1229	111.5254

the end of the season was due to a slight overgrowth of the apple tissues. Lewis, Murneek, and Cate in their pear harvesting studies found no important change in the average length and diameter of the pear stems, which they measured as well as the fruits. The general shortening of the stems towards the end was also due to the cortex of the pears protruding over the original stem. (12, p. 14-5) Cross sections obtained revealed what to me was most interesting, that by August and September the whole pith had become a mass of stone cells. This agrees with an incidental statement by Pieters to the effect that in the mature fruit stalk of the Rhode Island Greening the greater part of the cortex as well as the pith becomes lignified. (15, p. 119). A few measurements of the width of

the walls of these stone cells showed a tendency to greater thickness in September than in June. The data were too scanty to give reliable results, especially since a different set of pedicels and apples were measured at each picking and the number was not large enough to represent a fair average. The results, however, were interesting enough to lead me to desire to repeat such studies on a more satisfactory basis.

Work at Corvallis, Oregon

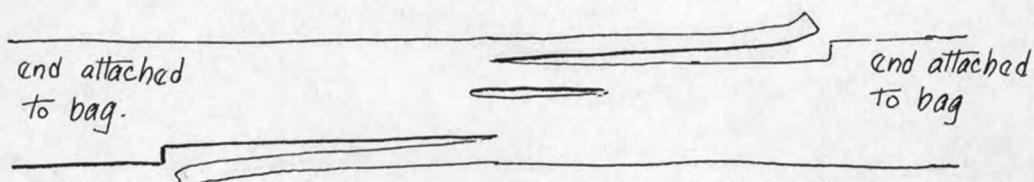
It seemed desirable to get the history of individual pedicels and their apples by periodic data taken through their course of development, that is, by weighing the apples while they were on the tree, without picking them, and by weighing the same ones each time. Furthermore, even though there apparently was a difference in development of stone cell walls between the earlier and later part of the season, might it not be merely a natural development? However, Vochting's pumpkins seemed to indicate that the tension does cause an intensification of cell wall development of the stem, even though the increase in weight is gradual. But suppose that the increased tension were sudden. Suppose the young pumpkin stalks or apple stalks had been made all at once to bear the weight which their fruit would have at maturity, what would be the effect?

In order to obtain such information an experiment was

set up in the experimental orchards at South Farm of the Oregon Agricultural College Experiment Station, with the idea of applying weights to certain apples and comparing the results with normal apples as checks, to discover, if possible, any response in the mechanical tissue of their pedicels to the sudden increased tension. Eighteen Wagoner apple trees, fourteen years old, with wide-spreading branches were selected because the fruit was relatively easy to reach.

Increasing the tension on the growing apples.---In order to apply the experimental tension while the pedicels and fruit were still in an early stage of development, weights were applied between May 19-23, 1925 when the young fruit was still small mostly from $7/8$ to $1\ 1/8$ in. in diameter, but giving promise of developing to maturity. The problem of using weights as a means of increasing the tension on the fruit pedicel called for such that would not injure or interfere with the growth of the apples; that could weather the season and that would lend themselves to the constant motion of the wind without unduly changing the downward pull. Bags of sand with shoulder straps one inch wide and $8\frac{1}{2}$ inches long seemed to answer all the foregoing requirements. Muslin bags were filled with sand to weigh 150 grams each, which was estimated to be about the weight of an apple at maturity judging from the mature weights of the Patton Greening apples weighed the previous

summer. In order to see whether the apple pedicel would endure a greater strain other bags were prepared to weigh twice as much or 300 grams each. 180 apples, numbered consecutively and labeled with celluloid tags were selected as unweighted checks. These checks, located all around the tree from about 2-7 feet from the ground, were distributed, ten per tree. Then 180 apples, numbered with the same numbers and a plus sign, located as far as possible on spurs adjoining the checks were weighted with the 150 gram bags of sand. These weights were applied by inserting the apple through a lengthwise slit cut to one side of the center of the shoulder strap and tied with strips cut from the edge of the shoulder straps.



Finally the 300 gram bags of sand were distributed five per tree, also as far as possible adjoining a check and a 150 gram weighted apple and given the same number but with a double plus sign.

Weighing the apple while it remained on the tree.--

Because the pedicel is subjected to an increasing tension due to the growth of the apple, it is desirable that the

normal rate of increase throughout the season be known. It is for this reason, as well as for a possible relationship between the development of the mechanical tissues in the pedicel and the rate of its apple growth, that apples were weighed. Since the results of the previous work were unsatisfactory because a different set of apples was weighed at each interval it was the aim to find some means of weighing the same fruits throughout the season. Both Whitehouse (17) in his apple variation study during the growing season and Lewis, Murneek, and Cate (12) in their pear harvesting studies, studied the form and increase in the size of their fruits by measuring the longitudinal and transverse diameters with special callipers at two and one week intervals beginning June 25 (1914) and July 12 (1917) respectively. (17, p.4 and 12, p.8). In both these investigations the same fruits were measured periodically. Could not some method be devised whereby the same fruits could be weighed periodically and still remain on the tree? In the search of the literature a method was suggested by the title and annotation of a reference as follows, Clark, K. B. Weighing Bunches of Grapes on the Vines. Ass. Grower 4:8,23,1922,--"By the displacement method and determination of the specific gravity." After some difficulty a simple method was worked out by using the lower sections of graduated cylinders, and various sized beakers (13 in all) ranging in diameter from 2.6 to 9.0 centimeters. These

beakers were calibrated in 5 and 10 c.c. divisions by means of adding water with a pipette, and marking the glass with a file. The beaker most nearly fitting the size of the apple was lifted up under the apple until the apple was completely submerged and the difference in the water level read. The object of using the smallest vessel available for submerging the fruit in question was to minimize as much as possible the error which is difficult to avoid in reading small volume changes in a large vessel.

It is evident from the foregoing discussion that in selecting apples as checks, such ones had to be found which would lend themselves to repeated submersion while allowing the beaker of water to remain in a vertical position for reasonably accurate displacement measuring. For hanging the weights, similar apples had to be selected so that the pull would be vertical and so that branches or spurs would not break when the added weight was applied. Since apples on long spurs in a vertical position, or at the ends of branches were suitable in both cases, a difference of position in choice between checks and weighted should not enter in as an element of error. This also accounts for the fact that whereas 25 apples for observation constitutes a small number compared to the total number of apples on a tree, nevertheless, it represented about all of the suitable apples the tree could accommodate in the given space for experimentation.

Collecting pedicels and recording other data concerning them.--The purpose in collecting pedicels at stated intervals was to observe the development of the strengthening tissues in the checks and to discover when the effect of the sudden increased tension began to be evident. A calendar plan for the taking and recording of the field data was worked out as follows. At the beginning of the experiment (May 19-23, 1925) the length and diameter of each pedicel tagged was measured with a millimeter rule and a calliper, if perchance there might be a relationship between this information and later findings. Also each apple was weighed. At two week intervals the checks were weighed. At four week intervals 2 checks, 2 lesser weighted, and 1 heavier weighted apples and pedicels from each tree were harvested and the pedicels preserved in 95 per cent alcohol for sectioning. Each apple was weighed when picked, the picked checks again in the laboratory where the beaker rested absolutely level--this for the purpose of checking the comparative accuracy of field measurements when the beaker had to be balanced in the hand.

Making sections of pedicels for microscope study.--In order to make a comparative study of the development of mechanical cells at various stages throughout the growing season, some preserved pedicels were put in a 50-50 solution of 95 per cent alcohol and glycerine which has a slight softening effect. A set of the center part of pedicels mostly from one tree was mounted, (not embedded)

with celloidin on wood blocks, for cross sections. This method proved reasonably satisfactory although no complete sections less than 20 microns in thickness could be obtained. Sections are extremely difficult to make since the mechanical tissues are very hard requiring a knife that is very sharp and very strong at the same time. Even though the hard cells can be satisfactorily cut by such a knife on a sliding or rotary microtome the softer tissues are readily torn due either to the strength of the knife or the snapping resistance offered by the hard tissues.

