

Anatomy of *Sarcocaulon*

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ABSTRACT

The anatomy of the leaf blade, petiole, stem and root of the genus *Sarcocaulon* (DC.) Sweet is discussed. On the basis of the leaf anatomy, the four sections recognized by Moffett (1979) can be identified: section *Denticulati* (dorsiventral leaves), section *Multifidi* (isobilateral leaves and adaxial and abaxial palisade continuous at midvein), section *Crenati* (isobilateral leaves, short curved trichomes and glandular hairs), section *Sarcocaulon* (isobilateral leaves and glandular hairs only). The anatomy of the stem is typically that of a herbaceous dicotyledon with a thick periderm. The root structure shows that the function of the root is not food storage.

RÉSUMÉ

L'ANATOMIE DES SARCOCAULON

L'anatomie du limbe foliaire, du pétiole, de la tige et de la racine du genre *Sarcocaulon* (DC.) Sweet est discutée. Sur base de l'anatomie de la feuille, les quatre sections reconnues par Moffett (1979) peuvent être identifiées: section *Denticulati* (feuilles dorsiventrals), section *Multifidi* (feuilles isobilatérales et tissu palissadique adaxial et abaxial continue au niveau de la nervure médiane), section *Crenati* (feuilles isobilatérales, trichomes courts et courbés et poils glandulaires), section *Sarcocaulon* (feuilles isobilatérales et poils glandulaires seuls). L'anatomie de la tige est typiquement celle d'une dicotylédone herbacée avec un périderme épais. La structure de la racine montre que celle-ci ne joue pas le rôle d'une réserve alimentaire.

INTRODUCTION

Sarcocaulon known by the common name 'Bushman's Candle' is one of the five genera belonging to the family Geraniaceae. The other four are *Geranium*, *Pelargonium*, *Monsonia* and *Erodium*.

Sarcocaulon plants are fleshy short-stemmed shrublets covered with a hard waxy bark which is inflammable due to being impregnated with wax. The root system is formed by a primary root and lateral roots. Leaves are long or short petioled with the long petioles persisting as spines. The short petioled leaves occur singly or in tufts in the axils of the spines. The leaves are simple or compound with the nature of the leaf margin of taxonomic importance. Moffett (1979) divided the genus into four sections primarily on the nature of the leaf margin. The following sections and species were recognized by Moffett (1979):

Section *Sarcocaulon* (leaf blade without lateral incisions). *S. camdeboense*, *S. l'heritieri*, *S. patersonii*, *S. salmoniflorum*, *S. vanderietiae*.

Section *Crenati* (leaf blade with lateral incisions, leaf unsegmented and leaf margin lobed). *S. ciliatum*, *S. crassicaule*, *S. flavescens*.

Section *Denticulati* (leaf blade with lateral incisions, leaf unsegmented and leaf margin not lobed). *S. inerme*, *S. marlothii*, *S. mossamedense*.

Section *Multifidi* (leaf segmented). *S. herrei*, *S. multifidum*, *S. peniculinum*.

The 14 southern African species are distributed over the more arid areas, ranging from the eastern Cape to southern Angola. The majority of species occur near the mouth of the Orange River. The plants grow in extremely hot, dry areas, remaining

entirely leafless throughout most of the year. The leafless plants may produce an occasional flower (Glass & Foster, 1970), but the plants only produce leaves after sufficient rain. After such rains, the plants are capable of bursting into flower and leaf almost immediately.

MATERIAL AND METHODS

Material from all the species except *S. inerme* and *S. peniculinum* was investigated.

The material used was obtained from plants in their natural habitats and plants collected and planted in the Botanical Garden of the University of the Orange Free State. The material was fixed in F.A.A., dehydrated by the tertiary butyl alcohol method (Gray, 1958), embedded in Histosec wax and sectioned at 10 µm. The sections were stained in Safranin and Fast Green and mounted in Entellan.

Leaves prepared for the scanning electron microscope were fixed in 3% glutaraldehyde in phosphate buffer (pH, 7.0), post-fixed in 1% osmium tetroxide, dehydrated in ethyl alcohol, critical point dried and sputter coated with gold.

