BULLETIN 339 OCTOBER, 1928

VASCULAR STRUCTURE AND PLUGGING OF ALFALFA ROOTS

By

E. L. LeCLERG and L. W. DURRELL

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VASCULAR STRUCTURE AND PLUGGING OF ALFALFA ROOTS

E. L. LeCLERG and L. W. DURRELL

ABSTRACT.—This bulletin briefly describes a disease of alfalfa commonly known of as "root rot." Investigations are reported on the relation of this disease to the anatomy of the alfalfa roots and their conduction of water.

The tracheids in diseased roots are filled with a gum deposit and the water can not pass up to the crown. Tests on water flow in diseased and healthy roots show that the plugged roots furnish the leaves with less water than the healthy roots. The tracheids are generally smallest at the crown of the root, and therefore, are more easily plugged. This small diameter of the water-conducting vessels at the crown, together with their short length, facillitates plugging.

The vascular-bundle arrangement is similar to that of a woody stem and the water-conducting tubes consist of short pitted tracheids.

In the young roots the tracheids are of small diameter, but as the roots get older the tracheids develop. The small ends of the old roots also have larger tracheids. Little, if any, anatomical difference is observed in one-, two- and three-year-od roots of Common, Baltic and Grimm. The diameter of the root and the area of conductive tissues increase with the age of the root.

The water flow in a root increases with age. The upper end of the root conducts less water because it has smaller tracheids in comparison to the younger roots.

Experiments conducted by the writers show that calcium sulphate, sodium nitrate, sodium carbonate, potassium phosphate, sodium arsenate and mercuric chloride in dilute solutions, when drawn into the roots, produce gum in the tracheids in a week to ten days. This gum reacts michorchemically the same as that found in roots from the field.

In the case of mercuric chloride (2:1000), gum formation is rapid and abundant. Since this salt is very toxic, there is little possibility of bacterial organisms being the cause of the gum formation in the roots in these experiments where it was used.

Some of the salts present in the soil or irrigation water have the ability to produce gumming in the cells of the alfalfa root. While bacteria in some cases may play a part in this disease, the action of salts in causing gumming and wilting, precludes bacteria from consideration as the sole cause.

INTRODUCTION

The vascular structure of the alfalfa root and its bearing on the water supply of the plant has received little consideration. Wilson,[15] in his anatomical study of the alfalfa plant, discusses the structure of the leaf and stem but makes slight mention of the root. The anatomy of the root and its conduction of water is, however, of special interest in connection with the wilt and root rot common to the alfalfa fields of Colorado. This disease is accompanied by gum formation in the tracheids of the root and it is for this reason that the following discussion of structure and the vascular plugging of the root is offered.

The wilt and root rot of alfalfa, so prevalent to Colorado, was first noted by the junior author in 1923 in Iowa and reported in June of the following year [2] with a brief description of the symptoms and vascular plugging of the root responsible for the wilting. The following year Jones [6] and Jones and Weimer [8] reported this disease in Wisconsin, and Durrell and Sackett [4] described it from Colorado.

As early as 1896, Headden [5] figured and wrote of a root rotting of alfalfa in Colorado, and in 1906, Paddock [10] in the same state briefly described a disease of alfalfa that blackened the stems and resulted in a dying of the crowns.

Weimer, [14] more recently, has described and figured a similar root rot of alfalfa.

Judging from the descriptions and figures, however, these writers record a disease different from the now-common wilt disease, or only the final stage of rotting.

Jones and McCullouch [7] present a careful description of the disease, and attribute it to a bacterial organism which they describe. They lay particular emphasis on this organism as the cause of the wilting of the plant and the discoloration of the root, but give little consideration to the structure of the root, the gum formation in the vascular system, or the decrease of water passage resulting from such gumming.

The wilt or root rot of alfalfa is so well known that but a brief description seems necessary. The diseased plants appear stunted and in the spring make but little growth, Figure 1. The stunting is accompanied by a wilting and flagging of the top, which is most noticeable in the spring at the beginning of growth or after the first cutting. Plants seldom show symptoms of the disease before they are three or four years old. The disease is progressive and increases in the plant with age. The immediate cause of the wilting and stunting is the lack of water because of the vascular plugging of the roots. A superficial observation of the root shows that the cut end is discolored. The discoloration appears as a brown or yellowish ring

Figure 1.—Normal alfalfa plant and a stunted, wilted plant with plugged vascular system.

or rings. Microscopic examination and microchemical tests show that the color is due to a gum deposited in the vessels of the root, Figure 2. In younger roots, only a few scattered vessels are plugged. In older roots, the plugged vessels occur in a continuous ring around the root and even several successive rings may be present, which increase with the progress of the disease.

