Anatomical relations of root formation in strawberry

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Summary: Anatomical relations of root formation are traced throughout the life cycle of the strawberry plant from the germinating seed up to the runners of the adult plant. Histological picture of the root changes a lot during the development of the plant. First the radicle of the germ grows to a main root, which makes branches into side roots and later adventitious roots are formed on the growing rootstock or rhizome. The anatomy of the different types of roots is also conspicuously different. First tiny branches appear relatively early after germination on the seedling's radicle, but soon the hypocotyl of the seedling thickens and develops side roots, which are already somewhat stronger. During this interval, the first true leaves are formed. The 4^{th} or 5^{th} of them being already tripartite, and the initiation of new roots extends into the epicotylar region of the shoot. The second years growth starts with the development of reproductive structures, inflorescences and runners starting from the axils of the new leaves. Near the tips of the runners below the small bunch of leaves, new root primordia are initiated. The tiny radicle of the germ develops a cortical region of 5–6 cell layers. Cells of the central cylinder are even smaller than the cortical parenchyma and include 3–4 xylem and 3–4 phloëm elements as representatives of the conductive tissue. Roots originating from the shoot region are much more developed; their cortical zone contains 17–20 cell layers, whereas the central cylinder is about half as large. In the next year, new roots are formed at the base of the older leaves. These roots differ hardly from those of the last season in size and volume, however, they are recognised by colour and their position on the rhizome. The roots of the last year are dark, greyish-black, and grow on the lower third length of the rhizome, on the contrary, the new ones, on the upper region, are light brown. Roots starting from the shoot or rhizome are, independently from their age or sequence, mainly rather similar in size and diameter, thus being members of a homogenous root (homorhizous) system, i.e. without a main root. Plants developed and attained the reproductive phase develop in the axils of the leaves runners being plagiotropic, i.e. growing horizontally on the surface of the soil. The runners elongate intensely, become 150–200 mm, where some long internodes bear a bunch of small leaves and root primordia on short internodes and a growing tip. Runners do not stop growing, generally, further sections of 15–25 cm length are developed according to the same pattern, with small leaves on the tip. The growing tip of the runners is obliquely oriented, and small, conical root primordia are ready to start growing as soon as they touch the soil. The roots penetrate the soil, quickly, and pull, by contraction, the axis of the runner downwards, vertically, developing a new rhizome. The short internodes elongate a little and start developing adventitious roots. At the end of the growing season, the plantlets arisen on the rooted nods of runners are already similar to the original plants with homogenous root system. On the side of the adventitious roots, new branches (side-roots) are formed. The root-branches are thinner but their capillary zone is more developed being more active in uptake of water and nutrients. The usual thickening ensues later.

Key words: strawberry, root, root formation, internode

Introduction

Morphology and anatomy of the strawberry raised, recently, the attention of students. Earlier, detailed analyses and some pictures of the adult strawberry plant have been published (*Dennert* 1894, *Filarszky* 1911, *Goebel* 1928–32, *Troll* 1937–1939, *Troll & Rauh* 1950), recently, the tracing of the outer and inner appearance of developmental processes and changes characterised the literature (*Muromcev* 1969, *Naumann & Seip* 1989, *Papp, Gracza & Lenkefi* 1999).

Our own initial morphological analyses suggested the conviction that the relatively small plant produces radical reorganisations of outer morphology as well as in its coherent inner anatomy each time when leaf-rosettes, then long runners are formed. Individual organs (root, stem, rhizome, leaf) have been analysed as for their histological structure, which could be compared with the outer morphological changes.

First, the development of roots has been analysed. Data on the structure of roots were published by *Muromcev* (1969), but only a single, the intermediate, developmental stage was represented. *Naumann & Seip* (1989) focussed their attention on the growing tip of the shoot, additionally, on the structure of the developed root.

Our own studies started with the analysis of the germinating seedling, the radicle, its branching and the initiation of adventitious roots followed by the older, thickening roots. The number of bundles in the cross section of roots, conductive xylem and phloem tissues is 5-5. The primary cortex and the central cylinder are separated by one cell layer of the pericambium. The pith consists of large thin-walled cells.