RESULTS AND DISCUSSION

Anatomy of the leaf

Trichomes

Glandular and non-glandular unicellular hairs occur on the leaves. The glandular hair is found on all the species. It consists of a short uniseriate stalk of three cells and a unicellular spherical head (Fig. 1). The non-glandular unicellular trichomes are of two basic types, namely short curved trichomes and long straight trichomes (Figs 2 & 3). The short curved trichomes are found in *S. ciliatum*, *S. crassicaule*, *S. flavescens*, *S. herrei* and *S. multifidum*. The long trichomes are only present in *S. herrei* and *S. multifidum*.

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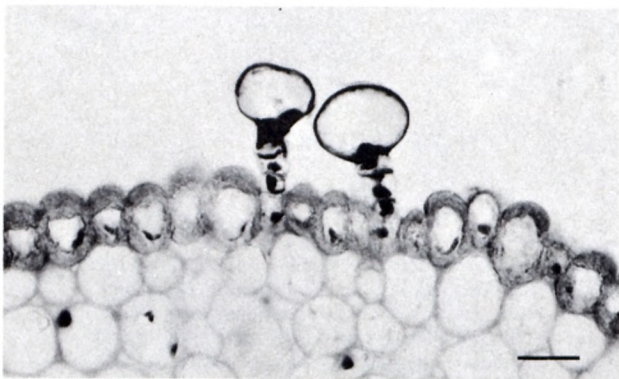


FIG. 1.—Part of a cross section through the petiole of *Sarcocaulon marlothii* to show the glandular hair. Bar = 20 μ m.

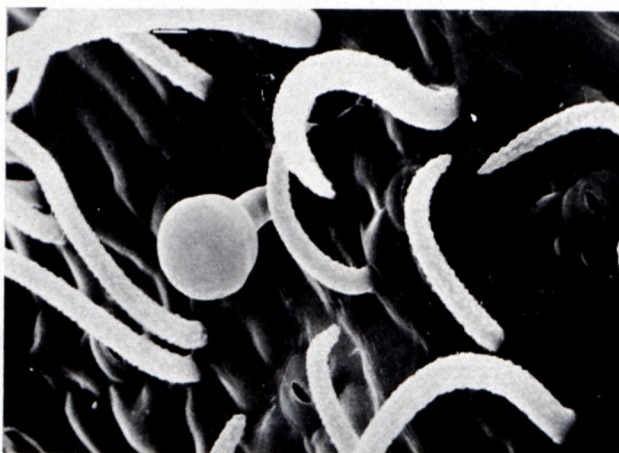


FIG. 2.—Scanning electron micrograph of glandular hair and curved trichomes on leaf of *Sarcocaulon multifidum*. Bar = 10 μ m.

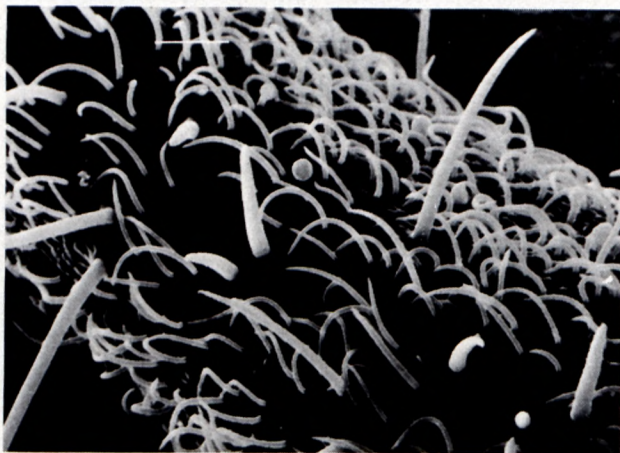


FIG. 3.—Scanning electron micrograph of glandular hairs, curved trichomes and straight trichomes on leaf of *Sarcocaulon multifidum*. Bar = 100 μ m.

According to the trichomes present two of the four sections recognized by Moffett (1979) can be identified. These are section *Crenati* with glandular hairs and short curved trichomes and section *Multifidi* with glandular hairs and both types of non-glandular unicellular trichomes. In section *Sarcocaulon* and section *Denticulati* only glandular hairs are found.

Lamina

Isobilateral in all the species, except *S. marlothii* and *S. mossamedense* where the leaf structure is dorsiventral. A thick cuticle is present. The adaxial and abaxial epidermal cells are of more or less the same size both containing cells of unequal size. Anomocytic stomata are found on both upper and lower surfaces of the leaf (amphistomatic leaf) and are on the same level as the other epidermal cells. The pores are irregularly orientated in surface view.