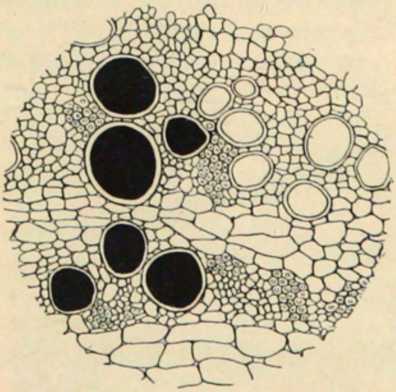

Figure 2.—Camera-lucida drawing from cross section of a root, showing some of the plugged water-conducting cells or tracheids.

The plugging is accompanied by a change in the composition of the walls of groups of cells surrounding the tracheids as indicated by a brilliant reaction to phloroglucin and hydrochloric acid. The gum deposit in the cells in some cases has the appearance of tyloses. In most tracheids, however, it plugs them as a solid core.

The plugging of the water-conducting vessels results in reduced water flow from roots to leaves with accompanying wilting of the tops of the plants. The reduced water flow and accompanying starvation is aggravated by the fact that the plugging of the root occurs largely at the crown and efficiently dams the rising water from the stems and leaves near to their junction with the root. Furthermore, the tracheids are of smaller diameter at this part of the root and are therefore more easily plugged. One of the indirect results of reduced water supply is reduced starch storage in the root. Diseased roots show little stored starch and the plant has but small food reserve available to start growth in the spring. This condition, continued over several seasons, results in a progressive weakened condition and ultimate death of the plant. Decay usually follows the plugging of the root and rotted areas are to be found in the older roots which extend deep down from the crown.

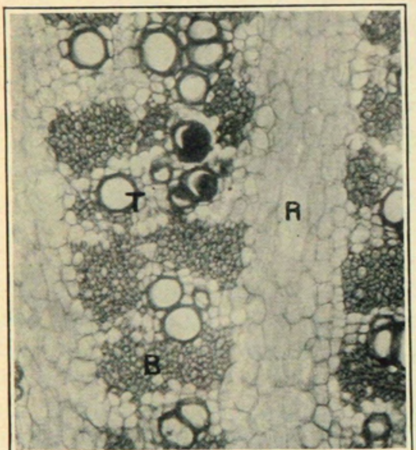

Figure 3.—Cross section of a three-year-old alfalfa root, showing: R-medullary ray, B-sclerenchyma tissue and T-tracheids of the vascular bundle.

ANATOMY OF ALFALFA ROOT

In order to better understand the effect of vascular plugging in the alfalfa root, a study of the anatomy of the root was attempted. Wilson's [15] study of this part of the plant was very brief and no other records have been found which deal with the character of the elements in the root or their arrangement. The roots studied were dug in the field at different seasons and plants of different ages were sectioned. Most attention was given to the upper part of the root as that region is the one that chiefly manifests plugging. Free-hand sections were made of some of the material tho the majority of the sections were from material embedded in paraffin and stained.

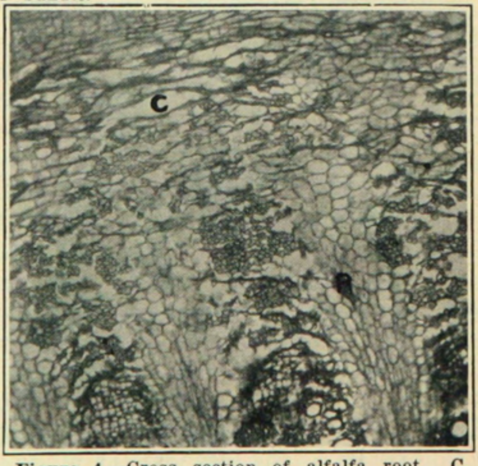

Figure 4.—Cross section of alfalfa root. C, showing loosely joined cells of cortex. R-rays extending fan-shaped into cortex.

In Figures 2 and 3, are shown cross-section views of the mature root. It will be noted that the bundle arrangement is similar to that of a woody stem. The vascular bundles are distinctly separated by medullary rays which are frequently traced far into the cortex, Figure 4. The bundles are well supplied with groups of sclerenchymous fibers dispersed among the vessels.

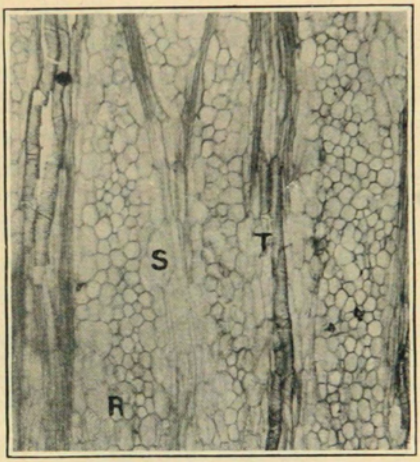

Figure 5.—Tangential section of a three-year-old root. R-ray, S-sclerenchymatous fibers, T-Tracheids.

