# The Influence of Fruit-bearing on the Development of Mechanical Tissue in some Fruit-trees<sup>1</sup>.

#### $\mathbf{B}\mathbf{Y}$

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#### HISTORICAL.

THE attention of botanists appears to have been first drawn to the difference between the anatomical structure of the flower-stalk and that of the leafy stem by the work of Oels in  $1879^2$ . Oels studied the Droseraceae, and found little difference between the structure of the axis of inflorescence and that of the leafy stem.

In a paper published in 1886, Klein<sup>3</sup> states that on passing upward from the axis of an inflorescence into the pedicels of the individual flowers the following changes were observed :— (1) an increase in the amount of cortex, this increase being at the expense of the wood and pith, chiefly at the expense of

<sup>2</sup> Oels, W., Bau des Stengels und der Blüthenstandaxe bei den Droseraceen. Inaug. Dissertation, Breslau, 1879. Ref. in Bot. Jahresbericht, 1879, 1. Abt., 43.

<sup>3</sup> Klein, O., Beiträge zur Anatomie der Inflorescenzen. Inaug. Dissertation, Berlin, 1886. Ref. in Bot. Jahresbericht, 1886, 1. Abt., 901, and Bot. Centralblatt, 1887, 32; 107-110.

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<sup>&</sup>lt;sup>1</sup> The laboratory work for this paper was done under the direction of Prof. F. C. Newcombe in the botanical laboratory of the University of Michigan. The writer desires to thank Prof. Newcombe for his kindness and assistance, not only while under his immediate direction, but also while preparing the notes for publication.

the latter; (2) in the flower-stalk there was often no pith, because the bundles were crowded together in the centre. This became even more marked in the fruit-stalk, in which the necessity of an abundant supply of building-material and of mechanical support for the fruit resulted in the bundles taking a more central position.

Nanke<sup>1</sup> in 1886 worked on *Pirus Malus* and on *P. com*munis, as well as on several other plants. He found that the cells in the fruit-stalk were smaller than those in the leafy shoot. This difference was most conspicuous in the woodcells.

In 1887 Dennert<sup>2</sup> published the results of an examination of 180 species. He found an increasing delicacy of structure in passing from the leaf-shoot into the axis of inflorescence and thence into the pedicels. This change consisted in a weaker development of wood and pith from below upward. Dennert found that at the time of ripening of the fruit there was an increase in the development of mechanical tissue. This was manifested by an increase in the extent of xylem and in the thickness of the walls of the wood-fibres. The medullary rays of the stem were usually lacking in the fruitstalk. An increase of hard bast did not occur where there was an abundance of wood, and vice versa.

In the same year Reiche<sup>3</sup> presented some work on additional species. His work confirms the results obtained by preceding authors.

In all this work the flower-stalk or the fruit-stalk was compared with the leafy stem. It was a study in the adaptation of organs to the demands made upon them, as

<sup>3</sup> Reiche, K., Beiträge zur Anatomie der Inflorescenzen; Berichte der Deutschen Bot. Gesells., 1887, V, 310-318.

<sup>&</sup>lt;sup>1</sup> Nanke, W., Vergleichend-anatomische Untersuchungen über den Bau von Blüthen und vegetativen Axen dicotyler Holzpflanzen. Inaug. Dissertation, Königsberg, 1886. Ref. in Bot. Jahresbericht, 1886, 1. Abt., 902, and Bot. Centralblatt, 1886, 32, 33; 145–147.

<sup>&</sup>lt;sup>2</sup> Dennert, E., Metamorphose der Blüthenstandaxen: Bot. Hefte, Forschungen aus dem Bot. Garten zu Marburg, Heft 2, 128–217, 1887. Ref. in Bot. Jahresbericht, 1887, 2. Abt., 647.

manifested in their histology. The same may be said of Laborie's work<sup>1</sup>, although he used fruit-bearing and vegetative shoots, instead of comparing fruit-stalks with vegetative This brings him nearer to the purpose of this paper, shoots. although he kept in view the study of adaptation to use as the principal end of the work, and made a more detailed histological study than is here contemplated. He found a marked preponderance of parenchymatous tissue, both cortical and medullary, and a more feeble development of the fibrovascular bundles, in the fruit-bearing shoot. The primary bast was nearly always lacking in the fruit-bearing shoot, or if present it was thin and scattered. In this shoot also the crystal-bearing cells and sieve-tubes were more abundant; and in the xylem there were fewer fibres, their place being taken by wood-parenchyma.