Mesophyll is differentiated into palisade parenchyma and spongy parenchyma. In the dorsiventral leaves (Fig. 4) (*S. marlothii* and *S. mossamedense*) the palisade consists of one cell layer and is not continuous above the main vein. The palisade parenchyma is well developed and in some cases can occupy at least half the thickness of the mesophyll.

In the isobilateral leaves (Fig. 5) the adaxial and abaxial palisade consists of two cell layers with the inner palisade layer consisting of shorter cells. The adaxial palisade layer is usually better developed. In *S. herrei* and *S. multifidum*, the two examples with compound leaves, the adaxial and abaxial palisade parenchyma is continuous at the midvein (Fig. 6). In the other species with isobilateral leaves, the abaxial palisade is always interrupted at the main vein but the adaxial palisade is continuous (Fig. 7) or interrupted in the same species. In the majority of material examined the palisade parenchyma was continuous.

Vascular bundles are collateral with each vein surrounded by a parenchyma sheath. On the abaxial side of the vascular bundle the sheath cells may be sclerenchymatous. A few fibres may be present between the sheath and the phloem. The parenchyma cells internal to the abaxial epidermis are often sclerenchymatous.

Calcium oxalate crystals in the form of druses are common in the mesophyll.

Based on the anatomy of the lamina the two sections *Denticulati* and *Multifidi* can be identified. However, in combination with the trichomes, all four sections recognized by Moffett (1979) can be identified. These are section *Denticulati* with dorsiventral leaves, section *Multifidi* with isobilateral leaves and adaxial and abaxial palisade

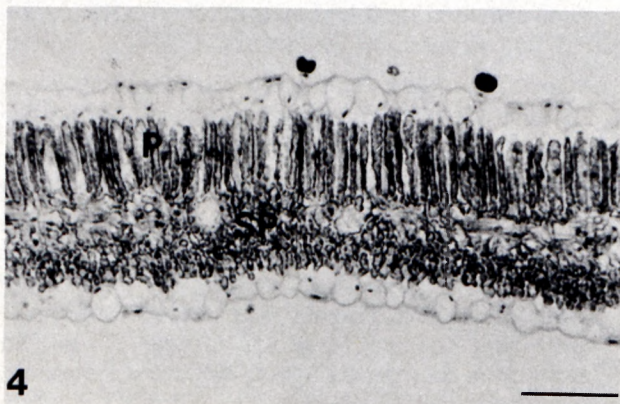


FIG. 4.—Part of a cross section through dorsiventral lamina of *Sarcocaulon mossamedense*. P, palisade parenchyma; SP, spongy parenchyma. Bar = 100 μ m.

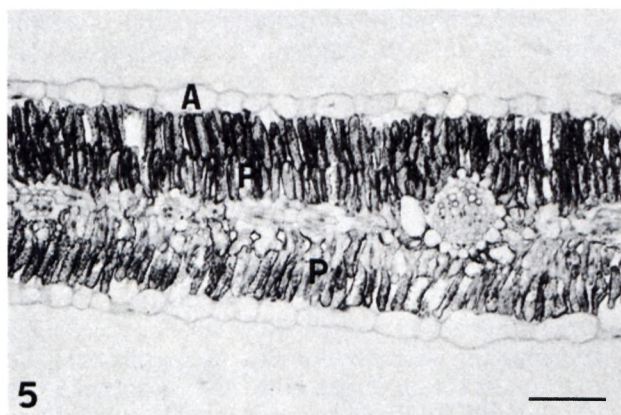


FIG. 5.—Part of a cross section through isobilateral lamina of *Sarcocaulon camdeboense*. A, adaxial epidermis; P, palisade parenchyma. Bar = 100 μ m.

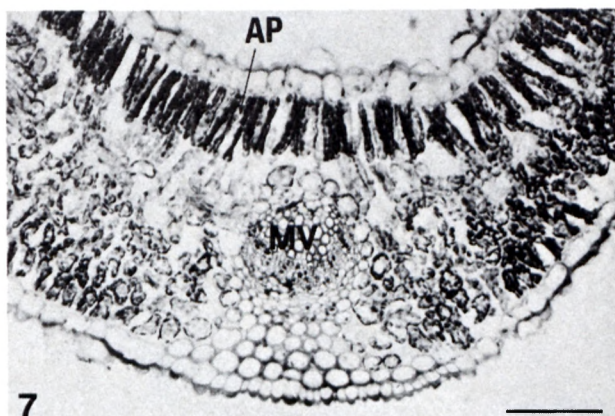


FIG. 7.—Cross section through midvein of *Sarcocaulon flavescens* to show the continuous adaxial palisade (AP). MV, midvein. Bar = 100 μ m.