Figure 5 represents a tangential section of the root, showing the width of the rays and the net-like spread of the bundles and fibers about them. There appears to be little pressure on the ray cells and they are rather large and loosely joined. In old decaying crowns the ray cells ret out quickly and leave the vascular bundles as porous, lace-like structures.

Figures 6 and 7 show in detail the wood fibers and the tracheids. It is of particular interest to note the character of the tracheids themselves. Judging by the speed of water flow in a normal alfalfa root it might be assumed that the water-conducting vessels were long tracheal tubes. In reality they consist of short, pitted tracheids, as no spiral or annular tracheids have been found. In the photograph, Figure 7, is shown more of the detail of such tracheids while the drawing in Figure 8, gives a representation of the pits and structure of the wall.

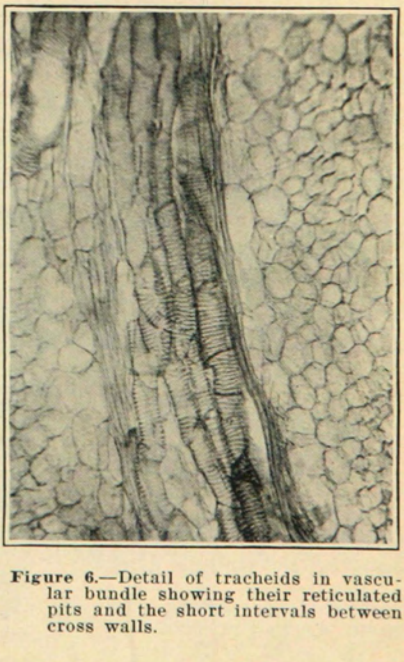
Figure 6.—Detail of tracheids in vascular bundle showing their reticulated pits and the short intervals between cross walls.

The cortex of the root consists largely of undifferentiated parenchyma cells extending to the outer corky bark, Figure 4. The bark or outer covering of the root consists of several lay-

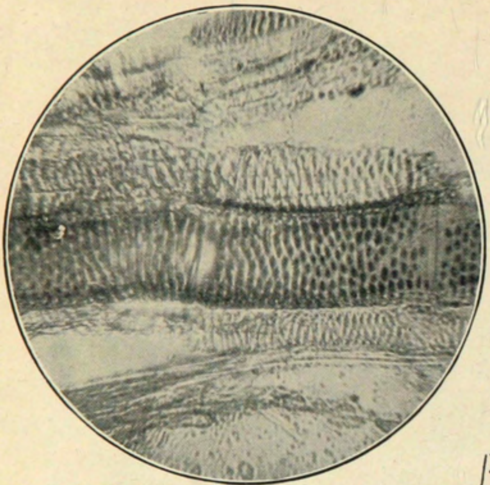

Figure 7.—Enlarged view of tracheid showing pitting.

ers of corky cells, Figure 9, terminating at the surface in a dead, scaly layer of varying thickness. Over the surface of the root are scattered lenticles, many of which are quite large. In Figure 10 is shown the nature of these. They are well plugged with cork cells.

Few, if any, visible differences exist in the main characters of the one, two- and three-year-old roots, that were sectioned, or even in the very old, healthy roots. Roots of Common, Baltic and Grimm varieties were examined, but no consistent differences were noted in root structure.

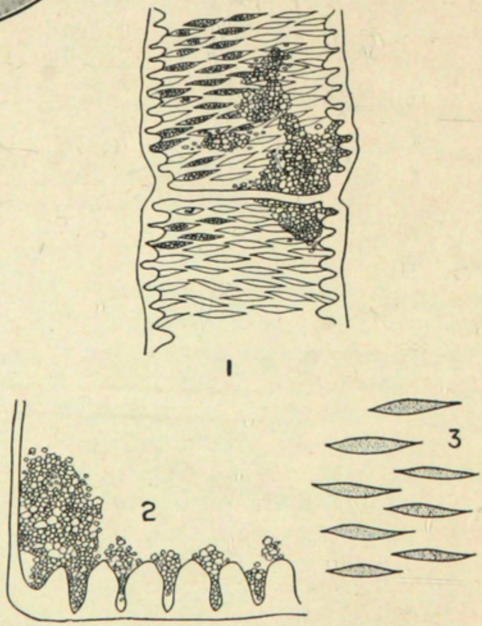

Figure 8.—Camera-lucid drawing of detail of walls and pits of tracheids. Numbers 1 and 2 show depth and shape of pits. In some tracheids the pits are very long, the thickenings almost giving the appearance of spiral thickenings such as are found in some trachea. In other cells the pits are more rounded. Number 3 shows greatly enlarged pits as seen with oil-immersion objective and 15-X eyepiece. The middle lamella is spotted with minute dots giving the appearance of extremely small pores. In 1 and 2 are shown the collection of particles of carbon of India ink caught in the pits after drawing dilute ink into the roots.