The first paper I found in which the influence of fruitbearing on the structure of the woody axis was considered was one by Sorauer<sup>2</sup>, who, in 1880, published the results of an investigation on the effect of fruit-bearing on the development of wood in some fruit-trees. I regret that I have not had access to the original paper, but I have made use of two excellent abstracts, one in the Bot. Centralblatt for 1880, p. 453, and one prepared for me by Prof. F. C. Newcombe while at Leipzig. The latter paper has been especially helpful, since it gives the gist of Sorauer's thought in a few concise quotations.

Sorauer made comparative measurements of the diameters of internodes in shoots of wild and cultivated pear-trees, and also of fruit-bearing and leafy shoots on cultivated trees. From these measurements he concluded that cultivated varieties are weaker (*weicher*) than wild ones, and that fruitbearing shoots are weaker than leafy ones; also, that in any

<sup>&</sup>lt;sup>1</sup> Laborie, Note sur les variations anatomiques et la différentiation des rameaux dans quelques plantes, Compt. Rendus, 1883, 97; 342.

<sup>&</sup>lt;sup>2</sup> Sorauer, P., Beiträge zur Kenntniss der Zweige unserer Obstbäume. Forschungen auf dem Gebiet der Agrikultur-Physik, 1880, Band III, Heft 2. Ref. in Bot. Centralblatt, 1880, 1; 453.

shoot the base is firmer than the apex. The interpretation of the term 'weicher' to mean mechanically weaker as well as softer seems justified by a sentence from the abstract in the Bot. Centralblatt, as follows: 'Bei den Kulturvarietäten bildet der Holzring einen kleineren Theil des Dickendurchmessers eines Zweiges als bei den Wildlingen. "Kulturvarietäten sind weichholziger," sagt die Praxis.' The entire argument also tends to show that the thought in Sorauer's mind was that a shoot on a cultivated tree was less able to bear mechanical strain than one on a wild tree. He tabulated his results to show the different percentages of wood and of cortex in the shoots examined. These percentages are in terms of the pith. No reason for using the measure of the pith as a basis is given in the abstracts, but there is one objection to this method which I wish to point out. The apparent difference in the relative amounts of wood in the different shoots is much greater than it would be were the percentages given in terms of the diameter of the shoot. Sorauer's last table, in which he summarizes his results, will serve as an illustration :---

		Cortex.	Wood.	Pith <sup>1</sup> .
Wild pear .	•.	75 %	80 %	100 %
Cultivated pear	•	91.4 %	58.2 %	100 %

This shows a considerable difference in the percentages of wood and cortex; but, if the percentages are given in terms of the diameter, we have the following for the same shoots:—

	Cortex.	Wood.	Pith.
Wild pear .	36.6	39.6+	23+
Cultivated pear	45 +	29+	26

The actual measurements from which all the above percentages were determined are as follows :----

	Cortex.	Wood.	Pith.	Wood.	Cortex.
Wild pear	24.8	27.9	33.3	25.4	25.2
Cultivated pear :					
Base of internode	58.7	42	67.3	42.7	72.3
Middle of internode	66.3	41	76.5	41.2	65.5

<sup>1</sup> The pith is not in the original, but it is put here for the sake of clearness.

When we use the diameter of the shoot as a basis, a truer conception is afforded of the difference between the two shoots; since the important question is not what relation the size of the wood-cylinder bears to that of the pith, but what relation it bears to the diameter of the shoot. It must be borne in mind, too, that, although the wood does not increase in the same proportion as does the cortex, yet there is a considerable increase in the diameter of the xylem-cylinder; and it still remains to be shown that it is necessary for the well-being of the tree that the proportion of increase shall be the same in all the tissues.

Sorauer thinks that the increase in cortex is due to the need for greater food-supply, and he states that the increased proportion of parenchymatous tissue brings with it a greater liability to injury by frost. Finally, he claims that absolute size has no value in a comparison of results. It is, he says, the proportionate amount of xylem that determines the strength of a shoot.

