

## Morphological Changes Induced In Roots Of Bromeliaceæ By Attack Of Heterodera SP

Rev. James Waterston B.D. B.Sc.

To cite this article: Rev. James Waterston B.D. B.Sc. (1912) Morphological Changes Induced In Roots Of Bromeliaceæ By Attack Of Heterodera SP, Transactions of the Botanical Society of Edinburgh, 24:1-4, 26-35, DOI: [10.1080/03746601209468935](https://doi.org/10.1080/03746601209468935)

To link to this article: <http://dx.doi.org/10.1080/03746601209468935>



Published online: 29 Nov 2010.



Submit your article to this journal [↗](#)



Article views: 3



View related articles [↗](#)

of sclerenchyma, outwardly they are bounded by much weaker tissues—protoxylem, soft phloem, and wood parenchyma. The walls thus unequally supported must be better able to resist distortion, owing to the presence at intervals of these strengthening bars.

Good preparations of these septa can be obtained by immersing the sections for twenty-four hours in aniline-water-safranin, washing out with weak acid alcohol, and then counterstaining with aqueous methyl blue. If the washing out is checked at the right moment, the red and blue of the bars and septum respectively are pure and their contrast decided.

MORPHOLOGICAL CHANGES INDUCED IN ROOTS OF BROMELIACEÆ BY ATTACK OF HETERODERA SP. By Rev. JAMES WATERSTON, B.D., B.Sc. (Plates IV., V.)

The object of this communication—which cannot claim to be more than a preliminary notice—is to give a short account of changes induced in the various root tissues of the Bromeliaceæ by the presence there of a species of *Heterodera*. A more thorough examination has been made of the parasite's ravages in *Pitcairnia* and *Billbergia*, but, while the following observations were made on species of these genera, the attack is not confined to them.

*Heterodera* is a genus of the Tylenchidæ, a family of Nematode worms. Tylenchi, the stem-eel worms, are only too well known to agriculturists in Britain and elsewhere from their devastation of cereals. *Heterodera*, first recognised in the early sixties, shares this evil family reputation. *H. schachtii*, Schmdt, *e.g.* causes "beet-sickness," sometimes so severe that one-third of the crop (5) is destroyed. Like Tylenchus it attacks wheat (2), barley, etc. Cabbage (3) has also been injured. *H. radicola* (4) was found in the Sahara to invade carrots, turnips, beets, tomatoes, the egg-plant (*Solanum Melongena*), onions, and celery.

It would be out of place to describe in detail the anatomy, etc., of *Heterodera*. But one or two points in its structure and life-history may be mentioned for an understanding of its characteristic attack.

The worm is well adapted to its specific life conditions (1). Both sexes have a strong mouth-prick, swollen proximally, by which the host's tissues are pierced and fixation there effected. When not exerted the style lies in a buccal groove immediately behind which is situated a bulbous muscular gizzard. This sucks in the juices of the host.

Marked sexual dimorphism occurs. The ♂, which when adult is recognisable by its six-rayed chitinous cap or "calotte," never loses its vermiform facies. But the ♀, which undergoes one ecdysis less than the ♂, and in fact retains its larval skin when adult, is greatly changed after impregnation. The reproductive organs and the alimentary tract become enormously swollen. Ultimately the worm is lemon- or citron-shaped. The genital pore from being lateral is shifted to a distinctly terminal position.

The larvæ of *Heterodera* are free living in the soil. At first they cannot be sexually distinguished. In some respects they resemble the adults, but differ in possessing pointed tails. After a time they attach themselves to the host plant, where the ♀ remains for life, falling off in the end either as an empty skin or as a brood-chamber for the young. The ♂ reaches maturity while attached to the plant. He then leaves it to find the ♀. Just before leaving he has assumed his peculiar head-dress. The larva is destitute of it; so too is the ♀, though in her case a covering of hardened sap simulates the "calotte" of the ♂.

Within the body of the gravid ♀ the embryos develop, and in their escape cause the death of their mother. The young may frequently be observed within a mucilaginous drop at the anal end of the parent. After hatching they make their way to the soil, where the life-cycle (four to five weeks) goes on as before. During the winter the unhatched larvæ of the last brood shelter in the skin of the dead mother.

*Heterodera schachtii*, Schmdt., does not penetrate at all deeply into the tissues of the plants attacked. *H. radicola*, and the form of which we are now speaking, on the contrary, live embedded in the host.