WATER CONDUCTION IN ALFALFA ROOTS

As vascular pugging of the root greatly affects the water supply of the alfalfa plant, measurements of the rate and volume of water flow thru roots were made and the avenue of passage noted.

In these tests, by the use of a pump similar to that described by Melhus, Muncie and Ho [9], water was drawn thru the roots by mild suction. This method was rapid and enabled definite measurement of flow. It had the advantage over using the transpiring top of the plant as a means of water pull, in being constant and capable of regulation.

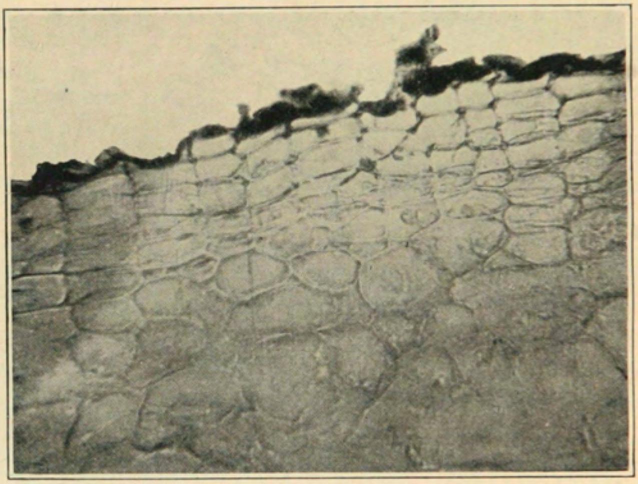

Figure 9.—Section of outer part of cortex showing cork cells at the surface.

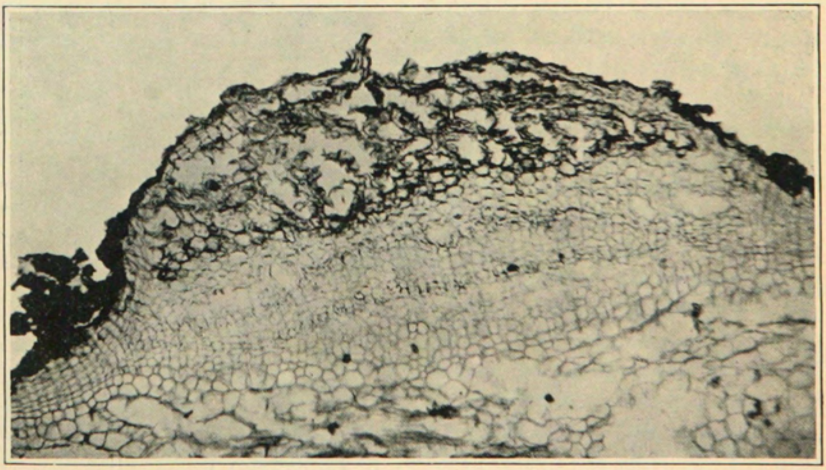

Figure 10.—Detail of section thru a lenticel of root showing protecting cork dam behind the lenticel.

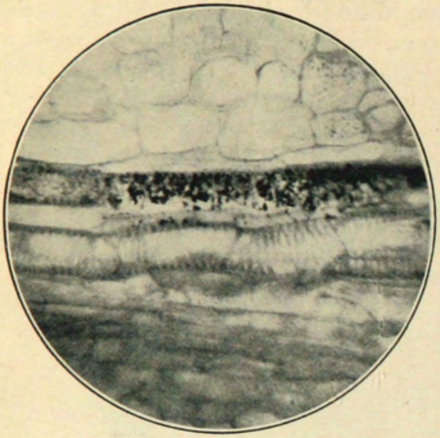

Figure 11.—Longitudinal section of tracheids showing particles of ink caught in pits.

By the use of soluble dyes the water flow could readily be traced in the roots and as would be expected, it followed the tracheids. When suspended material was drawn into the tracheids, however, some interesting results of an anatomical nature were obtained.