Measuring individual fibers.--While sections are of value in the study of arrangement, occurrence and development of tissues, the discovery of a response or its measurement, after all, must be found in the individual cell since it is the unit out of which a tissue is composed. Allen in his address on The Potentialities of the Cell (4) before the Botanical Society of America, substantiates this view by his statements: "Since all known living matter is organized into cells the possibilities or potentialities that inhere in the constitution of the living matter may be spoken of as the potentialities of the cell. Each function that the cell or one of its parts performs is the expression of a potentiality. (p.388). The passage of the cell from phase to phase is conditioned by stimuli. This is true at least to the extent that when a change is to take place, surrounding conditions determine just what that change shall be. Experiment shows that a very large proportion of the processes of change that constitute life are or can be brought about by environmental changes; and that, as between two or more possibilities at any point in the story, the environment largely determines which alternative shall prevail. To this extent, a particular potentiality may be described as the power of responding, by a certain activity to a definite stimulus or group or class of stimuli." (p.398).

Thus, the increased tension produced by the weights of sand was a normal stimulus suddenly intensified. The stimulus was new in that it occurred prematurely while the tension resisting cells were in the early stages of their development. A factor in the environment of these cells, therefore, was changed. Obviously then, since the apple and its stem did mature normally under this change, an adjustment must have taken place in response to this stimulus. The aim therefore, in this part of the present investigation was to measure individual cells, not as they occur in section but as they occur when seen individually. For this purpose the fiber cells were chosen since these constitute the chief tension-resisting elements of the pedicel. Since cell wall thicknesses or cross sectional areas of mechanical elements had been measured in the work of a number of researches, but not lengths of fibers, it was the aim first to measure lengths for the purpose of determining whether or not fibers in the weighted pedicels would respond by their property of elasticity which they possess in a marked degree (5) and thus become permanently lengthened. Researches recorded by Haberlandt (3) show that the tensile strength of bast, which is dependent on its fibers, lies between 15 and 20 kg. per sq. mm. of cross sectional bast fiber wall area, thus equalling that of wrought iron. It differs from wrought iron in that it is more extensible--at the limit of elasticity from 1-1.5 per cent, whereas wrought iron averages below 1 per cent.

Bast differs also in that the breaking point occurs soon after the elastic limit is reached, whereas a wrought iron rod endures nearly three times as great tension after its elastic limit is reached before it breaks. (p.163).

The weights used in this investigation of necessity could not approach the elastic limit because it dealt with response in the growing tissue and not torn tissue.

In preparing the material for fiber measurement, portions of the preserved pedicels--a 3 mm. length from the end to which the apple was attached--were macerated by the Shultze method described in Chamberlain's Methods in Plant Histology. (1, p.129). It consists in putting a drop of strong nitric acid over a small bit of tissue in a test tube and dropping in a small crystal of potassium chlorate and heating gently over a flame until the tissue is white. The fumes and acid are washed off with, and replaced by water. In order to avoid the possibility of fibers being mixed, each portion of pedicel was macerated in an individual test tube. The macerated tissue was well shaken and drops of it mounted on slides with a drop of glycerine to prevent drying out. These slides were then projected under low power by means of a microprojecting apparatus, and 100 fibers marked on ruled paper. In order to avoid measuring a fiber twice a mechanical stage was used on the microscope. Only fibers whose two tapering ends showed the ends of the cell cavity were measured in order to prevent

measuring broken ones. Although 100 fibers from one pedicel is a small number to measure, these 100 counts were localized in a small area and represented about the complete number that could be seen perfectly in the amount of tissue macerated.

PRESENTATION OF RESULTS

The normal rate of increase of the apple throughout the season.--The curve in figure 5 shows the average number of the cubic centimeter displacement of water of the apples measured at the two week intervals. Since the specific gravity of apples is so nearly 100 (98+%) these figures were not translated into weights. The number of cubic centimeters, therefore, is a near index to the number of grams representing the average weight of the Wagoner apples. The drop in rate shown on July 2, 1925 followed a few days' terrific heat just prior to that date. The drop after September 10th is probably due to the fact since the calendar plan extended only that far most of the best remaining apples were picked at that time, a few of them being allowed to remain as an afterthought. Also the apple crops were harvested during the last half of September. Figures 6,7,8,9, drawn from photographs, taken at four week intervals show typical sizes of the apple during the season.

Since the apples weighted with the double or 300 gram sacks persisted throughout the season as shown by figures 11 and 12 drawn from photographs, only the pedicels of these and none of the lighter or 150 gram weighted ones were used. Obviously if any response resulted, it would more likely be found in those in which the stimulus produced was greater.

C.C. of
Water
Displace-
ment.

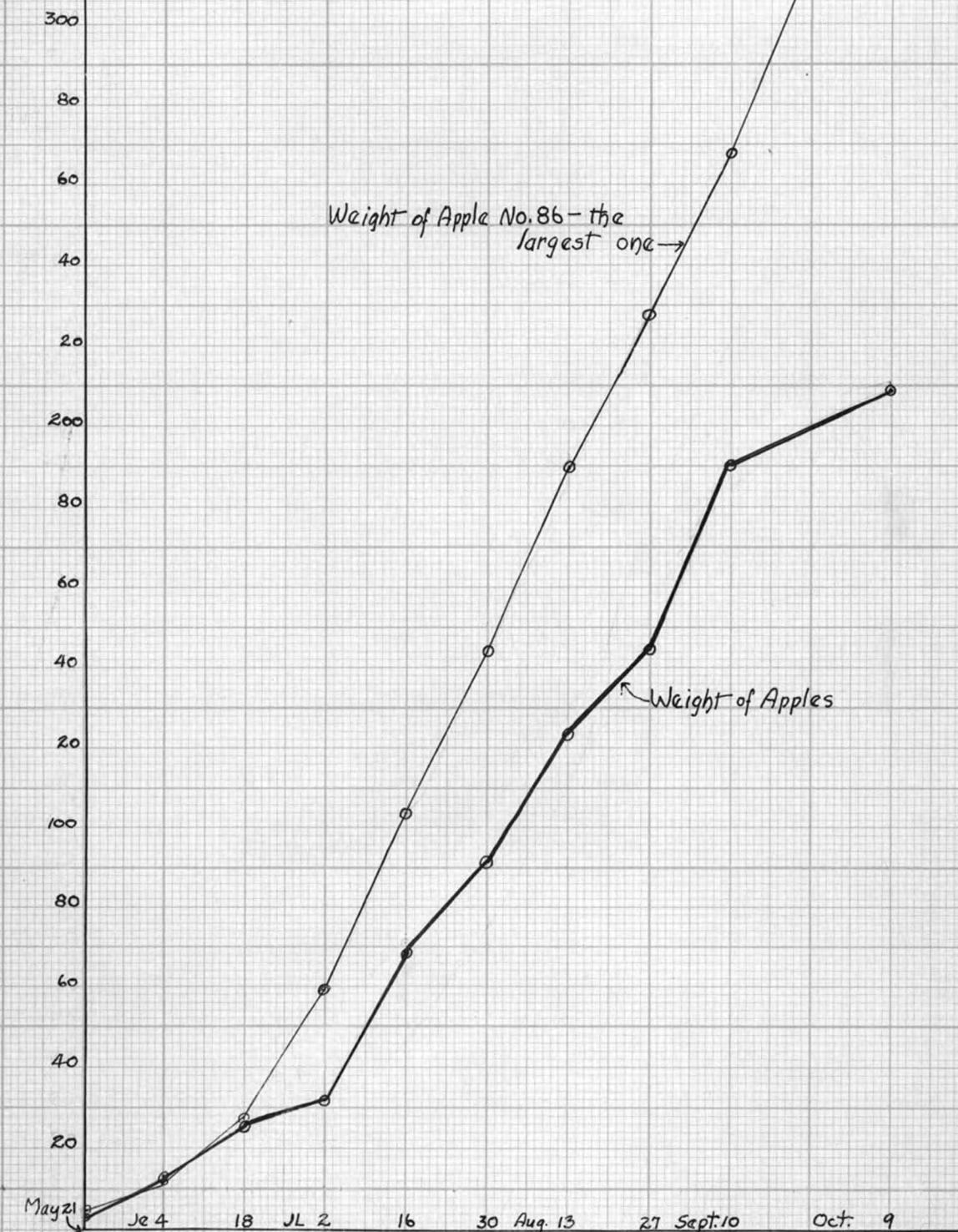


FIGURE 5 - AVERAGE RATE OF GROWTH OF THE APPLES WEIGHED.