With respect to the former, the account of Vuillemin and Legrain (4) is here given without comment. These investigators found at El Oued (Sahara) that the majority

of the market-garden plants in cultivation were attacked. But the results were not uniform. Turnips and carrots were injured; beetroot, etc., thrive when *Heterodera* was present, but languished in its absence. In the latter case, in fact, only stunted, immature plants could be raised. This fact was at first regarded as a coincidence merely. Histological investigation showed, however, that the worm had brought about a useful modification of the tissues. Vuillemin and Legrain thus regard the association "comme une véritable symbiose." Further, they conclude, *Heterodera*, which in a moist<sup>1</sup> environment makes such havoc among root crops, produces most salutary effects in plants grown among arid desert sands. The injured carrots and turnips already referred to, at an early stage succeed in overcoming the parasite's beneficent action. Hence in their dry surroundings it becomes impossible for them to develop succulent tap roots. *Heterodera* has great resisting power to drought, and can lie dormant for a time. It thus proves a useful ally of the higher vegetation, "dans un milieu dont l'aridité exclut les symbioses cryptogamiques."<sup>2</sup>

The external symptom of the presence of *Heterodera* was a swelling of the root, spindle-shaped in Monocotyledons, round more or less in Dicotyledons. Transverse sections showed the following state of affairs:—In the vicinity of the worm, certain of the elements, both in the primary and in the secondary wood, were transformed at an early stage into greatly swollen "utricles."<sup>3</sup> These bladder-like formations had collenchymatous walls with numerous water passages. The original cell had undergone division, without apparently formation of cell walls, till each "utricle" contained a multinucleated mass of protoplasm

<sup>1</sup> "Dans les serres ou dans les champs des contrées humides."

<sup>2</sup> For in the desert Leguminous plants when sown fail to produce mycodomatia on their roots.

<sup>3</sup> The value of this modification depended entirely on the environment. At El Oued the garden soil, to a depth of 50 m., is nothing but sand. Twice a day the soil is liberally watered. Thanks to the structure induced by the parasite's attack, the plants take up sufficient liquid to last them in the interval. Turnips and carrots resist the formation of those giant multinucleated cells. The collenchymatous "utricle" in their case collapses at an early stage, or it is filled by a cell formation in which starch deposits. Thus though the roots may survive owing to their fleshy nature, they never become so succulent as others in which the attack has been successfully established.

rich in reserve nitrogenous matter and without starch. As the structures just described abut on the vasa, they were able to draw water thence, store it for a time, and then pass it on to the thirsty cells around them.

In the Bromeliaceæ the roots frequently show swellings near the tip. But in general the effects of the attack of *Heterodera* can best be seen in fusiform enlargements some distance back. These are inconspicuous until they have split open.<sup>1</sup>

Rupture often takes place in the line of their long axis. The cortex is pierced. Sometimes even the vasa of the central cylinder are laid bare. Occasionally, with a lens, white specks in the innermost recesses of the fissure can be detected. These are, of course, the ♀ *Heterodera* swollen with eggs.

Now, because of the structure of the normal root, these ruptures, setting aside the hypothesis of some mechanical disturbance, challenged investigation. In the Bromeliaceæ the root cortex shows in its middle a sheath of exceedingly hard sclerenchyma (Plate V. fig. 1). Section cutting is often a matter of great difficulty. But wherever these white specks could be made out, the sheath had evidently been pierced by some agent. Transverse sections showed an even more remarkable state of affairs, viz. that the sheath appeared never to have formed at the spots referred to. On one side of the section the thickened libriform sclerenchyma was replaced by a mass of thin-walled cells.

The following is a general account of the changes observed :—

In some extreme cases the whole of the central cylinder with the inner cortex had perished. The root was reduced to a sheath of sclerenchyma surrounded by the dried remains of the outer cortex. Occasionally traces of the piliferous layer could be distinguished. More often every indication of it had vanished.

Where the destructive process had not gone so far the surviving tissues showed more or less disorganisation.

<sup>1</sup> The swellings at the tip have been investigated without, however, yielding any data that cannot better be taken from the second point of attack.

- (a) The pith, whose cells are, as a rule, wholly lignified, peripherally at least, was scarcely abnormal. The thickening<sup>1</sup> was hardly so pronounced as usual. Its outline might be distorted. It has, however, never been observed to be invaded by the parasite.
- (b) In the Bromeliaceæ the vasa of the main roots are symmetrically ranged about the pith. *Heterodera* often occurs in the vasa where these are large, as *e.g.*, in *Pitcairnia* spp. In some instances the parasites, dissected out from this position, were found to have attached themselves to the wall next the pith.