Carmine, suspended in water, was first drawn into the root, but the suspended particles did not penetrate far. Their size was such that they were to be found only a millimeter or two up the root from the point of entrance. Dilute India ink was then drawn into the roots in a similar manner. The particles of this substance penetrated much further into the root than did the carmine. Sections of the root showed particles of the carbon 20 to 50 centimeters up the root from the point of entrance.

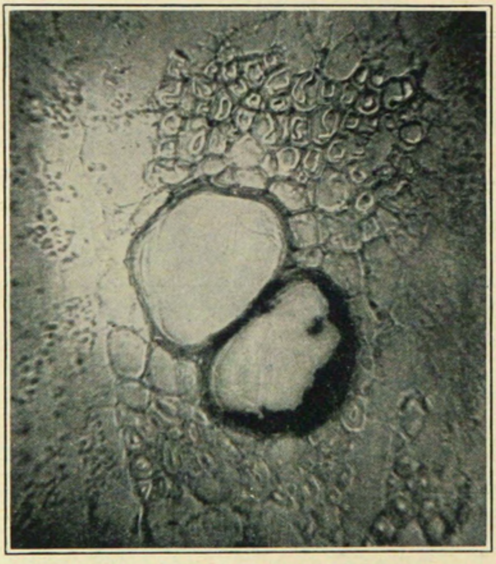

Figure 12.—Cross section of tracheids showing colloidal carbon caught in pits of walls.

In Figure 8, numbers 1 and 2, are shown camera-lucida drawings of the walls and pits of the water-conducting tracheids. In the center of these pits is the middle lamella separating the lumen of adjoining tracheids. The walls of the tracheids are rather thick and the pits are deep and often quite narrow. Observation of the middle lamella with a 1.9 objective and 15x eyepiece reveals a peculiar granular or stippled surface of this part of the wall which gives the appearance of minute pores, Figure 8, number 3.

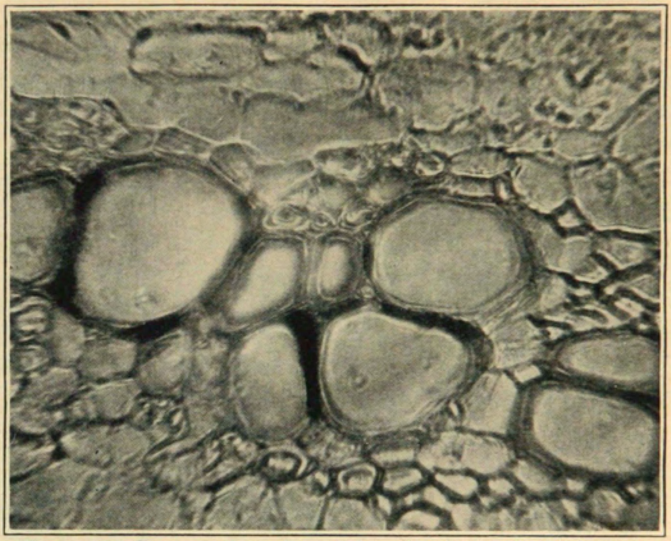

Figure 13.—Cross section of tracheids showing colloidal carbon caught in pits of walls.

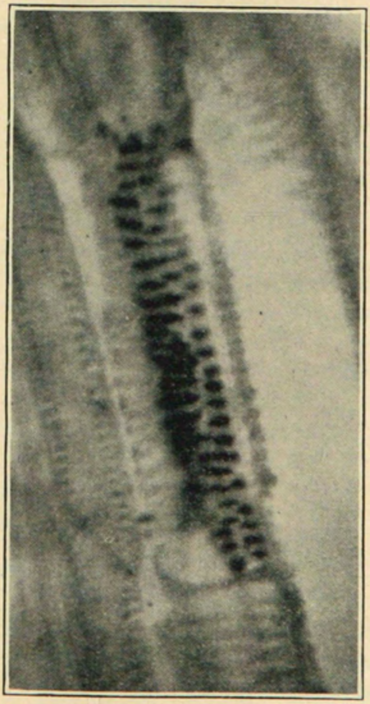

Figure 14.—Section of tracheid showing colloidal carbon caught in pits.

When India ink is drawn into the root the larger suspended particles are caught in the pits of the tracheids like drifted sand in a gutter and sometimes pile up in the ends of the cells. Figures 11 to 14 show sections of tracheids with ink particles lodged in the pits. The camera-lucida drawing in Figure 8, illustrates the same. The position of these deposits may no doubt give some indication of the course and direction of water flow. It is difficult to see, however, how the ink particles pass the middle lamella of the pits. The pressure of suction was only 24 inches of mercury and it is doubtful if this could rupture the thin wall. This suggests a porous structure of the lamella.