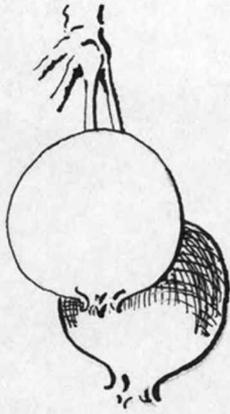


Fig.6 - May 13

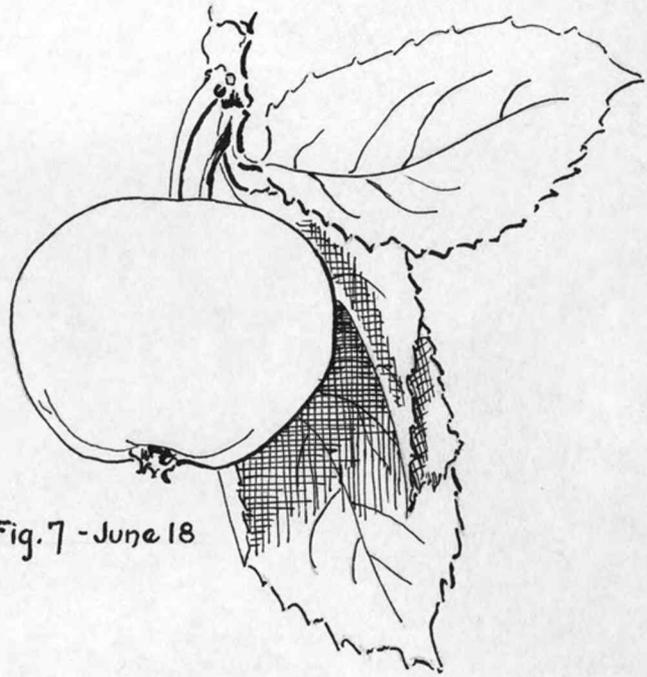


Fig.7 - June 18

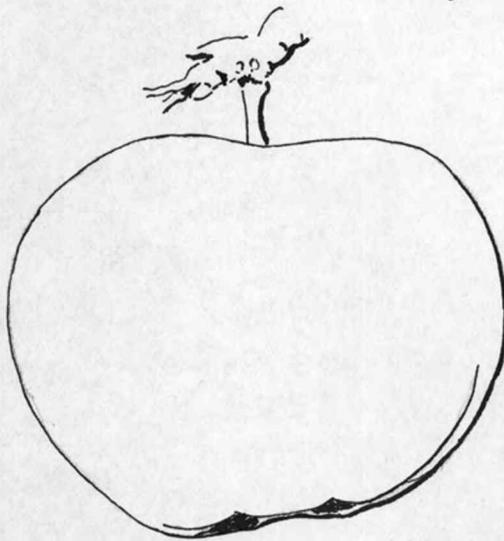


Fig.8 - July 16

Fig.9 - Sept. 10



WAGONER APPLES - NATURAL SIZE.



FIG. 10- A 300 GR. WEIGHT
APPLIED TO AN APPLE, MAY 20

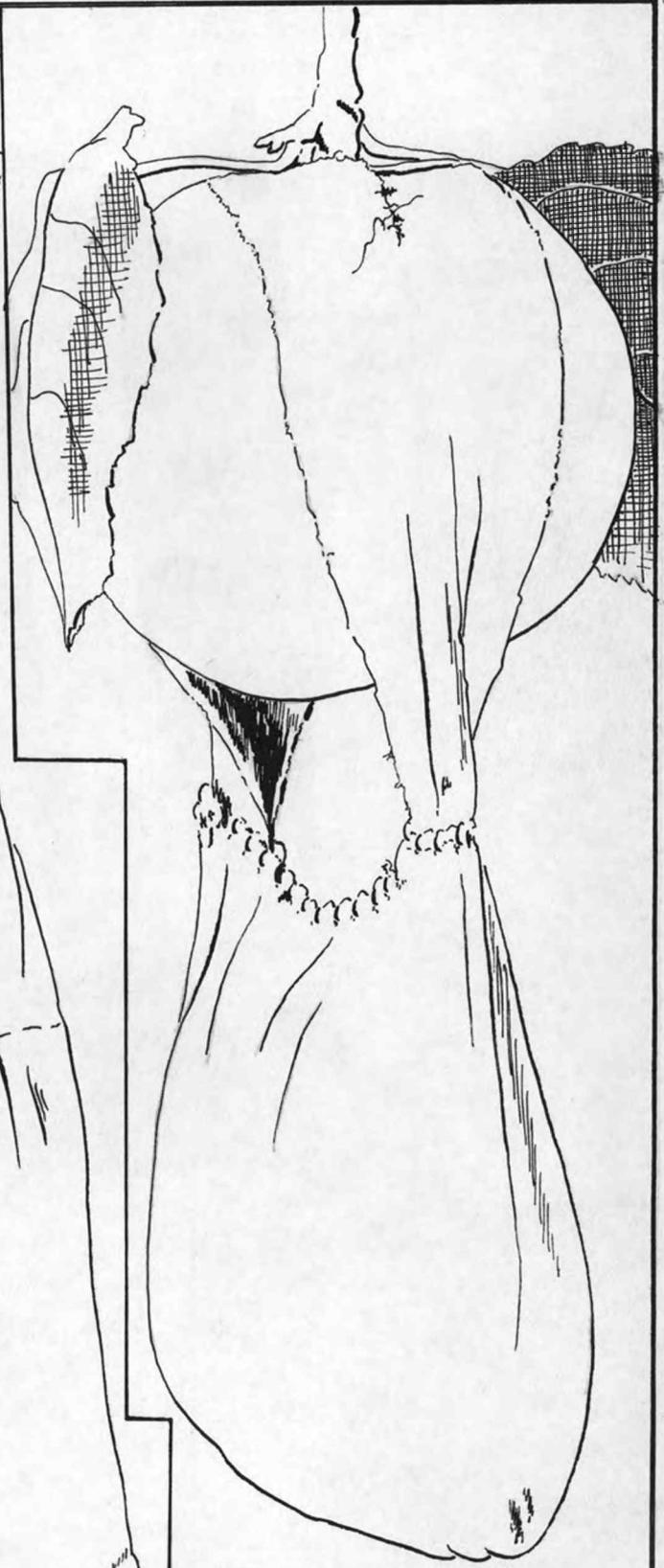


FIG. 11- A WEIGHTED APPLE
MATURED TO AVERAGE SIZE, Oct. 9.