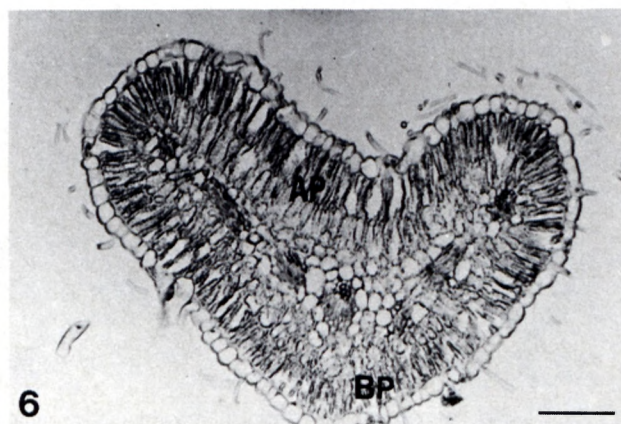


FIG. 6.—Cross section through isobilateral leaf of *Sarcocaulon multifidum* to show the continuous adaxial (AP) and abaxial palisade (BP) at midvein. Bar = 100 μ m.

continuous at midvein, section *Crenati* with isobilateral leaves, short curved trichomes and glandular hairs and section *Sarcocaulon* with isobilateral leaves and glandular hairs only.

Petiole

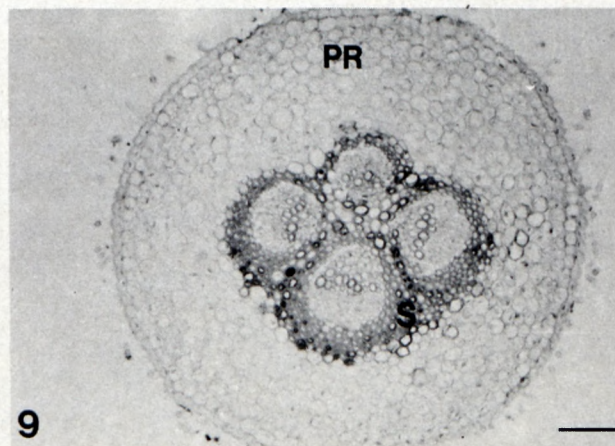
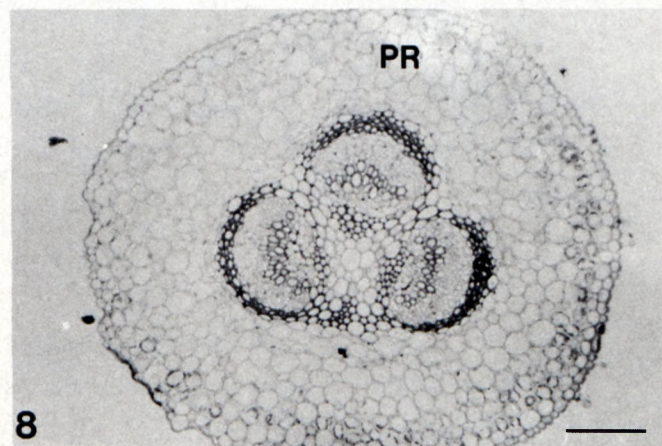
The anatomy of the petiole is the same in all the species. The outline is circular and a thick cuticle

present. The epidermis is composed of thick-walled cells. The cortex is parenchymatous with 1 or 2 cell layers subjacent to the epidermis often chlorenchymatous. Druse crystals are common in the cortex. Three (Fig. 8) or four (Fig. 9) vascular bundles are grouped together in the centre of the petiole with the fourth bundle usually smaller. The vascular bundles are each partially subtended or completely surrounded by sclerenchyma.

Spine (thorn)

The spine is formed from the long petiole after the lamina falls off. The anatomy of the spine resembles that of the petiole except that the four vascular bundles are arranged in a circle around the pith (Fig. 10). Between each of the four vascular bundles a smaller vascular bundle is often present. The thorn forms by lignification of the cells. Lignification begins around the vascular bundles and continues from the inside to the outside. The outer cortical layers may be lignified and persistent or are cast off together with the epidermis.