In a later paper Sorauer<sup>1</sup> reiterates his former conclusions. He also attributes to over-cultivation certain swellings on shoots, which he finds are due to a parenchymatous change in some of the wood-cells. I have not found any of these growths, and cannot therefore treat of them in this paper.

The inference drawn from Sorauer's work is that cultivation, and more directly fruit-bearing, may become injurious to a tree by reason of the greater development of cortex and the proportionally smaller amount of xylem produced in the fruit-bearing shoot, which renders it weaker mechanically and more liable to injury by frost.

I shall present here a study of the effect of fruit-bearing on the permanent mechanical<sup>2</sup> tissue of the tree, in order to

<sup>&</sup>lt;sup>1</sup> Nachweis der Verweichlichung der Zweige unserer Obstbäume durch die Cultur. Zeitsch. f. Pflanzenkrankheiten, Bd. II, 1892, pp. 66-70 and 142-148.

<sup>&</sup>lt;sup>2</sup> By 'mechanical tissue' is meant all those collections of cells having thick and lignified walls, and serving to give strength and firmness to the shoot. Since the wood-cylinder is the principal collection of such cells, and is the only one capable of accurate measurement, most attention will be given to it, with incidental reference to supplementary mechanical cells when these are of importance.

show the influence upon any tissue-system of the strain to which a tree is subjected in the production of fruit and seeds.

#### MATERIAL AND METHODS.

The trees studied are Apple, Pear, Peach, and Plum. The shoots to be compared were selected with reference to similarity in size and vigour, and were taken in each species from the same tree, often, indeed, from the same branch, in order to avoid, as far as possible, the influence of dissimilar conditions. When collected, these shoots were numbered and put into 50 per cent. alcobol, in which, to avoid unequal shrinkage, all were left for the same length of time.

To study the shoots, free-hand cross-sections were made, and the tissues measured with an eye-piece micrometer under a power of about 100 diameters. The measurements were made in two diameters at right angles to each other, and the average thickness of the zones of tissue determined<sup>1</sup>. For comparing fruit-bearing and vegetative shoots these figures were reduced to percentages, which are given in terms of the diameter of the shoot. The figures were carried to two decimal places, and the remainder, if less than 0.005, was ignored, and if greater was counted as 0.01 and added to the result. Further details concerning the material and methods used will be given when the different species are discussed.

#### DISCUSSION OF SPECIES.

The Apple<sup>2</sup>.—A study of the influence of fruit-bearing upon the mechanical tissue of a tree involves two points: (1) the immediate and temporary effect, and (2) the permanent effect.

<sup>1</sup> For illustration a sample measurement is given as follows :							
		Cortex.	Wood.	Pith.	Wood.	Cortex.	
Section 2 pear	First diameter Second diameter	70				70	
Section 2, pear	Second diameter	73	45	137	60	90	
	rage						
<sup>2</sup> The trees selected	for study were of	the Rho	de Islan	d Gree	ning var	riety.	

The first point can best be studied by a comparison of oneyear-old fruit-bearing shoots and one-year-old vegetative shoots, while a study of the second point requires that such shoots shall be chosen as promise to become permanent parts of the tree. Shoots fulfilling these conditions are found at the ends of the branches. Much of the fruit on both the Apple and the Pear is borne on short lateral shoots, which persist for a term of years, but which never become a part of the body of the tree. These shoots are known as 'fruit-stubs.' Their structure and its relation to the question under consideration will not be discussed in this paper.

By a one-year-old fruit-bearing shoot is meant that part of the terminal growth made during the season of collecting, and which lies between the scars left by the preceding winter's bud-scales at one end, and the bases of the fruit-stalks at the other. When collected in the fall, these shoots have completed one year of growth from their formation in the buds the previous year. The vegetative shoots selected occupied the same relative position, and were of the same age as the fruit-bearing shoots.