Where the worm is established the walls of the vas and those of the neighbouring wood parenchyma remain thin (Plate IV. fig. 5). Sometimes they are found broken down—thus preparing the way for the condition first described.

- (c) The phloem seems seldom to be invaded. But in the vicinity of an attack it may share in the hypertrophy induced (Plate IV. fig. 2, *ph.*).
- (d) The protoxylem may afford the parasite lodging and be obliterated. But even if the attack be only near a patch of protoxylem there may be marked increase in the size and number of the elements, *e.g.* a species with normally three small vessels has shown as many as seven or eight (Plate IV. fig. 3).
- (e) Generally *Heterodera* is found lying in a gall (Plate V. figs. 2, 3), whose long axis is roughly in a plane at right angles to the long axis of the root. Occasionally it may be placed otherwise—even parallel to the root axis. The gall itself is apparently formed from the innermost layer of the inner cortex, the endoderm, and the pericycle. Its walls consist of one or two layers of compressed cells which have been flattened against one another by the growth of the parasite.

Of the creature as found little can be said. Only the ♀ has been noted. Doubtless the ♂ and larvæ will be found when searched for in the soil. The ♀♀ occur commonly

<sup>1</sup> In one instance, however (Pl. IV., fig. 4), the pith consisted almost entirely of parenchyma.

in a large number of Bromeliaceæ in cultivation in the Royal Botanic Garden, Edinburgh. Plants from the Botanic Garden, Glasgow, also show the same attack.

No anatomical details can, as a rule, be made out in these ♀♀. Practically all examined have been in the last stage—nothing more than sacs of eggs or more or less empty skins containing some protoplasmic debris. Occasionally large nuclei may be seen—apparently the last traces of the alimentary canal. A section of the creature's attack in a vas thus often shows merely a clear thick zone lining the cavity. Within there is a film of protoplasmic matter (Plate IV. fig. 5). The clear zone referred to is, of course, the thick and practically unstainable epidermis characteristic of Nematodes.

I do not know of any measurements made in the case of *H. schachtii* and *H. radicicola*. The present attack may be the work of a distinct species or even of more than one species, should the form infesting plants in the Royal Botanic Garden, Edinburgh, prove to be different from that found in Glasgow. The following dimensions may be given:—

	Length.	Breadth.
1. Adult ♀ from <i>Pitcairnia</i> sp. (lemon-shaped). Edinburgh	·588 mm.	·35 mm.
2. Much younger ♀ from <i>Pitcairnia</i> sp. (shaped like a Florence flask) (This example began to narrow at a point genital aperture. It there measured ·07 mm. in breadth.)	·448 mm.	·168 mm.
3. Eggs of ♀ No. 1, still in the body of the mother . . .	·084 mm.	·028 mm.

Satisfactory measurements of the endodermal galls have not yet been obtained for all three dimensions. In a number of sections taken from a root of *Pitcairnia bracteata* (Glasgow Botanic Garden) the length of the gall is ·252 mm. and the breadth ·112 mm.

In a gall from an Edinburgh plant (*P. corallina*) the transverse measurements are ·154 and ·112 mm. respectively. The length cannot be determined.

The worm then, one would imagine, must be under pressure. Apparently, too, it may be folded on itself within the gall, but details are not easily made out.

Changes in the tissue near the gall have now to be described.

Very characteristic are the effects on the endodermis

itself. Sometimes all trace of this in the immediate vicinity is lost. But, as a rule, it persists with the radial walls slightly elongated where the cells abut on the point of attack. For some distance on either side of the gall the radial walls of the endoderm are unthickened. Further round the normal thickening reappears. Thus an attacked root in T.S. shows an endodermis consisting on one side of thin parenchyma, on the other are the usual horseshoe-shaped cells (Plate IV. fig. 2).

The pericycle, under the irritation of *Heterodera*, divides tangentially (Plate IV. figs. 2, 3, *p*), and may form a layer three to four cells deep.

The effect on the cortex too is distinct. In T.S. there appears a broad proliferation of thin-walled cells stretching outwards from the endodermis and widening as it goes. This mass of cells must originate from the inner cortex while that is still capable of division. The sheath of sclerenchyma, which forms in Bromeliads a mid-cortical layer, never is found opposite a gall (Plate V. figs. 2-4). *Heterodera* in some way inhibits the deposition of thickening matter on the cell wall. Two advantages in all probability directly follow. There is reduced pressure, while additional moisture may come in from the outside. Further, as rupture takes place latterly in this proliferated region the young *Heteroderae* find prepared a passage to the soil where the early stage of the life-cycle is passed.