It would seem that the flow of water thru the vascular system would, to some degree, follow the behavior of water flow in a system of pipes and that it would be governed to some extent by the number of tracheids and the size of the lumen of these cells. The water flow of 112 roots of different size and age was measured together with an antomical study of each. As the tracheids are the avenues of water flow, measurements of the diameter and area of these, and 224 camera-lucida drawings were made.

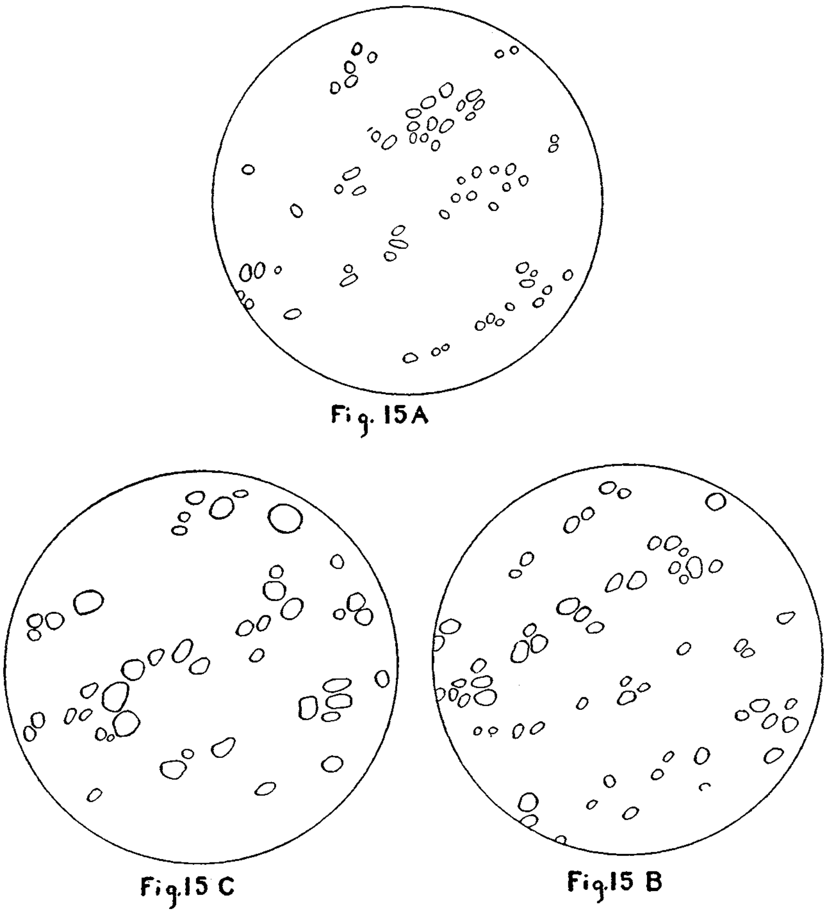

Figure 15.—Diagram of representative areas from cross sections of three-year-old alfalfa roots from camera-lucida drawing, showing relative size of tracheids. A-at crown. B-10 centimeters down from crown. C-10 centimeters on down from B.

In Figure 15 are the diagrams of representative parts of these roots showing the comparison between the size of tracheids in cross section at the crown of the root and lower down on the same root. Figure 16 shows a similar comparison of an old and a young root.

It is interesting to note in these diagrams, which are taken directly from camera-lucida drawings of representative areas of root sections, that young roots have smaller tracheids than old roots and also that the upper parts of the root have much smaller tracheids than the lower regions of the root. This seems significant when we consider that it is the tracheids in the upper part of the root that become plugged. Their small size naturally facilitates plugging and moreover, no matter how large the tracheids of the lower part of the root may be, the water supply to the leaves is gauged by that which can pass thru the tracheids of the crown region of the root.

Using the suction device above mentioned,[19] the water flow of 260 roots was tested. A summary of a part of these tests is given in Table I. In these tests pieces of tap root, approximately 10 cm. in length, were attached to the pump with one end immersed in water, and maintained under a constant suction equivalent to a vacuum of 24 inches of mercury. The rate and volume of water flow was measured in cubic centimeters for five-minute periods.

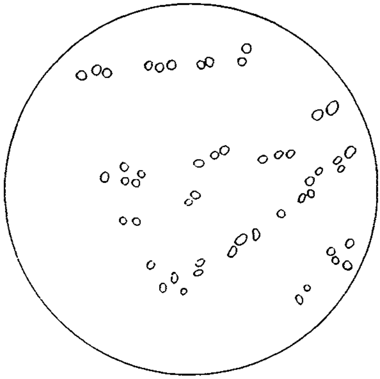

Fig. 16 A

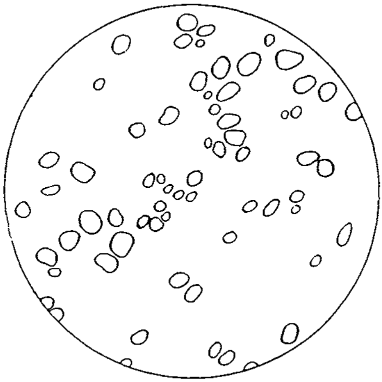

Fig. 16 B

Figure 16.—Diagram of representative areas from cross section of alfalfa root, from camera-lucida drawing, showing size of tracheids. A-one-year-old-root. B-eight-year-old root.