The four sections recognized by Moffett (1979) can be identified from leaf anatomy. Section *Denticulati* with dorsiventral leaves, section *Multifidi* with isobilateral leaves and adaxial and abaxial



FIGS 8 & 9.—Cross section through the petiole of *Sarcocaulon crassicaule* with three (Fig. 8) and four (Fig. 9) vascular bundles. PR, parenchyma; S, sclerenchyma. Bar = 100 μ m.

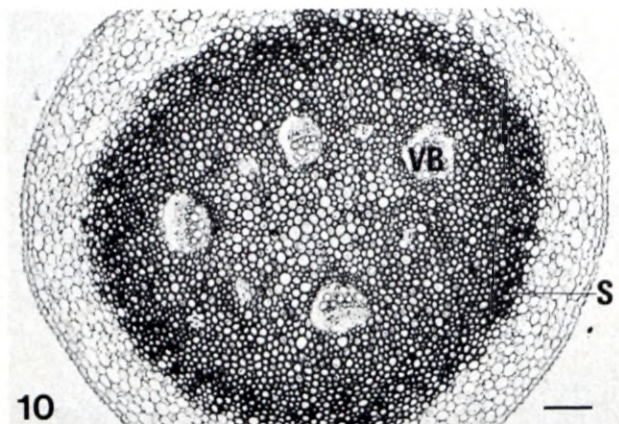


FIG. 10.—Part of a cross section through the spine of *Sarcocaulon crassicaule* to show the four vascular bundles in lignified tissue. S, sclerenchyma; VB, vascular bundle. Bar = 100 μ m.

palisade continuous at midvein, section *Crenati* with isobilateral leaves, short curved trichomes and glandular hairs and section *Sarcocaulon* with isobilateral leaves and glandular hairs only.

For plants growing in extremely hot dry areas, the leaves do not appear xerophytic with the stomata on the same level as the epidermal cells. Xerophytic features of the leaves are, however, the strongly developed palisade, small intercellular spaces, thick cuticle and dense covering of trichomes in some species. Although more xeromorphic features could be expected, it must be kept in mind that the leaves develop only after sufficient rain and are lost under unfavourable conditions.

Anatomy of the stem

The anatomy of the stem is very similar in all species. The stem is typically that of a herbaceous dicotyledon with collateral vascular bundles separated by wide parenchymatous medullary rays. The stem is covered by a layer of cork which peels off easily. A phellogen is formed early. In seedlings the phellogen originates in the subepidermal parenchyma while the cotyledons are still on the plant. The phellogen produces a conspicuous phellem to the outside and up to six layers of phelloderm cells toward the inside (Fig. 11)

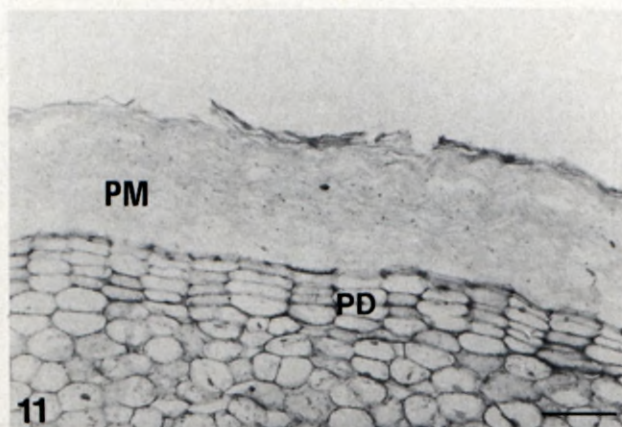


FIG. 11.—Part of a cross section through the stem of *Sarcocaulon flavesceus* to show the phellem (PM) and phelloderm (PD). Bar = 100 μ m.

The cortex consists of parenchyma cells containing druse crystals of calcium oxalate, tannin and abundant starch grains. The parenchyma cells immediately beneath the phelloderm are rich in chloroplasts, whereas the rest are filled with starch grains. Internal to the phelloderm, a few brachyscle-reids are sometimes present.