One curious feature of this mass of thin-walled cells is that here and there in it occur isolated elements over which *Heterodera* has had no inhibiting influence (Plate V. fig. 2). They are more or less completely lignified. Where the unthickened tissue joins the sheath there is frequently a gradual transition from such isolated cells to a broad continuous band of sclerenchyma. In other cases the line of demarcation is sharp.

As regards the final result of the attack, it has already been remarked that in extreme cases the entire central portion of the root is killed below the point of the worm's lodgment. In many instances—where the attack has been severe—the cells of the tissue a little above the parasite have been thickened or filled up. But as this condition is frequently observed in old normal roots



or where there has been mechanical injury, one can have no confidence in connecting it directly with the presence of *Heterodera*.

In one instance, however, the root had apparently reacted successfully against the worm. T.S. showed a triangular gaping wound reaching almost to the pith. In this space presumably the worm had been situated. Inside the thickened sheath a second, much narrower than the first, had formed. Opposite the wound this new sheath bent inwards, traversing the inner cortex, endodermis, etc., and effectually cutting off the injured area. About one-third of the functional central cylinder was thus saved. In the portion cut off the cells were either lignified or filled with gum, while the soft tissue which had caused the gap seem to have been suberised.

The nature of the tissue made no difference to its fate, cortex, endoderm, pericycle, phloem, and vasa were alike filled up.

There are some interesting points in a comparison of the present attack with that noted by MM. Vuillemin and Legrain. The Bromeliaceæ are epiphytes and xerophytes in tropical America. Their environment, therefore, is in some respects comparable to that of the plants grown at El Oued in the Sahara. In both cases the parasite is internal and causes hypertrophy of the tissues. There is, however, nothing in the cell proliferation noted in the Bromeliads analogous to the "utricles" of V. and L., with their multinuclear protoplasmic contents, which are supposed to benefit the host. So far as the Bromeliaceæ are concerned, it is extremely unlikely that at any time *Heterodera* comes under this beneficent category. Conceivably at the first it may stimulate the root tip to greater activity and cause a more copious water-supply. But for this there is at present no evidence. Everything points to the association of worm and root as one of malignant parasitism.

I have to thank warmly the following gentlemen :—

Professor Bayley Balfour, who has provided every facility for investigating the Bromeliaceæ under his charge in the Royal Botanic Garden, Edinburgh. Mr. L. Stewart has also assisted in many ways. I am indebted also to the Glasgow

authorities and to Mr. Rourke, superintendent of the gardens there, for some valuable material.

Mr. W. E. Evans, B.Sc., very kindly made slides from sections illustrating the attack.

To my friend Dr. Ashworth I have been greatly obliged throughout. He has helped me in the identifying of the parasite, in searching for literature, by several discussions, and by the loan of slides of the life-history of *H. schachtii*, Schmdt., which were shown to the Society when this communication was first read.

---

#### REFERENCES.

- (1) Drs. LEUCKART and NITSCHKE, *Erklärungen zu den zool. Wandtaf.*, Cassel, 1877.
  - (2) C. CLAUS, *Traité de Zoologie*, 12th French edition. Ed. by Moquin-Tandon, Paris, 1884, p. 527.
  - (3) SEDGWICK'S *Student's Text-Book of Zool.*, vol. i., London, 1898, p. 290.
  - (4) VUILLEMIN et LEGRAIN, "Symbiose de l'*Heterodera radicola* avec les plantes cultivées au Sahara," C. R. Acad. Sc., cxviii., 1894, p. 549.
  - (5) *Cambridge Nat. Hist.*, vol. ii. pp. 154-156.
- 

#### EXPLANATION OF PLATES.

##### PLATE IV.

Fig. 1. T.S. of Normal Bromeliad root, near endodermis. *Billbergia pallidiflora*.

„ 2. T.S. of root (from large vas to inner cortex) near attack of *Heterodera* sp. *B. pallidiflora*.

„ 3. Hypertrophied protoxylem. *B. pallidiflora*.

„ 4. Pith and vasa. Thickening inhibited. *B. Saundersii*.

„ 5. Attacked vas to show parenchymatous walls persistent. *Pitcairnia corallina*.

*i.c.* inner cortex. *ph.* phloem.