Soon after the primary organisation of the root tissues, the secondary growth, i.e. thickening of the conductive tissues ensues. As a first step, a remarkable new phenomenon appears. In the primary cortex, the thin-walled pith cells experience some conspicuous transformation, as their walls develop thickenings in an annular, spiral or reticular pattern. Their cytoplasm is meanwhile consumed, whereas their form elongates and adopts the appearance of conductive cells, i.e. tracheids. That peculiar type of cell transformation has been found in lower (ancient type) plants, where simple xylem and phloem bundles constitute the conductive tissue-system. Our former studies proved the occurrence of wall thickenings in the pith. In roots of Angiosperms, Ranunculus and some Gramineae species, this type of secondary differentiation of conductive tissues was recognised.

Subsequently, the typical thickening of the root followed as the third phase of the root growing process. The cambium layer appears, first in the typical undulate form between the xylem and phloem bundles, and so both type of conductive tissue are produced by the dividing cambium.

In addition to the former processes, the appearance of the cork-cambium has been observed as a rarely clear cut example, when the primary cortex is rejected.

Material and method

Young seedlings, larger plants with leaf-rosettes, young as well as developed runners of strawberry were collected. The variety "Elsantha" of the garden strawberry (*Fragaria ananassa* Duch.) has been selected for the purpose of investigation.

Each sample was subject to detailed morphological analysis. Descriptions were accompanied with drawings and photographs. At the same time, root samples of various size were also collected for quick tests. Sections made with a razor knife were examined in the light microscope stained with toluidine-blue. Anatomical details were fixed by photo pictures. The rest of the samples has been preserved in 40 % ethanol for the purpose of later, complementary examinations.

For additional tests by scanning electron microscopy, the cut surfaces were prepared according to the usual procedures.

Results

The present study deals with results of the morphological analysis of root initiation and development. First, the adult plant was attacked as being considered to be homogenous. Both, the original "mother" plant raised from a seedling as well as the rooted runners develop a rhizome, which produces the uniform adventitious roots.

Morphological observations

The seedling with the cotyledons develops a straight radicle of 20–30 mm length, without branching. With the appearance of the first true leaves, the "main" root starts branching and continues growing without thickening.

The plantlet attaining the height of 1–2 cm extends its tiny true leaves *(Figure 1)*. Incisions on the tip of leaves

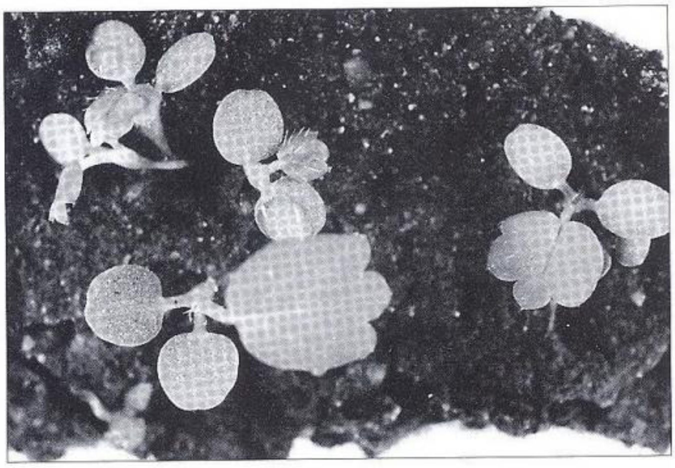

Figure 1 Young strawberry seedling with two coltyledons and one small true leaf

indicate the beginning of the future composed leaf form. Changes are occurring on the hypocolyl level. Thickening of the vertical organ is the first step of building a rhizome, and branching of adventitious roots starts first below, then above the coltyledons. The new roots start to grow horizontally, later turn downwards and continue growing obliquely. They grow more quickly and are more robust than the first main root and its primary branches.

Contractive shortening of the adventitious roots pulls the thickening rhizome downward into the soil, the shoot tip only remains on the surface. Meanwhile, the new leaves are already trifoliate. The vertical rhizome attains at the end of season a diameter of 3–4 mm *(Figure 2)*.