When growth begins in spring, the axis of the flowerbud lengthens rapidly, and bears at its apex a cluster of blossoms. Its complete growth in length is soon reached, and its continued vegetative existence is assured by the production of one or more lateral buds, which may or may not grow out into shoots during the same season. The fruit-bearing shoots average about 1.5 cm. in length, and are always more or less swollen. The swelling begins at the basal zone of scars, and is greatest at the apex of the shoot, just below the scar left by the breaking away of the fruit-stalk. By this scar, as well as by the swelling, a portion of a branch that has borne fruit during its first year may be recognized even until twelve years old. The age of such a part may be readily determined by counting the zones of bud-scars left at the base of each year's growth.

The shoots, both fruit-bearing and vegetative, were studied from cross-sections made serially from the basal zone of scars.

For a proper comparison of tissue-masses it was important that the sections should be cut at points having the same relative position. The basal zone of scars offered such a point, therefore only sections taken from this point were used for comparative measurements.

The material was studied with reference to the following questions :---

(1) Is the xylem-cylinder in a one-year-old fruit-bearing shoot less well developed than in a vegetative shoot of the same age and apparent vigour, and does it form a smaller proportion of the diameter of the shoot?

(2) What influence does fruit-bearing exert upon the lignification of cell-walls?

(3) Does the fruit-bearing shoot contain any supplementary mechanical tissue formed to supply a possible lack of development in the xylem-cylinder?

Although a detailed histological study of the swollen part of the fruit-bearing shoot is not contemplated, a general sketch of the arrangement of tissue, as found in a shoot gathered during October, may properly precede the study of tissuemasses.

At the base of the year's growth the structure is fairly uniform on all sides. The cortex is compact, the xylemcylinder is dense, and the walls of the wood-cells are well lignified. A little above the basal zone of scars, the cortex begins to enlarge and intercellular spaces become common. At this point also the wood-cells show thinner walls, though the thickness of the xylem-zone increases somewhat. Above the middle of the shoot, the symmetry of the wood-zone becomes disturbed to a marked degree. The bulk of the xylem is on the side of the lateral vegetative bud, and here also the wood-cells have thicker walls than those on the opposite side. Nearer the apex the walls of the wood-cells on the side nearest the fruit-stalk are still thinner, often indeed so thin that it becomes impossible to determine the exact position of the cambium. The cortex, on the other hand, greatly increases in size. The cells are larger, the intercellular

spaces more frequent, and the supply of crystals and of starch is abundant.

In the upper part of the shoot the parenchymatous character of the cells increases until, on the side nearest the fruit-stalk, very little wood is present, and such secondary wood-cells as are formed are not lignified. Above the lateral vegetative bud there is no cambium, and no secondary wood appears; but here the supplementary mechanical cells, bast and sclerenchyma, become prominent. Groups of sclerenchyma-cells appear in the cortex and in the medullary rays; the pith is usually lignified; hard bast is present in great quantity and continues, but decreases in amount down to the base of the shoot, where it disappears.

The presence and arrangement of the hard bast is interesting. In the fruit-bearing shoot it appears in great abundance, its distribution being the reverse of that of the wood, namely, the greatest amount at the apex, where there is least wood, and decreasing until there is none at the base, where the wood is well developed. In vegetative one-year-old shoots of Rhode Island Greening, I found no bast-fibres. In the mature fruit-stalk the greater part of the cortex as well as the pith becomes lignified.

It is clear that the upper portion of the fruit-bearing shoot has a weak development of xylem. The wood-cells decrease in number and in the thickness of their walls until the xylem disappears entirely. This is, however, the case only in the upper portion of the shoot, which subsequently dries up and falls away. But this weakness is more than compensated for by the abundant supply of well lignified sclerenchyma and hard bast-cells. These are found in groups and bundles where the xylem is weak, decreasing where the latter becomes strong.

The comparative development of the xylem-cylinder at the bases of the fruit-bearing and vegetative shoots had, of course, to be determined by measurements of the tissue-zones in the cross-sections of the two kinds of shoots. The results of these measurements are embodied in the tables given subsequently.

The first table shows the percentage of each tissue and the amount of difference in the development of the tissues in the shoots. In the second table are given the actual measurements of the tissue-zones. These furnished the data from which the percentages in the first table were derived.

TABLE 1.—Average percentage of tissue in one-year-old shoots of Rhode Island Greening Apple.