*e.* endodermis. *p.x.* protoxylem.

*p.* pericycle. *v.* vas.

*t.p.c.* thickened pith-cells. *u.p.c.* unthickened pith-cells.

*x.p.* xylem parenchyma.

## PLATE V.

- Fig. 1. *Tillandsia dianthoidea*. T.S., a normal root. The lateral thin parts of the cortical sheath are due to the emergence there of secondary roots.
- „ 2. *Pitcairnia bracteata*. *Heterodera* ♀ in situ in endodermal gall, apparently slightly doubled. Note the isolated thickened cell.
- „ 3. *Pitcairnia corallina*, badly attacked root. The endodermis and vasa have been occupied.
- „ 4. The same, more highly magnified.

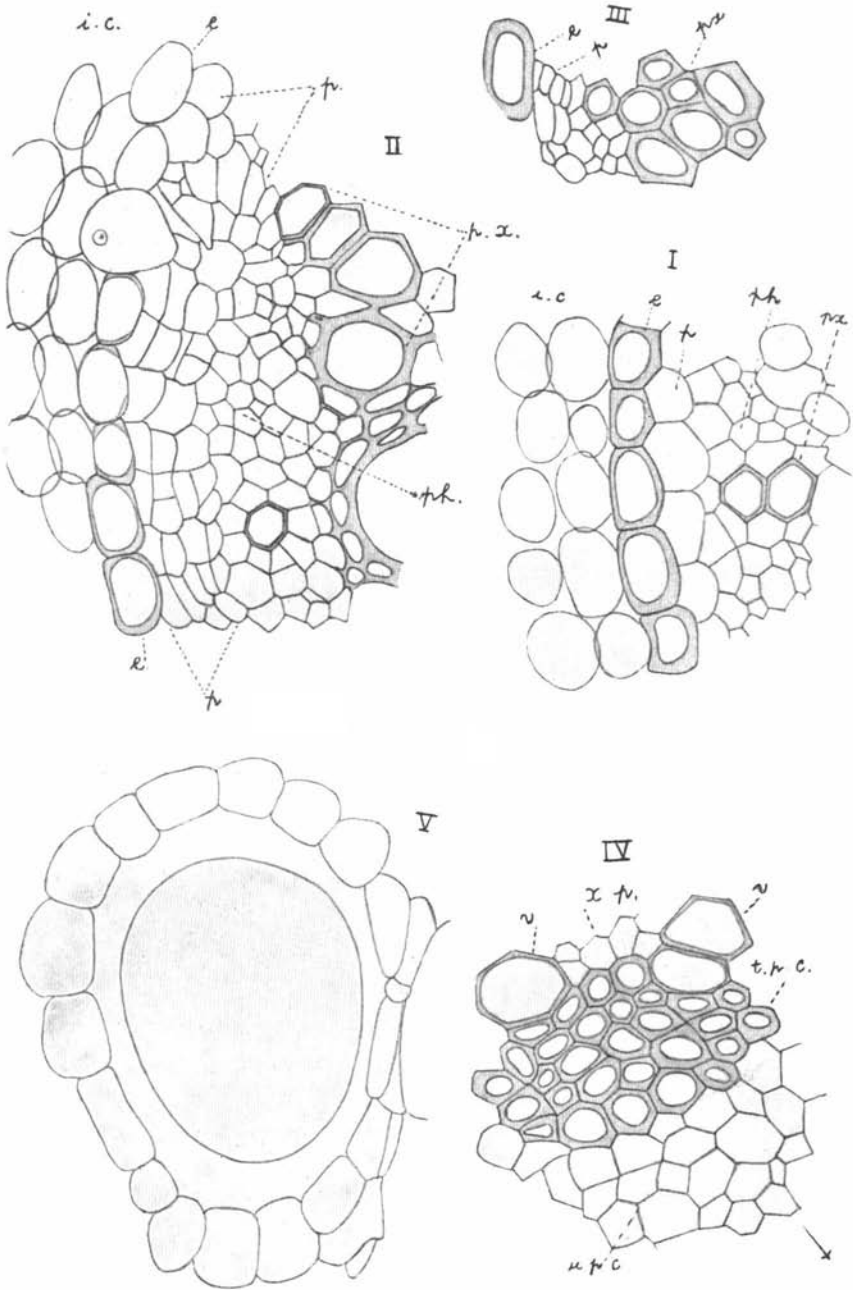
## EXUBERANT LENTICEL FORMATION ON AN OAK SEEDLING.