The actual area of the ducts was determined; also the average diameter of the segment of the root. From these measurements the percentage of conductive tissue of the root was calculated. These figures were obtained by projecting the root sections on a screen and measuring areas with a planimeter then reducing them to the actual size of root.

Table I.—Relation of Cross-section Area of Root and Tracheids to Age and Water Flow.

Consecutive pieces of root.	Average area of xylem in sq. cm.	Total area of tracheids in sq. cm.	Percentage area of tracheids	Water flow for 5 minutes in cc.
One-year-old				
Top 10 cm.	0.1263	0.0028	2.70	0.12
Second 10 cm.	0.0561	0.0021	4.17	0.39
Third 10 cm.	0.0423	0.0023	5.08	0.70
Two-year-old				
Top 10 cm.	0.4378	0.0158	3.79	3.06
Second 10 cm.	0.2459	0.0207	4.43	6.68
Third 10 cm.	0.2192	0.0105	4.92	15.60
Three-year-old				
Top 10 cm.	0.5637	0.0223	3.88	7.66
Second 10 cm.	0.2954	0.0140	4.92	14.48
Third 10 cm.	0.2515	0.0143	5.26	29.50

In the above table, representing tests on 260 roots, it may be noted that the diameter of the root and the average area of tracheids increases with the age of the root. The average percentage area of the xylem composed of tracheids increases with age, altho as shown previously, Figure 16, the diameter of the tracheids themselves is generally smaller in the older parts of the root. As might be expected the water flow in a root also increases with age, the older roots carrying more water than the younger roots.

Curiously, however, the upper end of the root conducts less water, under the same conditions, than the lower section of the root, because it has smaller tracheids in comparison to the younger parts.

The effect of gumming on water flow in alfalfa roots is evident and it has been shown by the junior author [2] and by Melhus et al. [9] that the gum deposit in the tracheids materially reduces the amount of water furnished the plant by the root. To put this water flow on a definite, comparative basis, a number of tests were made which are summarized in the following table.

Table II.—Effect of Gum Deposit on Water Flow in Alfalfa Roots.

	Average area of xylem in sq. cm.	Average area of tracheids in sq. cm.	Percentage of tracheids	Water flow for 5 min. in cc.
Diseased roots	0.4459	0.0241	5.42	7.3
Healthy roots	0.5637	0.0223	3.88	7.6

In the above tests, approximately equal water flow was obtained in diseased and healthy roots regardless of the fact that the percentage of conducting tissue in the diseased roots was 5.42 percent of the xylem area while in the healthy roots it averaged but 3.88 percent. On a ratio basis, the diseased roots should have conducted 10.6 cc. of water, considering their tracheil capacity, when in reality they transported but 7.3 cc. water in the same time.

NATURE OF PLUGGING OF ALFALFA ROOTS

Altho the mechanism of the plugging of the alfalfa root and the subsequent reduction of water flow to the plant is obvious, the cause of the gum formation is obscure. Prillieux, [11] in his study on gum formation in fruit trees, concluded that the gum filling the lumen of wood cells and bast of the bundles was due to infiltration of starch which became changed to gum.

Trecul [13] mentions rain as a causal condition of gum formation and Aderhold [1] recorded one or two experiments in which an increased gumming followed watering. The effect of high water content of the soil on increasing the susceptibility of Prunus and Citrus to gumming has been mentioned by most writers. These records are of interest in connection with the gum deposition in the alfalfa root for it is a matter of constant observation that wilted alfalfa plants resulting from gum-plugged tracheids are to be found in the parts of the fields where water has stood for a short time or in fan-shaped areas where irrigation water has been admitted to the field. In the few non-irrigated alfalfa fields, which the writers have examined, no gummed plants have ever been found.

The association of an organism with the disease as demonstrated by Jones [6] suggests it as an agent in the plugging of the tracheids. The plugging material which is a gum, as indicated by microchemical tests, [4] may perhaps be developed by the invading organism or by the host plant in the presence of the organism. In the spring of 1924, the junior writer was able to produce such plugging in the roots by injection with suspensions of three different soil bacteria that were taken at random from several cultures in the laboratory. These suspensions were in a physiological salt solution. In all cases plugging was developed in the tracheids. As the organisms could hardly be specific, the salt solution suggested itself as a cause of gum formation.