	Cortex.	Wood.	Pith.
	Per cent.	Per cent.	Per cent.
Twelve vegetative shoots .	40·74	21·48	37·77
Twelve fruit-bearing shoots .	47·97	19·36	32·66
	+ 7.23	- 2.12	- 5.11

The percentages given in the above table were computed from the figures in the following table :---

TABLE 2.- Average absolute amount of tissue in 1-

	Cortex.	Wood.	Pith.	Total.
Twelve vegetative shoots	90.6	47.77	84	222.37
Twelve fruit-bearing shoots	102.8	41.50	70	214.30
	+ 12.2	-6.27	- 14	-8.07

Both the above tables show a larger amount of cortex in the fruit-bearing than in the vegetative shoot, while the wood and pith are more abundant in the latter. The difference in the amount of wood is small, reaching little more than 2 per cent., or only 94.05 micromillimetres in absolute measure. At the base the fruit-bearing shoot is smaller than the vegetative shoot. The characteristic swelling begins a little above the basal zones of scars. Above this point both the cortex and the wood increase in size, but the proportion of cortex increases most rapidly.

To determine the relative thickness of the walls of the

<sup>1</sup> In terms of the spaces of the eye-piece micrometer. Each space equals 15 micromillimetres.

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wood-cells in the fruit-bearing and in the vegetative shoots, sections were taken near the bases of both; camera drawings were made of the wood-cells in a certain area; and the paper covered by the drawing was weighed. The portions representing cell-cavities were then cut out and the remainder again weighed. It was found that the weight of the paper representing cell-wall was 63.64 per cent. of the weight of the entire section in the case of the vegetative shoot, and 46.72 per cent. in the fruit-bearing shoot. This difference in the thickness of the walls became greater near the apex of the shoot, where many of the cells remain thin-walled until the following year, when their walls become thicker and are The lignification of the wood-cells proceeds from lignified. below upward, and from the younger secondary cells inward to the older primary ones. The primary vessels themselves are always first lignified, but the cells surrounding them and the secondary cells, formed early in the season, remain softwalled until after the more lately formed secondary cells have become lignified.

The figures given above as representing the relative thickness of the walls of the wood-cells in the two kinds of shoots must not be regarded as average ones, since only one test was made. But there is no doubt that, as a rule, the woodcells in the one-year-old fruit-bearing shoot have thinner walls than the cells in vegetative shoots of the same age.

The young fruit-bearing shoot must support the weight of the apple, but ample provision has been made for this in the abundant supply of hard bast and sclerenchyma. In view of this splendid development of supplementary mechanical tissue, the slightly smaller proportion of xylem in the fruitbearing shoot cannot be considered a serious weakness for the first year. But it remains to be seen whether the relations existing at that time continue during the life of the shoot. To answer this, small branches were gathered, portions of which, now three and five years old, showed by their swellings and fruit-scars that they had borne fruit during their first year's growth. Other portions of branches were gathered, of the same age as the first, but upon which fruit had never been borne<sup>1</sup>.

A study of these shoots showed a remarkable development in the fruit-bearing ones, both in size of the xylem-cylinder and in the thickness of the walls of the wood-cells. Most of this increase had been on the side nearest the fruit-scar, thus making the radii of the xylem-cylinder more nearly equal. The walls of the wood-cells were apparently as thick and as well lignified in the fruit-bearing shoots as in the vegetative shoots. Measurements of the tissues showed that the woodcylinder in the fruit-bearing shoot had not only outgrown its former weakness, but that it now formed a greater proportion of the diameter of the cross-section than was the case in the vegetative shoot.

TABLE 3.—Amount of wood in the fruit-bearing and vegetative shoots at the end of the first, third, and fifth year of growth.

Twelve vegetative shoots, first year				47.77
Twelve fruit-bearing shoots ,,	•			41.50
				-6.27
Seven vegetative shoots, third year				123.5
Seven fruit-bearing shoots "		•		133.8
				+ 10.3
Six vegetative shoots, fifth year .				164.66
Six fruit-bearing shoots ,, .				188.33
				+ 23.67

This increase in the development of the xylem, as well as in the walls of the wood-cells, indicates that the weakening effect of fruit-bearing upon the wood is temporary, and is quickly outgrown. That even the temporary effect is compensated for by the great development of supplementary mechanical tissue is shown above.