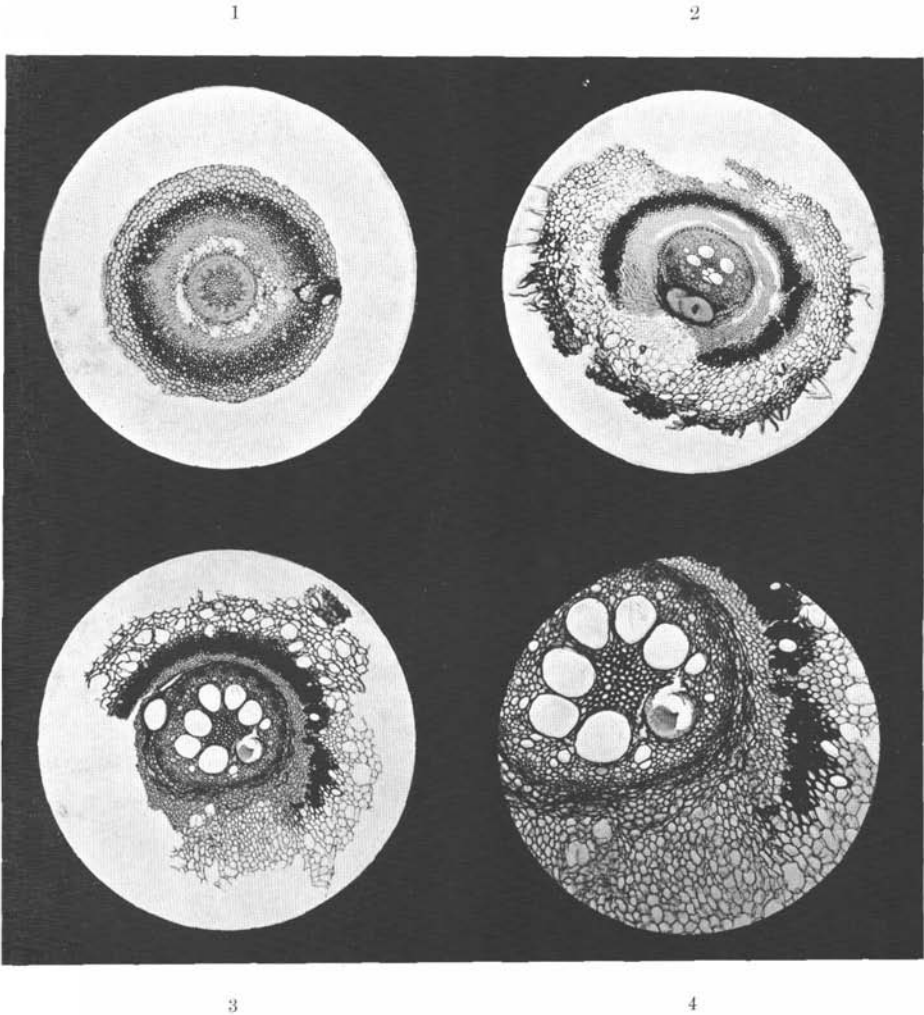
By Miss BERTHA CHANDLER, M.A., B.Sc. (Plate VI.)

At a former meeting of the Botanical Society Mr. Rutherford-Hill showed an oak seedling which had been sown in water, exhibiting, in consequence, abnormally developed lenticels on the roots. The specimen, which was eleven weeks old, was kindly given me by Mr. Rutherford-Hill, with another, seven weeks old. The photographs are from the former, the older specimen, which exhibited these outgrowths to a more marked extent than the latter.

Before examination under the microscope, these structures were thought to be “pneumathodes,” but sections showed that they were rather lenticels having no differentiated structure apart from the lateral root which these encircled. The production of abnormal lenticels is very much akin to the artificial production of aerial roots, for the same factor, excess of moisture, favours the development of both structures. Just as pneumathodes can be induced in plants by cultivation under water, so abnormal lenticel formation, caused by the accelerated division of the lenticel initials, can also be induced. The oak seedling figured is an example. Terras,<sup>1</sup> speaking of abnormal lenticels occurring on stems, says that under similar conditions the same thing occurs on roots. The two main factors, the abundance of moisture and the reduction of the pressure owing to the slight resistance of the medium in which the seedling is grown, account for the abnormal development of these

<sup>1</sup> “Trans. Bot. Soc. Edin.,” xxii. p. 450.





Photographed by W. EDGAR EVANS.