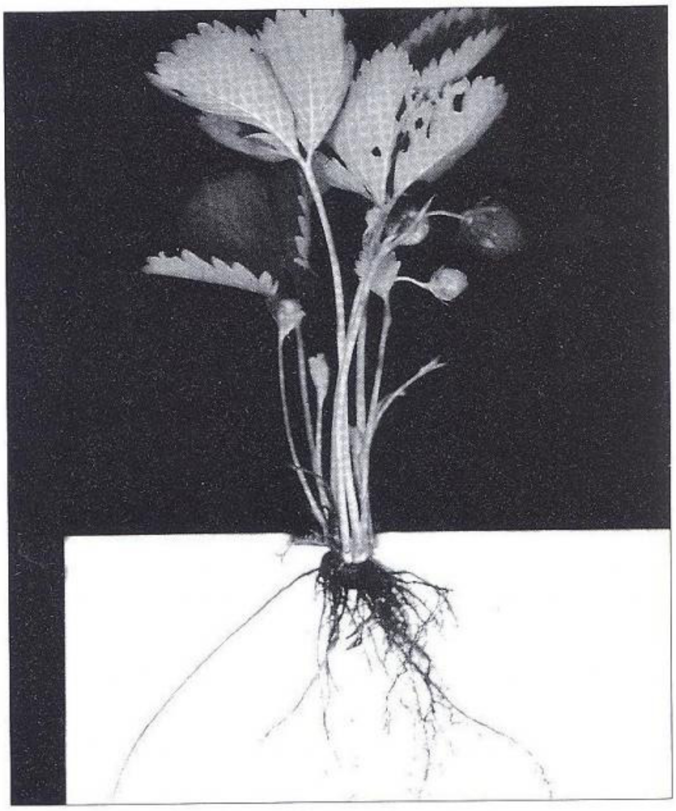

Figure 2 Adult plant with well developed root system

Histological findings

Substantial differences are stated among the roots of different origins and positions, e.g. the seedling's radicle, the "main root", the side branches of the former, which are tiny, whereas the adventitious roots growing from the thickening rhizome are stronger.

The primary cortex and the central cylinder of the radicle are narrow. The cortex harbours 5–6 cell layers. The shape of cells are iso-diametric, their size is medium large. In the central cylinder there are more cell layers with smaller size. Xylem and phloem bundles alternate 3–3 of each; later in larger ones 4–4. On the surface of the central cylinder is a single layer of pericambium *(Figure 3)*. The pith is built up of thin walled cells as visible in the longitudinal section *(Figure 4)*.

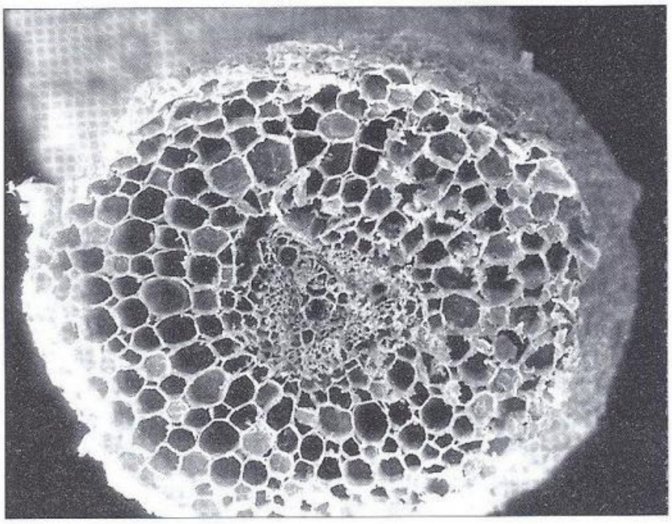

Figure 3 Root cross section of a young plant

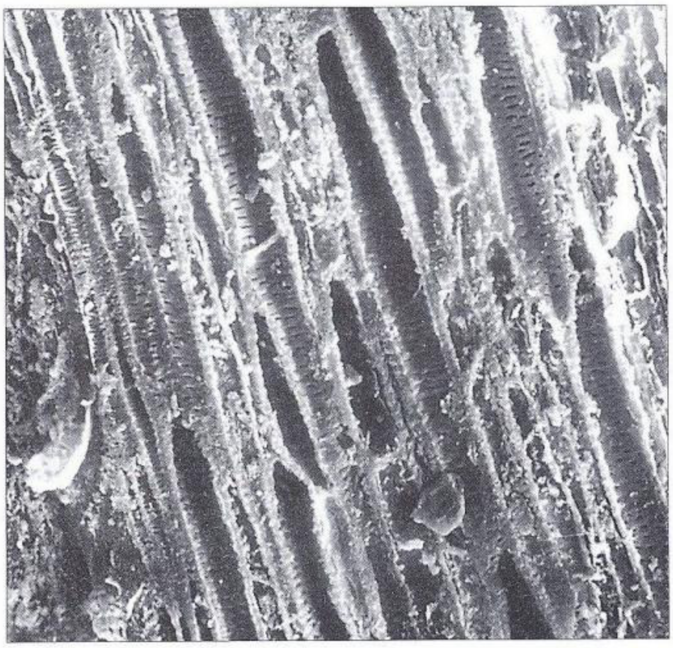

Figure 4 Longitudinal section of root in a young plant with large, elongated, thin walled cells