Pear.—The fruit-bearing one-year-old Pear-shoot resembles

<sup>&</sup>lt;sup>1</sup> To avoid using a cumbersome descriptive phrase, these three- and five-year-old portions of branches will hereafter be designated as three- and five-year-old fruit-bearing and vegetative shoots respectively.

that of the Apple in every way, except size. It is larger, and the swelling is greatest near the middle, decreasing from this point in both directions. The upper part withers after fruitbearing. In arrangement and division of tissue the part below the insertion of the lateral vegetative bud is similar to the corresponding part of the Apple. Instead, however, of bast-fibres, the supplementary mechanical tissue is scleren-The sclerenchyma-cells are slightly elongated and chyma. taper-pointed, with thick and strongly lignified walls. Bundles of these cells are placed just outside of the fibro-vascular bundles, and are scattered throughout the cortex, medullary rays, and pith in the upper part of the shoot. Like the bastfibres in the Apple, they decrease in number near the base of the shoot.

An early variety of Pear, of unknown name, was selected for study. Measurements were made in the same manner as for the apple, the sections being taken near the base in each case. Although the largest possible vegetative shoots were used, they were, as a rule, no longer than the fruit-bearing ones.

		Cortex.	Wood.	Pith.
Five vegetative shoots .		42.20	23.12	34.68
Five fruit-bearing shoots	•	41.36	22.10	36.54
		-0.84	— I·O2	+ 1.86

TABLE 4.—Average percentages of tissue in one-year-old shoots.

There is very little difference in the proportionate amount of tissue in these shoots, but an examination of the tables of absolute measure will show that the advantage, as far as amount of mechanical tissue is concerned, is largely with the fruit-bearing shoot.

TABLE 5.—Average absolute measure of tissues in the same shoots as in Table 4.

Vegetative shoots Fruit-bearing shoots	•	Cortex. 106.6 146.0	Wood. 5 <sup>8.</sup> 4 78.0	Pith. 87.6 129.0	Total. 252.6 353.6
		+ 39·4 N n 2	+ 19. <b>6</b> 2	+ 41.4	

The diameter of the fruit-bearing shoots at the base is much greater than that of the vegetative shoots. This is largely because the swelling begins at the base, involving the basal zone of scars. It is impossible to get entirely below it and still be within the year's growth.

The tables show that the amount of woody tissue is greater in the fruit-bearing than in the vegetative shoots, although the percentage is slightly less. This is due primarily to the increased size of the pith, since the proportion of cortex is also greatest in the vegetative shoots. The cortex, however, increases rapidly in size toward the middle of the shoot, and soon greatly exceeds that in the vegetative shoot. The walls of the wood-cells in the fruit-bearing shoot at the base were of usual thickness, as far as could be ascertained by careful inspection. No measurements were made.

It is clear that the base of the fruit-bearing shoot is not mechanically weak.

*Plum.*—The material for this work was collected in the latter part of July. Two sets of shoots were taken, both in their third year of growth. One set bore mature fruit at the time of collecting, and the other had borne no fruit that season.

In the Plum, as in the Peach, the axis of the fruit-bud is but slightly developed, and the fruit-stalk seems to proceed directly from the branch upon which the bud is borne. The sections of the Plum were taken 1 or 2 centimetres below the point of attachment of the fruit, and, in the vegetative shoot, at a point as nearly similar to this as possible. The tissue from  $\frac{1}{2}$  to I centimetre below the fruit shows the effect of fruit-bearing. The zone of cortex is larger than either above or below this point; the zone of xylem and the pith are also larger. The development of all the tissues is greatest on the side toward the fruit, making the section of the stem at this point oval instead of circular. The walls of these wood-cells are thin and but little lignified. The measurements were taken from sections cut below the swollen portion in order that those from fruit-bearing and from vegetative shoots might be comparable.

The Plum-shoots bear fruit during their second and third years. The scars left by the fruit-stalks are so small that their presence cannot be certainly determined. It is therefore not known whether any of the three-year-old shoots used bore the previous year or not.

