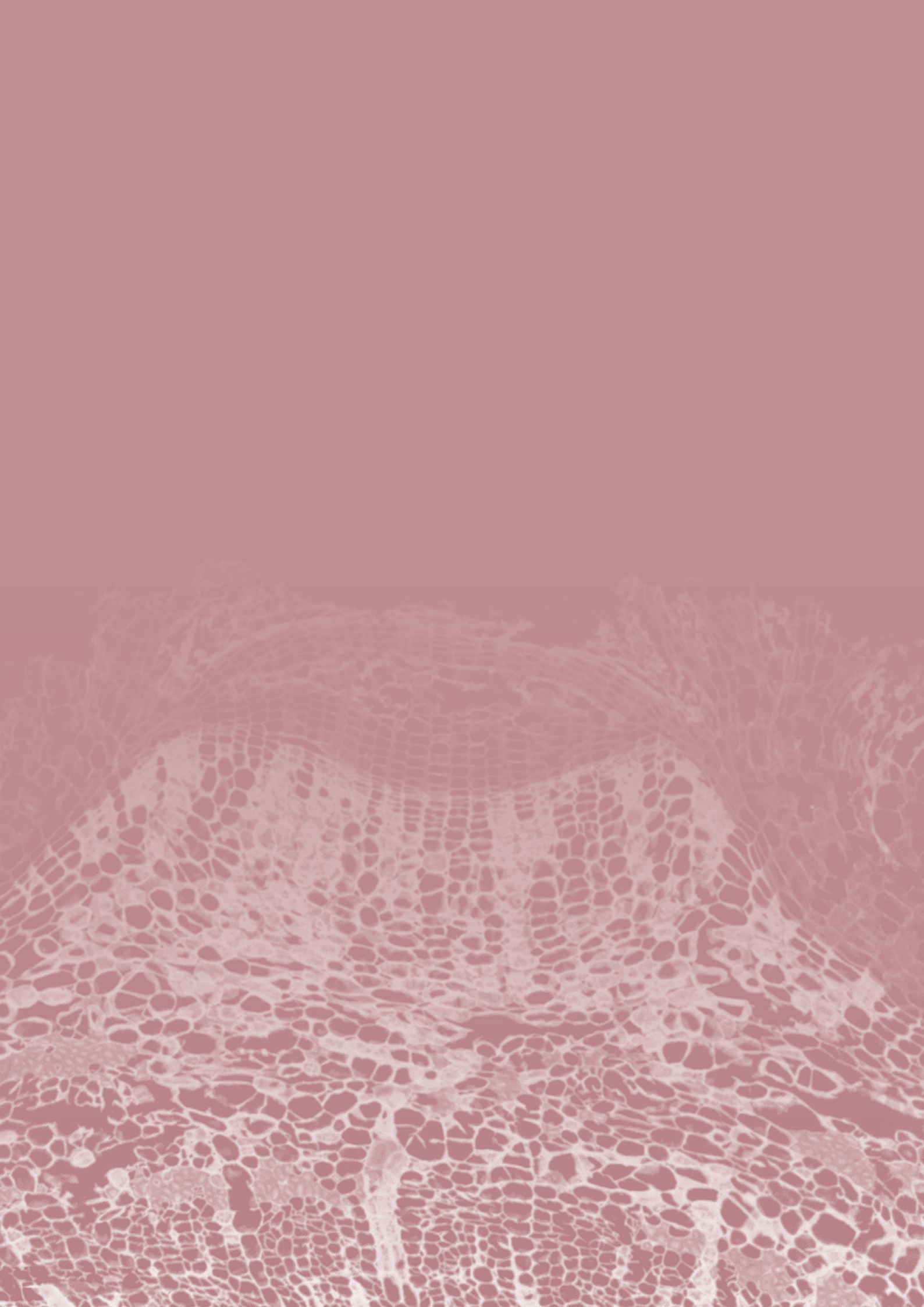
Tanja Mrak • Jožica Gričar

ATLAS OF WOODY PLANT ROOTS

Morphology and Anatomy with Special Emphasis on Fine Roots



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Foreword

Fine roots of most plant species form a symbiotic organ with fungi, called mycorrhiza. In temperate and boreal stand-forming forest tree species in the Northern Hemisphere, the predominant form of mycorrhiza is ectomycorrhiza, in which the fungal mycelium forms a fungal mantle, a shield of fungal hyphae around fine roots, a labyrinth of hyphae called the Hartig net around the cells of the primary cortex, and differently organized extramatrical mycelium growing out from the ectomycorrhizal root. Ectomycorrhiza colonizes almost all fine roots of trees from the families Pinaceae, Fagaceae, Betulaceae, Salicaceae, Dipterocarpaceae in the Southern Hemisphere, and a few other genera of woody plants.