With secondary growth, a fascicular and interfascicular cambium develops (Fig. 12) The vascular cambium produces secondary xylem and phloem in radially arranged groups. Rays up to six cells wide separate the vascular bundles. Ray cells are often filled with starch grains (Fig. 13). External to the phloem, the pericycle is represented by a few fibres. In some cases, fibres are also present in the primary and secondary phloem.

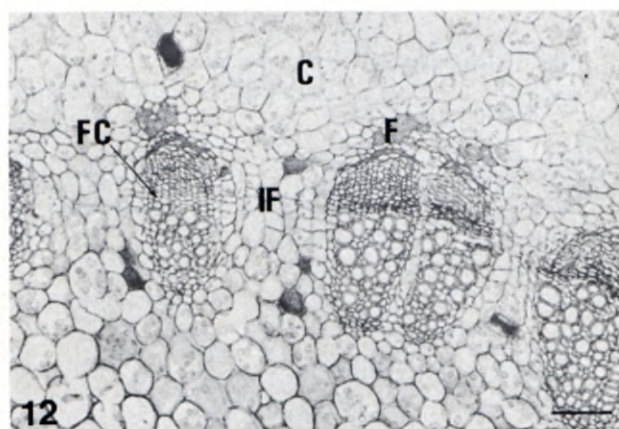


FIG. 12.—Part of a cross section through the stem of *Sarcocaulon flavesceus* to show the separate vascular bundles and beginning of secondary growth. C, cortex; F, fibres; FC, fascicular cambium; IF, interfascicular cambium. Bar = 100 μ m.

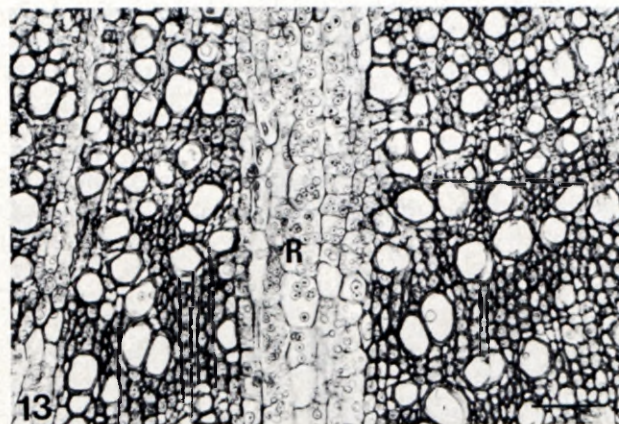


FIG. 13.—Part of a cross section through the secondary xylem of *Sarcocaulon mossamedense* to show the ray cells filled with starch grains. R, ray. Bar = 100 μ m.

The pith is similar in structure to the cortex.

The ability of the plants to survive the long dry seasons can probably be ascribed to the phellem, chloroplast rich parenchyma cells beneath the phelloderm, and the starch grains serving as reserve material.

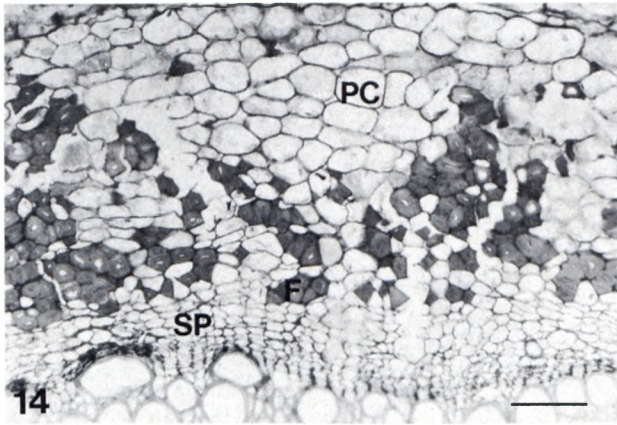


FIG. 14.—Part of a cross section through the root of *Sarcocaulon ciliatum* to show the fibres (F) in the secondary phloem (SP) and pericycle (PC). Bar = 100 μ m.

Anatomy of the root

Material of a young root showing the primary state before secondary growth takes place was not available for study. In the secondary state of growth

the root consists of primary xylem in the centre surrounded by secondary xylem. The xylem appears homogeneous because of the narrow rays (1–2 cells wide). The secondary phloem and pericycle are rich in fibres (Fig. 14) and are enclosed by the phellem.

From the root structure it is clear that the root's function is not food storage.

ACKNOWLEDGEMENTS

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