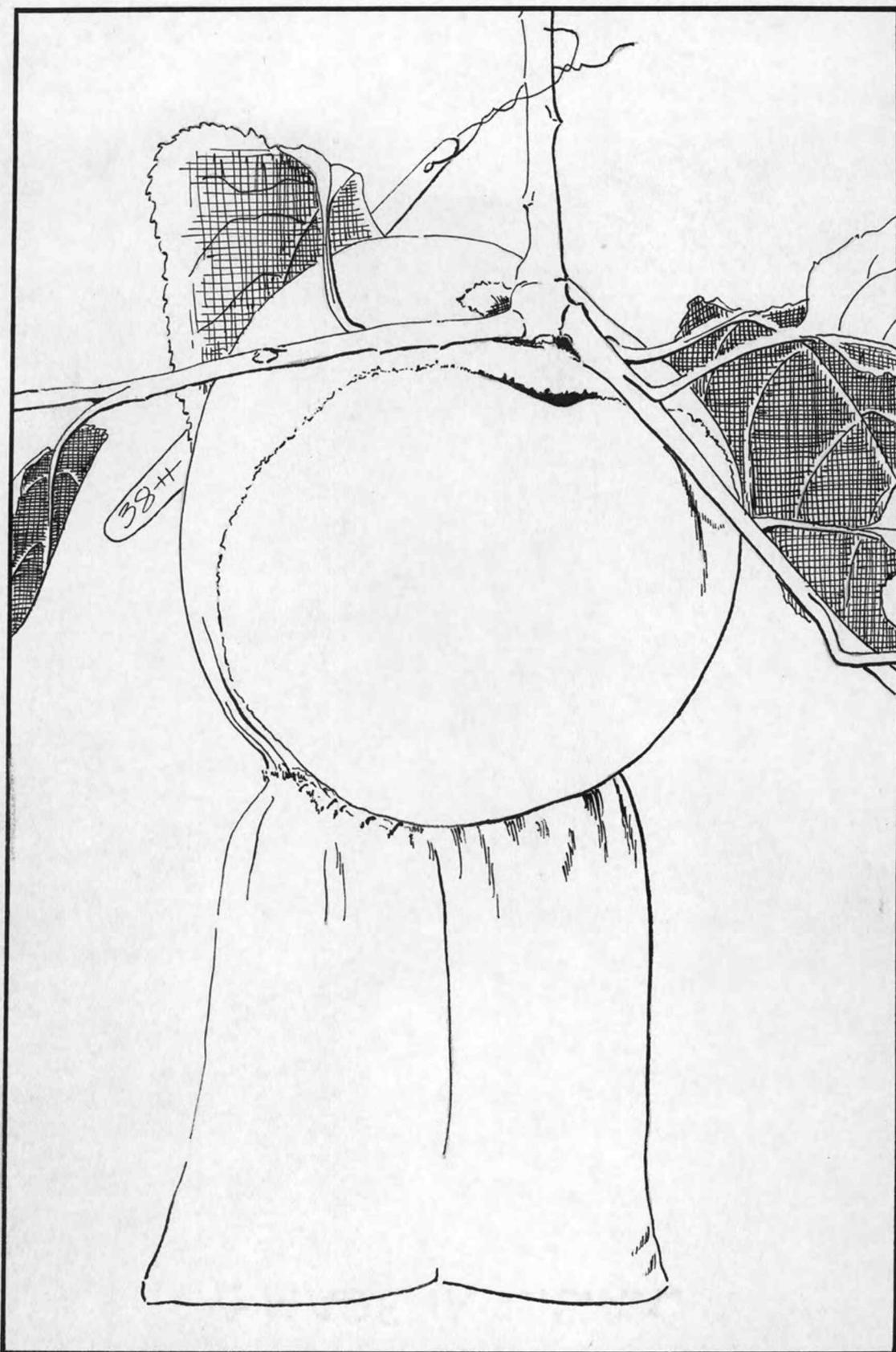


FIG. 12 - Largest Weighted Apple. Wt. May 20 - 2.5 gr. — Oct. 9 - 358.0 gr.

Anatomy of the pedicel.--Nanke (14) in his researches on the anatomy of fruit and vegetative shoots of dicotyledonous woody plants extended his study into the fruit pedicel which he compared with the shoot. He finds in the apple that the cells of the pedicel throughout are smaller than those of the stem. This difference is greatest in the cells of the secondary xylem. Stone cells are found in the pedicel only. The pith has large patches of thick walled elements which do not occur in the stem.

Kline (10) in a paper published in 1886 on studies made on the anatomy of inflorescence axes found that in the need for mechanical strength there is a conflict for position between the mechanical elements and the nutrition elements. Since the mechanical elements in accordance with mechanical principles take the peripheral position. In cross section the vascular bundles are crowded together in the center, which is particularly marked in the fruit stalk, that is, an increase in the amount of cortex at the expense of wood and pith.

While these researches throw some light on the anatomy of the pedicel they are concerned primarily with stems bearing fruits rather than fruit stems and do not cover the anatomy of the pedicel during stages of its development.

The drawings on Plates 1-4 represent a series of cross section diagrams of pedicels made at the intervals indicated, showing the distribution of mechanical

EXPLANATION OF PLATE I

(Supplementary)

Figure a. A cross section diagram of a Wagoner apple pedicel picked April 10, 1926, when the petals were beginning to fall.

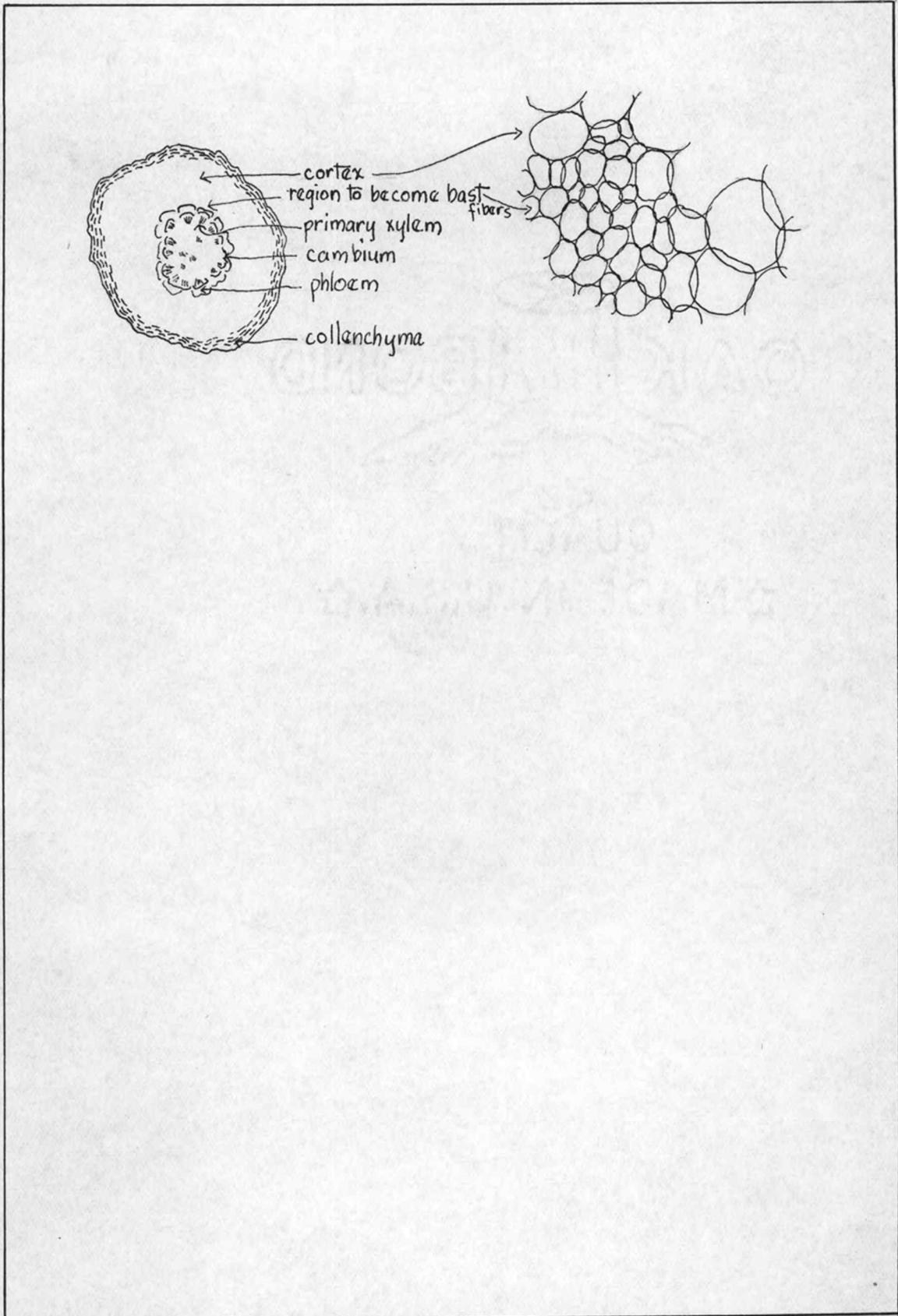
At this stage beginnings of the vascular bundles appear in an irregular ring near the center.

The collenchyma is well developed and serves as the chief supportive element.

A cross section of a pedicel made 20 days later was similar to c on Plate II.

Figure b. A detail of cell structure from a, in the region of fibers just outside of the phloem.

PLATE I.