Studies of ectomycorrhiza biodiversity were undertaken at the Slovenian Forestry Institute in 1985, first concentrating intensively on Norway spruce, later followed by European beech, and then several isolated studies on oaks, sweet chestnut, pines, and poplars. The identification of the fungal partner in ectomycorrhiza followed primarily the Atlas of Ectomycorrhiza created by Prof. Reinhard Agerer from the Ludwig Maximilians University in Munich, based on morphological and anatomical characterization, which was soon complemented with molecular identification. The comprehensive identification of *Lactarius lygniotus* on Norway spruce by anatomical and molecular tools (in 1995) from Slovenian forests was thus the very first publication combining classical identification methods with the ITS-RFLP identification of the fungal partner. Since the quantification of the different ectomycorrhizal types occurring in a forest ecosystem was needed, all future studies were also based on a combination of morphotyping and molecular identification, this latter following development in molecular tools.

However, over the decades, the identification of fine roots of forest trees remained a problem when dealing with heterogeneous sites and samples. Some approaches were taken into molecular identification of fine roots, following the work by Dr. Ivano Brunner and his colleagues at WSL in Birmensdorf. Yet, a need for a comprehensive identification key of fine roots, based on their morphological and anatomical characteristics, remained a must. Therefore, it was also stated as one of the key issues in the proposal for the RegPot Capacities project EUFORINNO, which finally provided the means, and time, for the best possible scientists to approach the problem.

The authors, Dr. Tanja Mrak and Dr. Jožica Gričar, have approached the need for developing a fast and reliable method for identification of fine roots of woody plants systematically. They reviewed all existing literature, studied a number of fine root samples from a number of forest tree species, defined the key characteristics that differentiate them, and organized these characteristics into a morphological and anatomical key for identification, enriched with outstanding microphotographs of fine root morphology and anatomy.

The ATLAS OF WOODY PLANT ROOTS: Morphology and Anatomy with Special Emphasis on Fine Roots provides the first identification key for roots of twelve forest tree species. Some are ectomycorrhizal, some form arbuscular mycorhiza, and some can form both, or an intermediate form, ectendomycorrhiza.

I am certain that the Atlas will be widely used by students and researchers studying belowground processes, roots of woody plants, mycorrhizal symbiosis and other complex interactions in forest soils. The Atlas of Woody Plant Roots in its first edition describes twelve forest tree species, and I am already looking forward to later editions, adding further tree species and including other mycorrhizal forms.

Prof. Dr. Hojka Kraigher, coordinator of EUFORINNO project

The atlas includes descriptions of the root morphology and anatomy of the twelve most frequent temperate European tree species: *Abies alba* Mill., *Picea abies* (L.) Karsten, *Larix decidua* Mill., *Pinus sylvestris* L., *Prunus avium* L., *Castanea sativa* Mill., *Fagus sylvatica* L., *Quercus petraea* (Matt.) Liebl., *Carpinus betulus* L., *Acer pseudoplatanus* L., *Populus nigra* L., and *Fraxinus excelsior* L.

Root anatomy is generally regarded as a lesser known area of science ("The hidden half of tree; Meinzer *et al*. 2011 or, as the saying goes "Out of sight, out of mind"). It is all the more commendable that the authors addressed the topic.

The objectives were to elaborate (1) a morphological (dichotomous) key for the identification of roots thinner than 5 mm based on the description of colour, surface structure, ramification pattern, diameter, mycorrhizal status and morphotype of mycorrhizal root tips, and (2) a microscope combination key based on (1) IAWA List of microscopic features for softwood identification (2004), (2) IAWA List of microscopic features for hardwood identification (1989) and (3) IAWA List of microscopic features for bark identification (2016 - in preparation).

The study represents the first atlas dealing with the morphology and anatomy of roots thinner than 2 mm. The coded descriptions of the root tissues make it possible to design a modern combination identification key.

The methods used are appropriate to the aims of the study with sufficient information for sampling and sample preparation. The general description of root anatomy, including types of mycorrhizal symbioses and the definition of the anatomical features of wood and bark, is adequate and competent. The accompanying photomicrographs are excellent and support the text well.