Adventitious roots starting from the rhizome are substantially thicker than the derivatives of the radicle. The anatomy of the root express the difference clearly, as their cortical zone is 17–20 layer thick, whereas the central cylinder is relatively smaller in diameter, almost half as large, but larger than that of the seedling root's. The number of conductive bundles grows to 5–6 of xylem and the same number of the phloem bundles *(Figure 5)*. The pith is also larger with larger thin walled cells, whereas the pericambium is equally present on the boundary of the cylinder.

Roots are growing larger clearly and the changes in the anatomy are also progressive. The conductive tissue does not follow the accustomed way, as instead of the undulated cambium ring having been formed to produce secondary xylem and phloem elements, transformation of the pith sells ensues. The thin walled pith cells develop spiral, annular and reticulate cell wall patterns, meanwhile the cell content disappears, and finally, the whole pith is transformed to a conductive tissue *(Figures 6, 7, 8)*. This type of conductive tissue formation has not been published yet, though it exists also in other plant species but was not followed up during its development. An overlook of the phylogeny of plants reveals its occurrence in ferns and ancient fossilised pteridophytes, which had woody organs well maintained. It is evident in

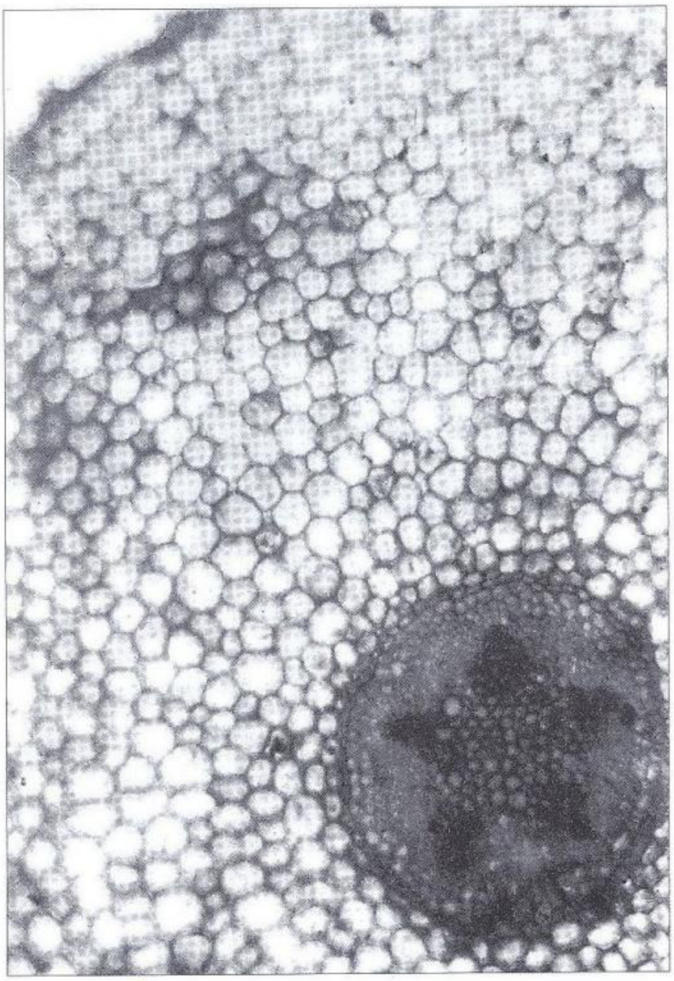

Figure 5 Root cross section of an adult plant with xylem and phloem bundles, 5 of each, and pith tissue in the centre whit large, thin walled cells