In 1925 the writers injected the following solutions into alfalfa roots: M-1 NaCl, M-1 K_2HPO_4 and a saturated solution of Na_3AsO_4. Twenty-two roots were used with the result that all became plugged in one to two weeks.

Subsequent tests at different dates in the succeeding year resulted as follows:

M-100 $CaHPO_4$—very little gum formation.
M-100 $CaSO_4$—trace of gum formation.
M-100 NaCl—abundant gum formation.
M-100 Na_2CO_3—abundant gum formation.
M-100 $NaNO_3$—abundant gum formation.
Distilled water—slight gum formation.

On the assumption that the organisms might be contributory to the gum formation, a number of additional tests were made using mercuric chloride in place of the above salts. The first result of these tests was gum formation which occurred also in later tests under varying conditions.

TABLE III.—Gum Formation in Tracheids with $HgCl_2$ (Two parts to 1000).

	Room temperature	Freezing temperature outdoors	30° C.
Saturated atmosphere	vessels discolored gum formed	no gum formed	vessels discolored gum formed
CO_2 atmosphere	vessels discolored gum formed	vessels discolored gum formed	no gum formed
Oxygen atmosphere	vessels discolored gum formed	vessels discolored gum formed	vessels discolored gum formed
Oxygen-free atmosphere	vessels discolored gum formed	vessels discolored gum formed	vessels discolored gum formed
Saturated atmosphere, distilled water injected	no gum formed	no gum formed	no gum formed

It is interesting to note, in connection with the data in Table III, that Ruhland [12] believed that atmospheric oxygen was an active agent in gum formation and that Beijerink and Rant [3] obtained abundant gum formation in peach in four to seven days after injection of mercuric chloride. In the case of alfalfa, the injection of mercuric chloride produced abundant gum in the tracheids and the high concentration used precludes the association of a parasitic organism.

From the above resume of tests of injections of salts, some of which are found in Colorado soil, it would appear that some of them, in sufficient amounts, can cause gum formation in the tracheids of the alfalfa root. Furthermore, the appearance of such gumming of the roots is identical with that developed in the field. These tracheids are filled with a yellowish core of gum which also reacts chemically in the same way as that of the roots taken from the field.

SUMMARY

A study has been made of the anatomy of the root of the alfalfa plant and its conduction of water which is of special interest in connection with the wilt and root rot common to the alfalfa fields of Colorado.

The wilt or root rot of alfalfa is characterized by a stunting and the plants make but little growth in the spring. The stunting is accompanied by a wilting and flagging of the top. The tap root, when cut, shows the cut end to be discolored, which appears as a brown or yellowish ring or rings. This discoloration is due to a gum deposited in the vessels of the root. The plugging of the tracheids results in reduced water flow to the leaves and wilting of the tops occurs.

The plugging of the roots occur largely at the crown. Diseased roots show little stored starch and the plant has but small food reserve available to start growth in the spring.

The vascular-bundle arrangement is similar to that of a woody stem. The water-conducting tubes consist of short pitted tracheids.

The cortex of the root consists largely of undifferentiated parenchyma cells extending to the outer corky bark, which is made up of several layers of cork cells terminating at the surface in a dead scaly layer of varying thickness.

Little, if any, visible structural differences are evident in the one-, two-, and three-year-old roots or in the roots of Common, Baltic, or Grimm varieties of alfalfa.

By use of soluble dyes the water flow in the roots could be traced. The dye was drawn up by mild suction, and was observed to follow the tracheids.

The walls of the tracheids are rather thick and pitted, the pits being deep and often quite narrow. The middle lamella appears to be perforated with minute pores.

Young roots have smaller tracheids than old roots and the upper parts of the roots have much smaller tracheids than the lower regions of the root.

The diameter of the root and the area of conducting tissues increases with the age of the root.

The water flow in a root increases with age, the older roots carrying more water than the younger ones. The upper end of the root, however, conducts less water because it has smaller tracheids in comparison to the younger roots.

Diseased roots conduct less water than healthy ones of the same age.

It has been demonstrated that a plugging, similar to that found in the field, can be produced by injection of various salts into the alfalfa root. Solutions of $CaHPO_4$, $CaSO_4$, NaCl, Na_2CO_3 and $NaNO_3$ injected into healthy roots each resulted in a plugging of the conductive tissue in one to two weeks. The fact that mercuric chloride (2:1000) gave similar results would indicate that bacteria are not the sole cause of vascular plugging.

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