EXPLANATION OF PLATE II

- Figure c. Are cross section diagrams of 3 pedicels
" e. picked May 20, 1925 from one spur on
" g. tree No. 4. Diameters x24

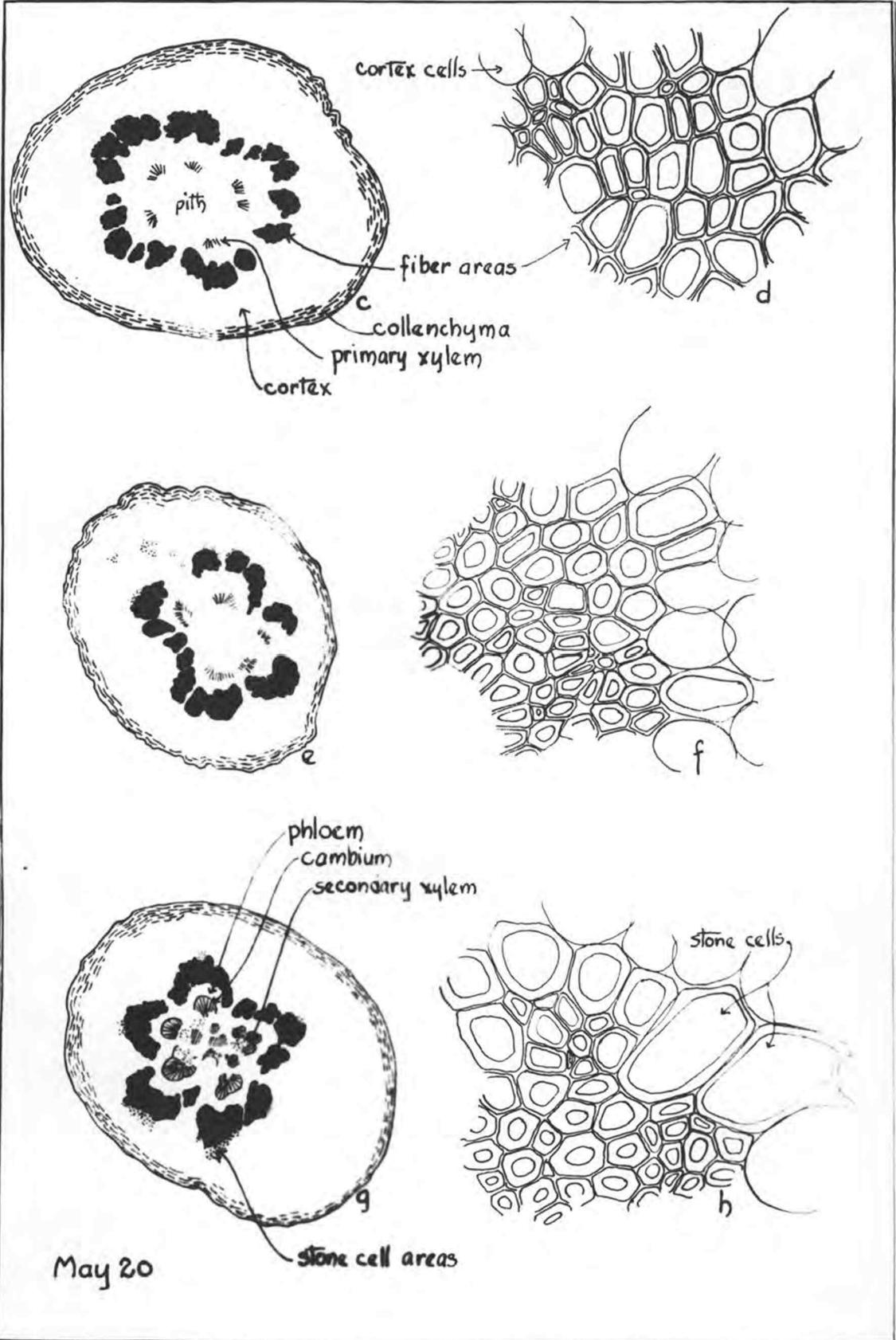
The apples of c and e were very small-- about $3/8$ inches in diameter, displacing 0.5 cc. In these the fiber areas are well differentiated. Stone cells are beginning to appear in e.

In g the cambium and secondary xylem are distinct. The apple of this pedicel displaced 3.2 cc. (Av. for May 20,--3.4).

- Figure d. Corresponding outline cell structure drawings
" f. of portions of the fiber area adjoining
" h. the cortex region. Diameters x2050.

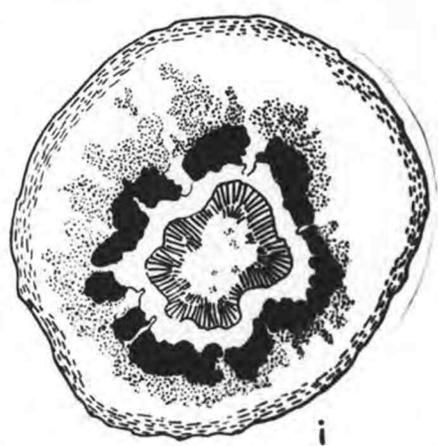
Note that in d the fiber walls are apparently not as thick as in f and h. Also in these some of the cortex or ground tissue cells are differentiating into stone cells.

There is no apparent line of demarcation between the pericycle and the cortex. Morphologically the fibers are in the pericycle region and, therefore, are more correctly called pericycle fibers than bast fibers.

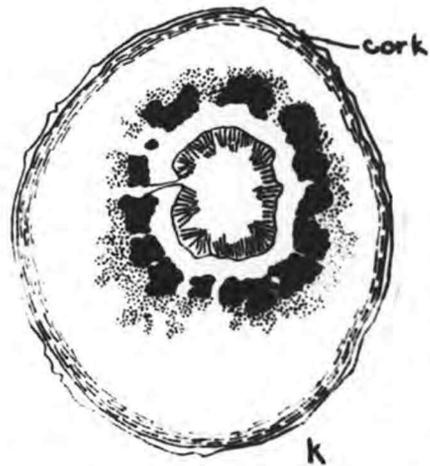
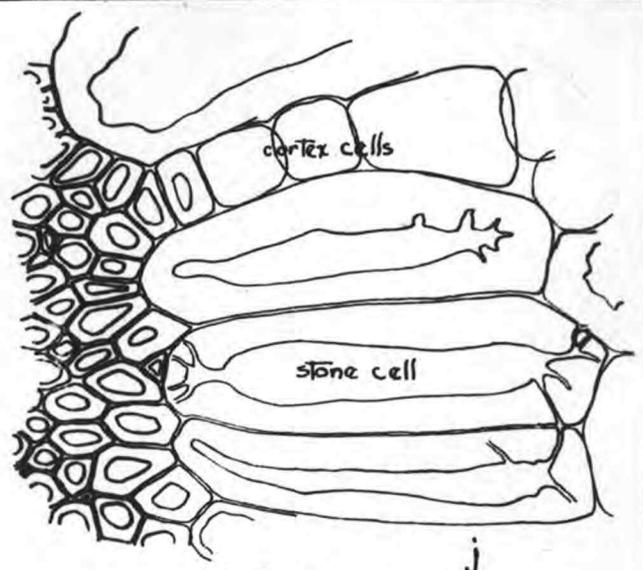


EXPLANATION OF PLATE III

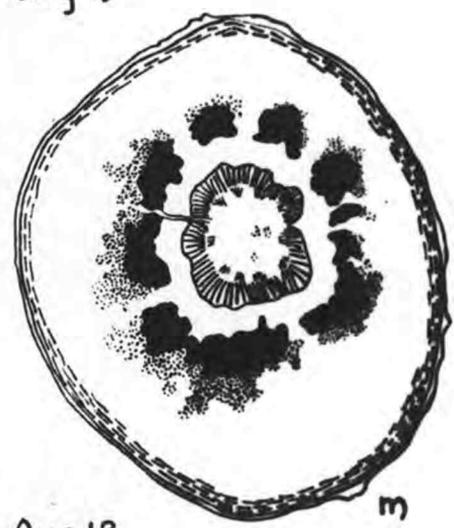
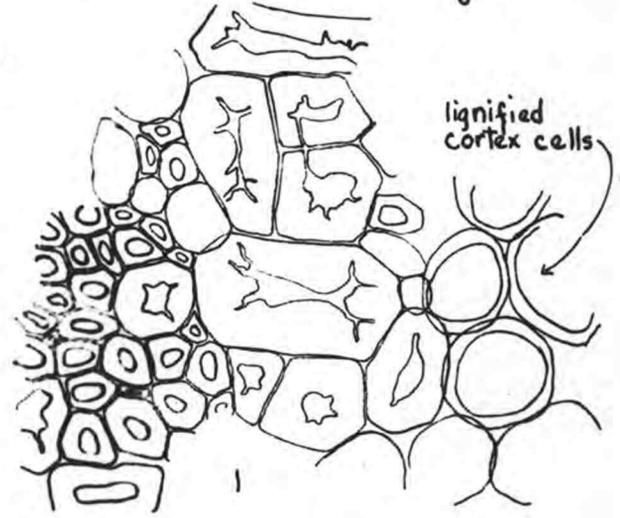
- Figure i. Cross section diagram of pedicel No. 6, tree 1.
Apple displaced 28 cc. (Av. for
June 18,--25.9).
- Figure k. Cross section diagram of pedicel No. 38,
tree 4. Apple displaced 69 cc. (Av. for
July 16,--68.3).
- Figure m. Cross section diagram of pedicel No. 39,
tree 4. Apple displaced 123 cc. (Av.
for Aug. 13,--122).
- Figure j. Corresponding outline cell structure drawings.
" l. Note that the walls of the fibers are
" n. increasingly thicker. The walls of the
stone cells are thicker. In l some
cortex cells are also thicker walled.