By the term vegetative shoots is meant those not bearing fruit during the season of collecting, and by fruit-bearing shoots those of the same age bearing mature fruit at the time of collecting.

TABLE 6Average proport	tions of tis:	sue in—	
	Cortex.	Wood.	Pith.
Five vegetative shoots three years old	26.6	50.8	22.6
Five fruit-bearing shoots ", ",	30.79	44.77	24.44
	+ 4.19	-6.03	+ 1.84

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The figures given in this and the following tables on the plum may not be entirely reliable, because the history of the shoots used is unknown. If the vegetative shoots of 1894 bore fruit during 1893, the apparent influence of fruit-bearing would be decreased. It would show that the effect of previous fruit-bearing did not prevent the shoot from developing a greater amount of wood than was formed in the fruit-bearing shoot of 1894. In this case the difference in the amounts of tissue would have to be attributed to unknown accidental causes. If, on the other hand, the vegetative shoot had not borne fruit the previous year, it would tend to verify the supposition that all the difference between the shoots was due to fruit-bearing. The figures in Table 6 were computed from the data given in the following table :—

TABLE 7	-Average	absolute	amount	of	tissue	in—	
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			Cortex.	Wood.	Pith.
Five vegetative shoots			65.4	125	55.6
Five fruit-bearing shoots	•		73.6	107	58.4
			+ 8.2	- 18	+ 2.8

A greater difference between the two kinds of shoots in the amount of woody and parenchymatous tissue is found in

the Plum than was found in the Apple or Pear. However, satisfactory results could only be obtained by taking sections of shoots whose fruit-bearing history was known for several years past, and measuring the amount of wood formed each year. A comparison of the amount formed during fruitful and unfruitful years would show the effect of fruit-bearing and whether any such effect was constant.

A few trees of the Wild Goose variety of Plum were found whose history for the past three years was known. During 1891 the trees bore a heavy crop of fruit, but bore no fruit at all during 1892 and 1893. In the spring of 1894 shoots were cut from different parts of one of these trees for the purpose of studying the effect of a heavy crop upon the amount of wood formed during the fruit-bearing year, but with no special reference to the shoot upon which the fruit was borne.

In the following table the measurements are given, as before, in terms of the eye-piece micrometer, each having a value of 15 micromillimetres<sup>1</sup>.

		1893.	1892.	1891.	1890.	1889.	Aver. of
1 year old		62					4
2 years old		54	37				5
3 years old		35	52	45			6
4 years old	•	30	34	34	42		4
5 years old		25	43	30	35	29	2
		No fouit	No famit	Fruit-bear	IIn	Un-	
		borne.	borne.	ing year.	known.	known.	

#### TABLE 8 .- Average amount of wood formed during

The average amount of wood formed in the shoots three, four, and five years old, during 1891, the fruit-bearing year, is 36; during 1892, 43; and during 1893, 30. The average annual amount formed in these shoots during these three

<sup>&</sup>lt;sup>1</sup> It should be borne in mind that throughout the paper all actual measurements are given in units of the eye-piece micrometer, each unit being equal to 15 micro-millimetres.

years is  $36\frac{1}{3}$ , only a trifle more than the average of all of them for 1891. If fruit-bearing was the principal factor in reducing the amount of wood, we should expect its effects to appear more strongly in 1892 than in 1893; but more wood was formed in both 1891 and 1892 than in 1893.

*Peach.*—The material for the study of the Peach was collected while the ripe fruit was still on the tree. Some of the shoots used bore two peaches, so near together as to be almost opposite. The vegetative shoots were selected as nearly like the fruit-bearing ones as possible, and of course of the same age. Sections near the base of the fruit-stub, as well as from points above and below the fruit, were studied. Measurements, with one exception, were made from sections cut about 2 centimetres below the attachment of the fruit. This avoided the local effect of fruit-bearing.

The peach is borne on the shoot making its second season's growth. It is supported by a rigid stub 2 or 3 millimetres in length. This stub is remarkable for the great amount of mechanical tissue it possesses. The wood-cylinder is dense, the walls of the wood-fibres are thick and well lignified.