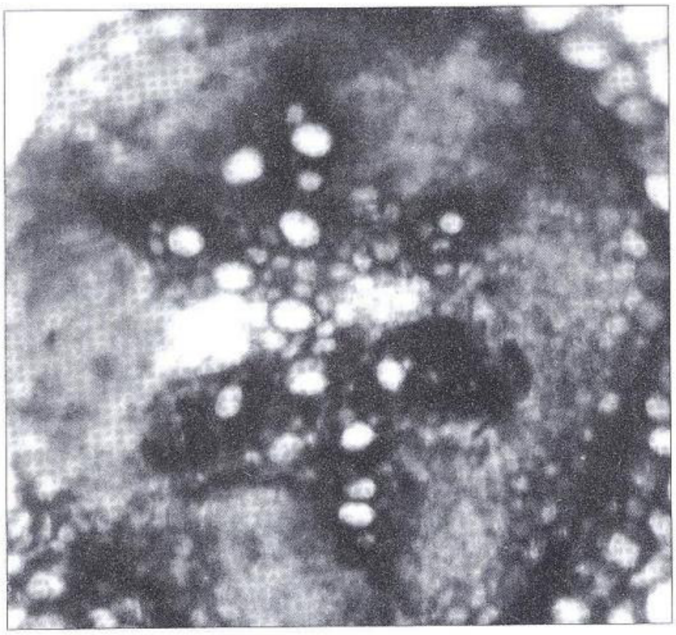

Figure 6 Cell walls start to develop thickening

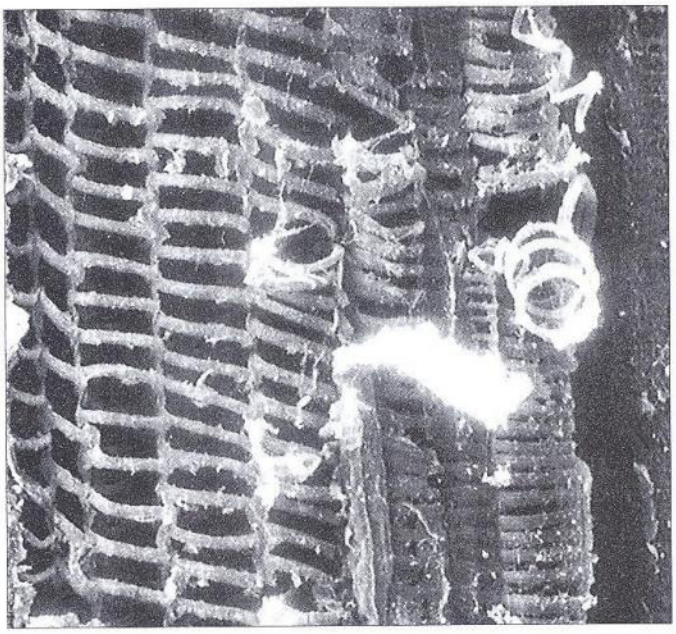

Figure 8 Secondary conductive elements display spiral, annular patterns on the cell wall