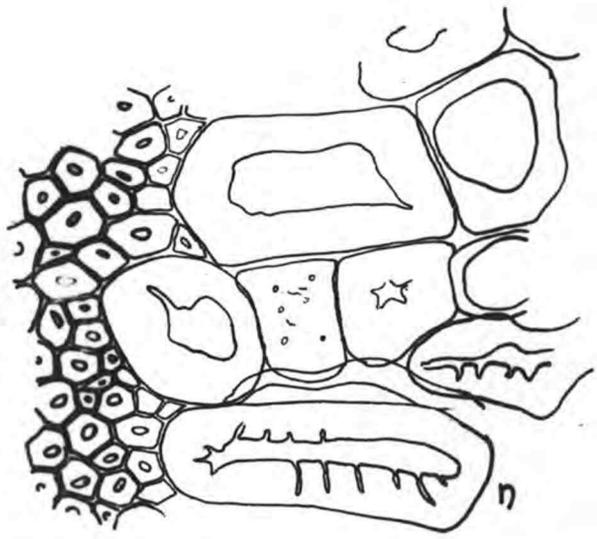
June 17



July 15

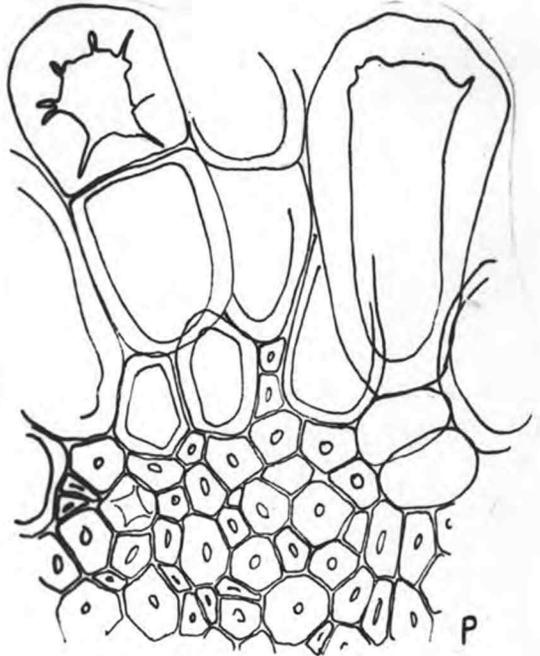
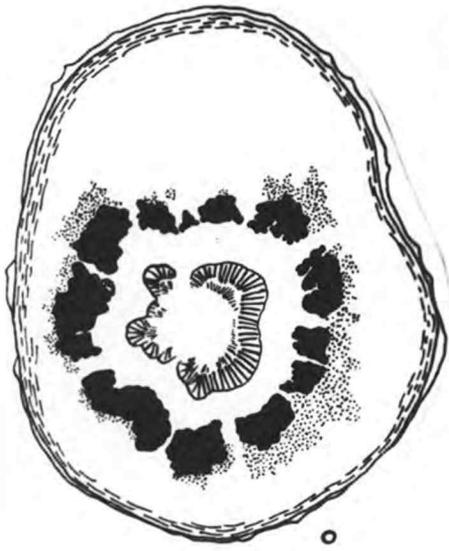


Aug. 12

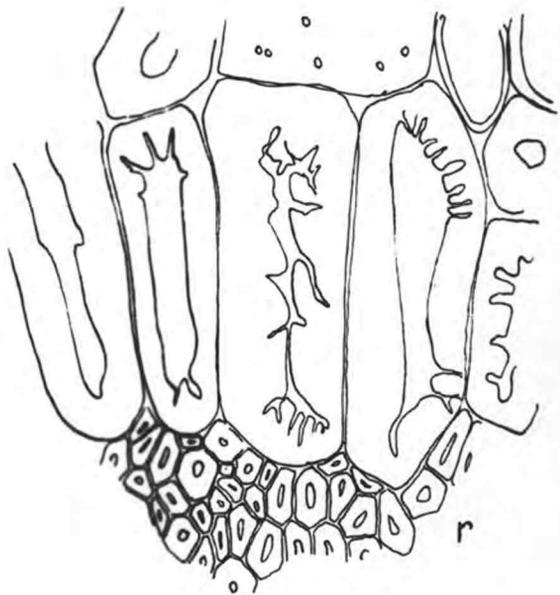


EXPLANATION OF PLATE IV

- Figure o. From pedicel No. 117, tree 12. Apple displaced 258 cc. (Av. for Sept. 10,--190)
- Figure q. From pedicel No. 32, tree 4. Apple displaced 133 cc. (Av. for Oct. 9,--209.3).
- Figure p. Corresponding outline cell structure drawings.
" q. Cell walls are very thick. In these the whole cortex and collenchyma exhibit increased wall thickening.



Sept. 9



Oct. 9

EXPLANATION OF PLATE V

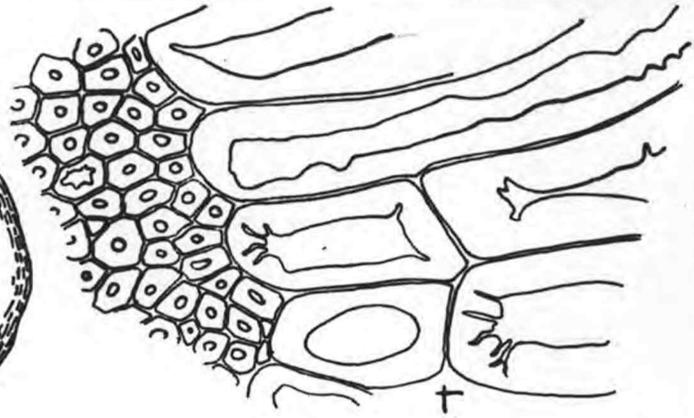
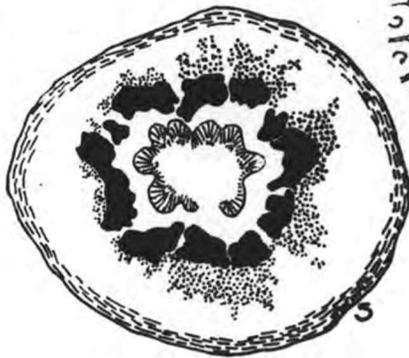
Cross section diagrams and cell drawings of
300 gram-weighted pedicels.

Figure s. Of pedicel No. 35†, tree 4. Apple displaced 28 cc. which is the same as the check of June 17, shown in i of Plate III. Note that the fiber cell walls of t are thicker than those of j in Plate III.

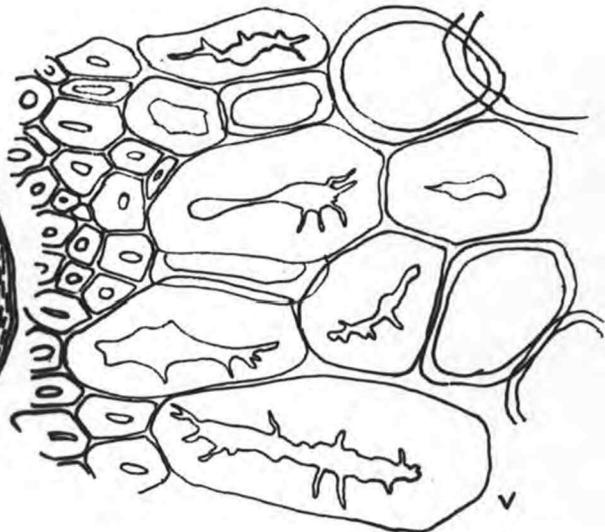
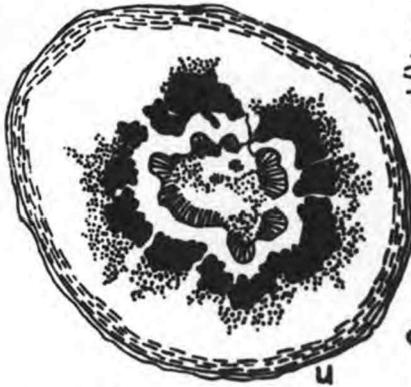
Figure u. Of pedicel No. 31†, tree 4. Apple displaced 51 cc.