The modifications described above for the Plum also occur in the Peach-shoot. Just below the stub the stem is swollen and the tissues have the greatest development on the side toward the fruit. This irregularity is local; at a distance of I to 2 centimetres it has entirely disappeared.

Great care was taken to cut the sections for measuring the tissues from points as closely comparable as possible and to have the shoots alike in size and vigour. All the shoots used were two years old. The tables which follow show that, in the Peach, fruit-bearing certainly does not produce a weak development of xylem. The effect is local and is confined to a very limited area. The proportion of xylem in the fruit-bearing shoot is greater than that in the vegetative, while the proportion of cortex is greater in the latter. The cortex in the fruit-bearing shoot of both the Plum and Peach is not as well developed as in the corresponding shoots of the Apple and Pear ; the proportion of pith is smaller in the

fruit-bearing than in the vegetative shoot, and relatively smaller in the swollen portion than elsewhere.

TABLE 9.- Average proportion of tissues in-

			Per cent.		
Five vegetative shoots . Five fruit-bearing shoots	•	35·22 30·91 - 4·31	33.98 $39.69$ $+ 5.71$	$ \begin{array}{r} 28.78\\ \underline{19.25}\\ -9.53\end{array} $	

In the small swollen area at the base of the fruit-stub the zone of wood is thicker than it is a little lower in the same shoot, but the walls of the wood-cells are thin and mostly unlignified.

 

 TABLE 10.—Actual average measurements of the shoots and measurements through the swollen part.

	Cortex.	Wood.	Pith.	Total.
Five vegetative shoots .	65	63	53	181
Five fruit-bearing shoots .	59	77	55	191
Five fruit-bearing shoots				
through swollen part .	78	87	53	218

#### SUMMARY.

The study of these four species seems to warrant the following conclusions, in answer to the questions proposed at the beginning of this paper :—

1. The one-year-old fruit-bearing shoots of the Apple and the Pear have less wood in proportion to their diameter than does the vegetative shoot of the same age. This is due, in the Apple, largely to an increase in the cortex, and in the Pear solely to a great increase in the cortex and the pith, of the fruit-bearing shoot. It does not, however, appear from the structure of the shoots that the fruit-bearing shoot is weaker than the vegetative. The former is well supplied with supplementary mechanical tissue, which is distributed at those points where it is most needed, and thus gives it an increase of strength for the fruit-bearing year which fully makes up for the difference in xylem-development.

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2. In the Peach the fruit-bearing shoot has more wood than the vegetative shoot, and the walls of the wood-cells are as thick in the former as in the latter.

3. In general it may be said that the effect of fruit-bearing upon the tissues is local. In the Apple and Pear it is perceptible throughout the one-year-old shoot; in the Plum and Peach it is confined to a small area in the immediate neighbourhood of the fruit-stalk.

4. The local effect of fruit-bearing tends to an increase of cells, with a decrease in the thickness and lignification of the walls of the wood-cells. The cortex is especially enlarged, giving rise in the Apple and Pear to the swollen condition of the fruit-bearing shoot.

5. In all cases the increase in growth is greatest on the side near the fruit-stalk, although the wood in the Apple and Pear is best developed on the side of the lateral vegeta-tive bud.

6. The local effect of fruit-bearing on the wood-cylinder disappears with time. The study of Apple-shoots that had borne fruit during their first year showed that in the two or four years following there had been a rapid increase of wood, especially on the side of the fruit-scar. This side was weakest at the end of the first year. These shoots at the end of three and five years had a better xylem-development than shoots of the same age that had never borne fruit.

7. Fruit-bearing has a temporary local effect upon the lignification of the walls of wood-cells. It prevents their lignification wholly or in part, according to their distance from the fruit-stalk. The lignification of other cell-walls is promoted by fruit-bearing. In the fruit-stalk the greatest part of the tissue has become lignified, and in the upper part of the Apple- and Pear-shoot there is an abundance of welllignified sclerenchyma and hard bast, which is either not found in the vegetative shoot or only sparingly so.



Pieters, A. J. 1896. "The influence of fruit-bearing on the development of mechanical tissue in some fruit-trees." *Annals of botany* 10, 511–529. <u>https://doi.org/10.1093/oxfordjournals.aob.a088625</u>.

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