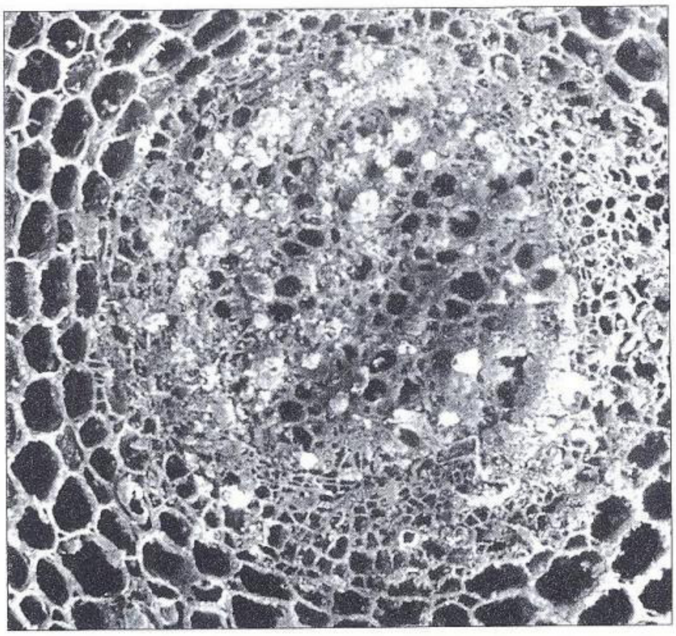

Figure 7 Formation of water conducting tracheids is observed in the pith

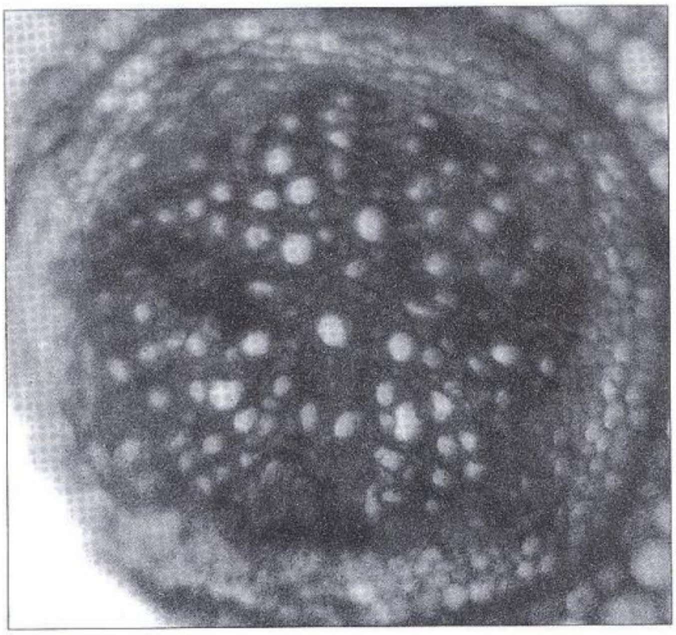

Figure 9 Formation of the undulate cambium with centrifugally produced conductive tissue elements

Psilotum triquetrum, but it is found in the stem region. In the stem region of the ferns, the xylem and phloem are first organised in separate bundles, then the pith cells start to develop spiral, annular and reticulate patterns. The transformation of the pith is a way to build out conductive tissue. Thus the transformation of the pith is an ancient ability of secondary anatomical changes. The stem has been exposed to weather and other environmental adversities, consequently, the conductive system developed by several steps.

Transformation of the pith to become conductive tissue appears also in higher, angiosperm plants, but the transformation of the root was preserved. In some Gramineae, Ranunculus, and here in the root of *Fragaria* we recognise the transformation of the tissue.

In the root of *Fragaria* and *Ranunculus* the development did not stop with that, but the typical secondary thickening with further formation of xylem and phloem of the root continues. It is the third phase of root development, when the undulate cambium produces, bilaterally, tertiary wood cylinder and a tertiary ring of bark, i.e. continuous wood and bark *(Figure 9)*.

In the structure of the root one more significant change has been observed. The original pericambium develops to a cork cambium starting cell division quickly 5–6 layers of

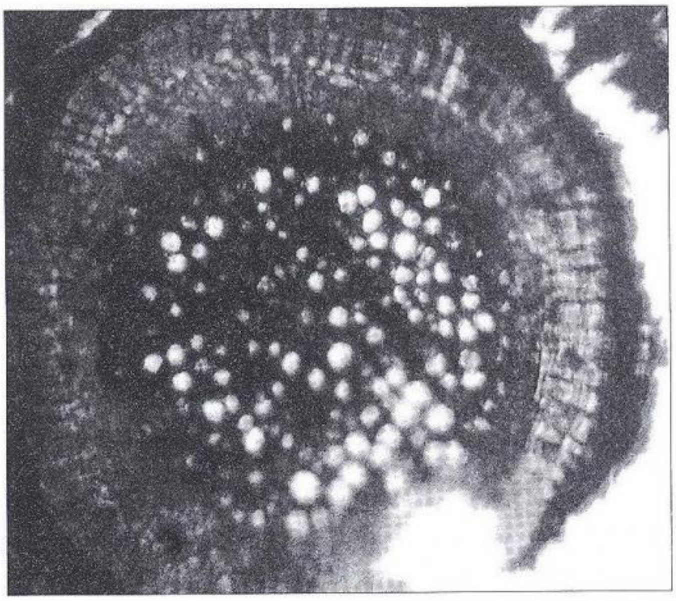

Figure 10 With the cork cambium and the cork tissu the primary bark has been pushed outwards and dies off

periderm on the outer surface of the central cylinder. The cork tissue closes the translocation between the primary bark and the conductive cylinder. The colour of the primary bark turns dark greyish black and is rejected *(Figure 10)*.

Acknowledgements

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