Figure w. Of pedicel No. 38†, tree 4. Apple displaced 358 cc. See illustration of this apple in Figure 12.

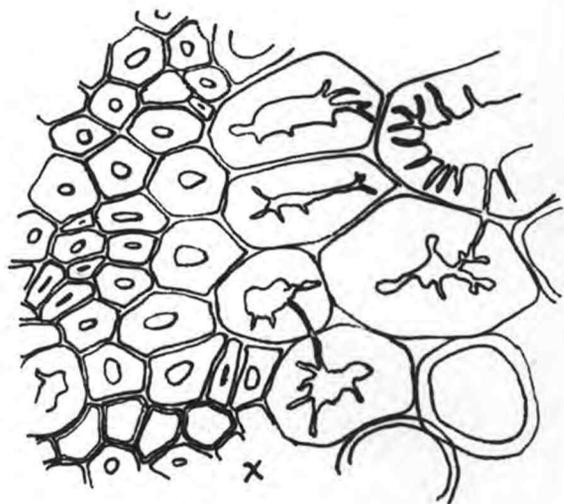
The outline cell structure drawings seem to show that an increase in thickness of the walls of mechanical elements occurs sooner than in the checks.



June 17



July 15



Oct. 9

elements. The diagrams were drawn from tracings made by projecting the cross sections under low power with a 6x eye piece at a distance which increased the diameter about 24 times. The cell structure drawings were made from tracings under high power with a 10x eye piece at a distance which magnified the diameter 2050 times. A study of these cross section diagrams shows how admirably the arrangement of the mechanical elements (collenchyma, stone cells, bast fibers, and xylem) coincides with that of flexible inextensive organs as outlined on page 12 of this paper. It will be noted, particularly in the mature specimens, how the fibers (both in the xylem and the bast, in the pericycle region) which are the tension resisting elements, are aggregated in two broken hollow cylinders near the center. This makes for great tensile strength. The sclerenchyma (stone cells) and collenchyma increase the cross sectional area of mechanical elements and thus also contribute to the power of enduring the pulling strain. The fact that the fiber areas occur not in solid cylinders but in broken, rope-like strands and that the stone cells skirt irregularly around them combines flexibility with the tensile strength. The collenchyma by its continuous peripheral position gives form to the pedicel and protects the softer tissues from collapse.

A study of the cell structure drawings of Plates 1-4 which were taken from a small area of bast fibers adjoining the cortex showing some cortex cells, show how the

walls of the bast fibers gradually increase in thickness as the season progresses. The same development is also shown in the walls of the stone cells although not as evenly. A thickening of the cortex parenchyma cell walls is definitely apparent in June, although the tendency begins to show itself earlier. The collenchyma cell walls also become very much thicker as the season progresses, particularly the tangential walls.

Plate 5 shows drawings at 3 intervals from pedicels weighted with 300 gram weights. A comparison with the June 17th drawings on plate 3 shows that the bast fiber walls of the 300 gram weighted pedicels are thicker than in the normal ones. Also in June the fiber walls are already apparently as thick as they ever will be.

Fiber length measurements.--The results of the fiber length measurements are shown in tables 2 and 3 and presented graphically in figure 13.

The figures in table 2 and 3 were worked out as follows: The mean for each pedicel was found by averaging the lengths of the 100 fibers measured. These lengths were arranged into 6 classes ranging as indicated, each range having its middle point as its value. The number of fibers called variaties, fitting in each range, were tabulated. This constituted the frequency. The difference between the mean and the class value constituted the deviation from the mean. The standard deviation was commuted by extracting the square root of the sum of the frequencies times the

Table 2. AVERAGES AND CLASSIFICATION OF LENGTH, MEASUREMENTS OF FIBERS FROM CHECK OR UNWEIGHTED PEDICELS.

The actual length of the average mean fiber designated 6.25 is 1.15 mm.

Tree No.	Pedicel No.	Mean length of 100 fibers	Frequency of fibers in each class						Standard deviation from the mean	Probable error of the mean
			Class 1	Class 2	Class 3	Class 4	Class 5	Class 6		
			Range	R 3.51-	R 5.51-	R 7.51-	R 9.51-	R 11.51		
			-3.50	5.50	7.50	9.50	11.50	-		
			Val 3.0	Val 4.5	Val 6.5	Val 8.5	Val 10.5	Val 12.0		
1	1	6.36	4	25	50	15	5	0	1.37	.0928
1	4	6.00	3	43	37	15	2	0	1.63	.1102
1	10	6.52	0	27	48	21	4	0	1.59	.1076
2	13	6.92	0	20	47	22	8	3	1.89	.1282
2	19	6.10	4	41	32	20	3	0	1.78	.1205
3	24	6.19	3	32	42	18	4	1	1.81	.1224
4	32	6.13	2	39	40	15	2	1	1.69	.1144
5	42	6.60	2	34	35	18	7	2	2.03	.1374
5	49	6.65	4	28	38	23	6	1	1.96	.1327
9	87	5.89	2	43	38	14	2	0	1.60	.1079
14	134	5.43	4	46	42	7	1	0	1.42	.0959
Total		68.79	28	378	449	188	44	8	18.77	1.2700
Average		6.25	2.5	34.3	40.8	17.0	4.0	.72	1.76	.1154

Table 3.

AVERAGES AND CLASSIFICATION OF LENGTH MEASUREMENTS OF FIBERS FROM WEIGHTED PEDICELS OF CORRESPONDING TREES
The actual length of the average mean is 0.94 mm.

Tree No.	Pedicel No.	Mean length of 100 fibers	Frequency of fibers in each class						Standard deviation from the mean	Probable error of the mean
			Class 1	Class 2	Class 3	Class 4	Class 5	Class 6		
			Range	R. 3.51-5.50	R. 5.51-7.50	R. 7.51-9.50	R. 9.51-11.50	R. 11.51-		
			Val 3.0	Val 4.5	Val 6.5	Val 8.5	Val 10.5	Val 12.0		
1	1#	6.42	1	37	49	9	3	0	1.55	.1045
1	3#	4.59	13	76	9	2	0	0	.86	.0582
1	4#	4.77	13	62	24	2	0	0	1.19	.0806
2	13#	6.84	0	24	39	29	7	1	1.83	.1235
3	24#	6.90	1	21	47	23	6	1	1.75	.1186
4	31#	5.50	1	55	36	7	1	0	1.38	.0934
4	36#	6.54	10	17	38	23	8	1	2.12	.1434
4	38#	5.20	7	56	33	4	0	0	1.22	.0828
5	41#	5.70	10	43	31	11	4	1	1.93	.1304
9	82#	6.68	0	21	51	22	6	0	1.61	.1085
14	134#	5.45	6	50	37	5	1	0	1.39	.0943
Total		64.59	62	462	394	137	36	4	16.83	1.1382
Average		5.87	5.6	42.0	35.8	12.4	3.2	.36	1.53	.1034

Total
Frequency

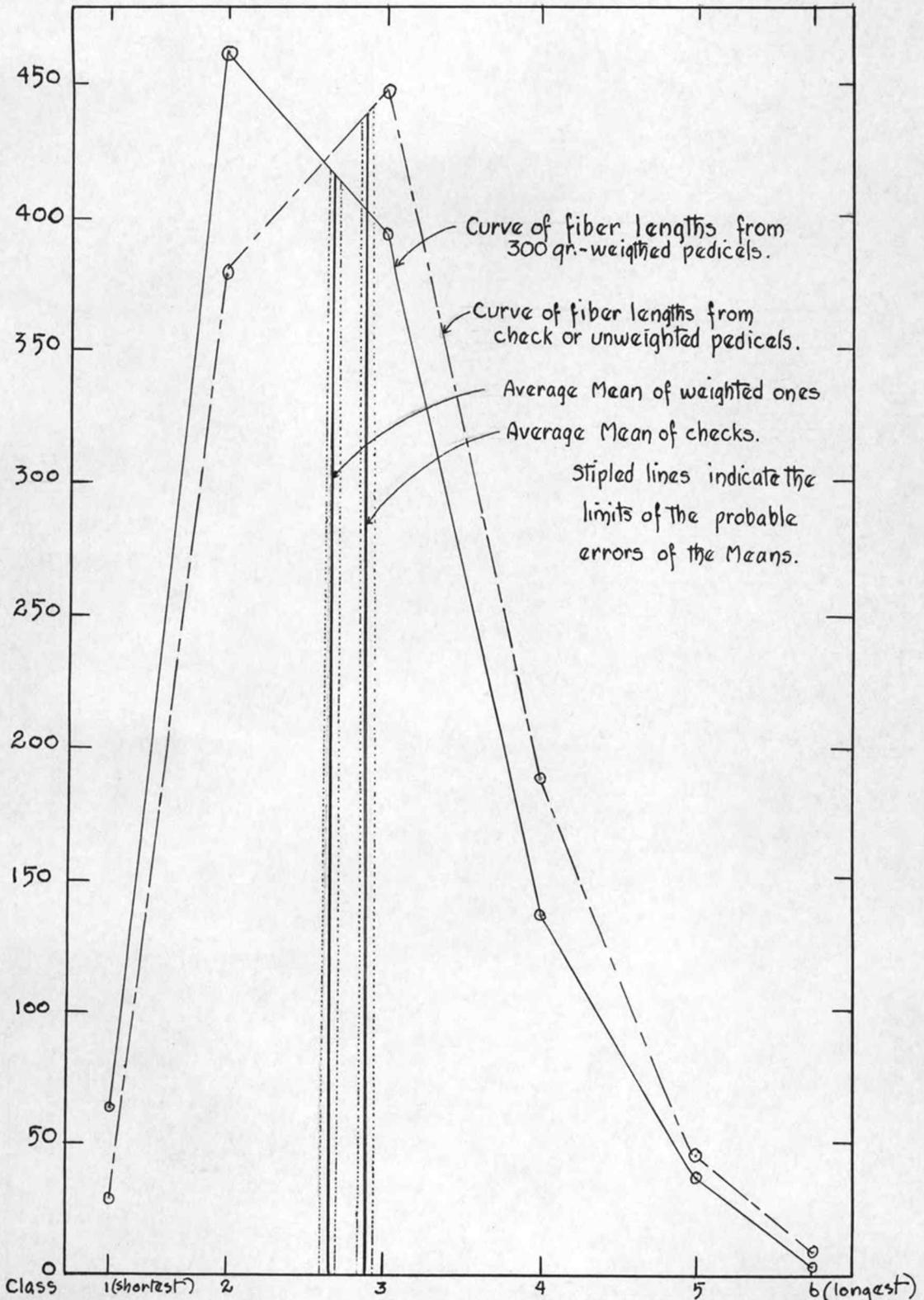


FIGURE 13 - RESULTS OF FIBER LENGTH MEASUREMENTS.

square of the deviations (of the six classes) divided by the total number of the variates, or as represented by

the formula
$$\sigma = \sqrt{\frac{\text{Sum of } f \times d^2}{\text{Total number of variates}}}$$

By means of the standard deviation it was possible to compute the probable error of the mean, as indicated by

the formula
$$\pm .6745 \times \frac{\text{standard deviation}}{\sqrt{\text{Total no. of variates}}}$$

These computations were worked out from methods given by Davenport in his Statistical Methods. (p.15-16). The tabulations of the 11 checks (6 of which were picked July 15th, and 5 on Oct. 9th) were then totaled and averaged as put forth in Table 2. The same was done with the 300 gram-weighted pedicels, set forth in Table 3. Table 2 includes a measurement of 1095 fibers; table 3 measurement of 1098 fibers.

These tabulations show a difference in the average mean length between the checks and the "treated" pedicels --the "treated" average mean being less. This is not what had been anticipated, namely that those fibers on which the tension had been increased might be longer. The graph shows that whereas the difference in the means is not spectacular it does not lie within the inner limits of their probable errors. The polygon of the check measurements approaches the normal curve. This is further indicated by the fact that 5 out of the 11 means come within twice the probable error (on one side of the mean)

and 9 of the 11 means within eight times the probable error.

The graph also presents a skewed polygon, showing a larger number of shorter fibers and a smaller number of longer fibers. This skewness is also further shown by the fact that 1 out of the 11 means comes within twice the probable error, 2 within four times, and 7 within eight times the probable error of the mean.

Relationship between length of pedicel and length of fiber.--The question of a probable relationship between the length of pedicel and the length of fiber led to a tabulation of the average fiber lengths presented in the third column of table 4 arranged in order from the lowest to the highest average. The lengths of their corresponding pedicels were compared in the fourth column. There appears to be no correlation. A trial tallying, according to methods given by Babcock and Clausen, in Genetics in Relation to Agriculture, (p.49-52) showed no semblance of swarming, the distribution of the variations in the four quarters of the tally table being 5,5,5,7. This precluded any necessity for working out the coefficient of correlation.

Apparently also there is no correlation between length of fiber and weight of fruit, the varying weights being pretty well distributed up and down the line in the last two columns of table 4.

When fiber measurements were begun there seemed to

be an indication that fiber length might be a tree characteristic. This led to making comparable measurements from the same trees, as tables 2 and 3 show. The first column of table 4 shows, however, of the seven trees represented, that the different pedicels from one tree are not necessarily bunched among the shorter or longer fiber length averages.

TABLE 4. THE AVERAGES OF FIBER LENGTHS FROM TABLES 2 AND 3 ARRANGED IN ORDER FROM THE LOWEST TO THE HIGHEST, AND COMPARED WITH THE TREE, THE LENGTH OF PEDICEL, AND THE WEIGHT OF THE APPLE FROM WHICH THE FIBERS CAME.

Tree No.	Ped-icel No. of 100 fibers	Mean length	Length of Pedicels in cm.	Weight of Apple in c.c. of displacement. July 15	Weight of Apple in c.c. of displacement. Oct. 9
1	3†	4.59	1.6		147
1	4†	4.77	1.4	64	
4	38†	5.20	2.0		358
14	134	5.43	1.6	81	
14	134†	5.45	1.8	112	
4	31†	5.50	1.9	51	
5	41†	5.70	2.3		250
9	87	5.89	2.2	103	
1	4	6.00	1.6	57	
2	19	6.10	1.7	60	
4	32	6.13	1.7	28	133
3	24	6.19	1.5	50	104
1	1	6.36	2.3	39	139
1	1†	6.42	2.1		227
1	10	6.52	2.0	67	
4	36†	6.54	1.4		107
5	42	6.60	1.8	45	140
5	49	6.65	1.8		191
9	82†	6.68	1.8	68	
2	13†	6.84	1.8	61	
3	24†	6.90	1.6		172
2	13	6.92	1.7	69	
Average of total		6.06	1.79	64	180

In passing from the presentation of results to conclusions it may be of interest to note that at no time

both during setting up this investigation and throughout the course of the season did a pedicel break. There were accidents when applying the weights and weighing the checks. There were also fatalities between field trips.

But in every case where an apple or a weight dropped it was due to breaking of the spur or at the spur. And this was not ~~was~~ due to the fact that the pedicels had at the stage when the weights were applied attained their maximum strength. Even though no measurements of tensile strength were made, at the early stage the pedicel could easily be broken apart whereas at maturity it could not. In fact this is a matter of common experience.

Also, in no case did the pressure of the cloth strap cause an abnormal development of the apple cortex or flesh.

Summary and Conclusions.

The ability of the Wagoner apple pedicel to withstand tension is very great almost from the start. Results of this investigation show that as early as May 13, at a stage of development when the apple is less than an inch in diameter and weighs about 2.5 grams, the pedicel is able to endure at least 143 times the normal weight it is naturally called upon to hold.

The mechanical elements in the Wagoner apple pedicel seem to develop in the following order: Collenchyma and xylem are differentiated first; then the bast (or, ^{more correctly} pericycle) fibers and next irregular amounts of stone cells

out of the cortex fringing the bast fibers. Patches of pith cells may also become sclerified. There appears to be an increasing thickening of the walls of all these cells including the remaining cortex parenchyma and medullary ray cells which goes on almost to fruit maturity.

When compared with normal Wagoner pedicels there appears to be a more rapid thickening of the walls of the bast fibers in pedicels on which the longitudinal tension was artificially increased to the extent of 300 grams.

Fiber length measurements seem to indicate that the artificially increased tension caused a divergence from the normal expressed in the presence of a larger number of shorter and a somewhat smaller number of longer fibers.

The displacement method as used in this investigation seems to be a highly satisfactory method for weighing the growing fruit on the tree, expeditiously, safely, and with reasonable accuracy. It has been found, however, that unless a particular fruit is weighed at the same hour of the day at each successive weighing, errors will be liable to creep into the growth curve thus obtained due to the rapid rate of weight increase which the fruit undergoes even within a single day.

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