Prof. Dr. Dr. h.c. Niko Torelli, Professor of Wood Science and Technology

This work was financed by the 7th FP Infrastructure project EUFORINNO (REGPOT No. 315982) and the Slovenian Research Agency through Research Programme P4-0107. It is dedicated to the identification of fine roots of selected temperate tree species, for which at present no comprehensive identification key exist. Fine roots of the following tree species were analyzed: European Silver Fir (*Abies alba* Mill.), Norway Spruce (*Picea abies* (L.) Karst.), European Larch (*Larix decidua* Mill.), Scots Pine (*Pinus sylvestris* L.), Wild Cherry (*Prunus avium* L.), Sweet Chestnut (*Castanea sativa* Mill.), Common Beech (*Fagus sylvatica* L.), Sessile Oak (*Quercus petraea* (Matt.) Liebl.), Common Hornbeam (*Carpinus betulus* L.), Sycamore (*Acer pseudoplatanus* L.), Black Poplar (*Populus nigra* L.) and Common Ash (*Fraxinus excelsior* L.).

Roots were sampled from natural forest stands in Slovenia. A very detailed description of sampling, sample preparation, and processing is given. The atlas has the following chapters: 1.Introduction, 2.Methods, 3.General remarks on root morphology, 4. Root morphological key, 5. Plates with morphological descriptions, 6. Root anatomy (with integrated key), 7. Coded description of anatomical structures of the selected tree species, 8. Plates with anatomical descriptions, 9. Anatomical identification of roots thinner than 1 mm, 10. Acknowledgements, and 11. References.

The emphasis of the atlas is on morphological and anatomical analysis of fine roots, their ramification pattern, mycorrhiza type and tissue structure in primary and secondary growth, where detailed information on wood and bark structure is given. All morphological and anatomical analyses and descriptions are supplemented with very well prepared illustrations (microphotos of tissue sections and images of fine root ramification) of the tree species analyzed. I found the root atlas well prepared, using proper and standard terminology for fine roots morphology and anatomy, and illustrations are especially helpful in using the key in tree species identification.

The fine root atlas will be used as an excellent and appropriate tool for researchers and students in analyzing fine root dynamics in forest and other types of ecosystems.

Prof. Dr. Franc Batič, Professor of Applied Botany

Introduction

This atlas is the result of a pilot study that looked for the most appropriate approach to identify roots thinner than 5 mm. The atlas includes twelve common European temperate species, four conifers, and eight broadleaf species that are presented in colour plates showing their morphology and anatomy. Having in mind the procedure for sample preparation for any sort of root analysis, which normally requires cleaning and sorting of roots according to species, we constructed a morphological key as a first step. If this step is insufficient, or if additional confirmation of identification is desired, anatomical descriptions with the characteristic features of each species in bold letters are supplemented in a systematic way. Preceding the anatomical descriptions is a comprehensive chapter on anatomical features that are encountered or are expected to be encountered in roots, prepared in the form of a key. This chapter can be used by the reader to construct her or his own anatomical key for the species of interest, and includes the most recent findings of the International Association of Wood Anatomists on the wood of softwoods and hardwoods and the properties of bark, as well as available knowledge on the differences between root and stem wood.

As far as we know, this is the first atlas with root morphological features included. Kutschera and Lichtenegger (2002) provide information on gross morphology of root systems of a number of temperate tree species in their atlas of roots, but fine morphology properties such as colour, structure of bark, properties of the periderm, and type of mycorrhiza are not included.

We perceive this atlas as a living structure, with many possibilities to upgrade it, add new species and improve the keys. The challenge that remains are the most distal roots, where morphological and anatomical features become very similar among species to the untrained eye. Still, in this work a chapter on the anatomical identification of roots thinner than one mm is included, with problems that are encountered when trying to identify such a thin root pointed out. However, with this work, the minimum size limit for successful anatomical identification, considered by Agerer (1987-2012) to be 2 mm, has been moved to 1 mm. Agerer (1987-2012) based his key for sixteen tree genera on an earlier comprehensive anatomical identification key with more than 100 temperate tree and shrub genera, published by Cutler et al. in 1987, which is unfortunately now out of print. Agerer's key (1987-2012) was constructed with the special assistance to scientists who work on ectomycorrhizas, but our intention is also to have species with other types of mycorrhiza included. For this reason, three of the included species are hosts for endomycorrhizal fungi, while another one can be host to both ectomycorrhizal and endomycorrhizal fungi.

Methods

SAMPLING

Sampling of roots was performed from February 2014 until October 2015 at different sampling sites in Slovenia (Fig. 1). For each species, two to five (six) individuals were sampled. Roots of diameter up to 5 mm were carefully dug out of the soil, following thicker root for which connection to tree stem was clearly evident. After digging, roots were cut by using garden scissors and put into a labelled plastic bag together with some soil to avoid drying out and sealed. The label listed the tree species, consecutive number of the sample, soil layer from which the sample was taken, and date of sampling. The label of the sample was kept throughout the procedure.

Fig. 1: Map of sampling sites

MORPHOLOGY

Sample preparation

After transfer to the lab, samples were first processed for anatomy (see next section), and the morphological investigations were performed within a week at most. Until then, samples were kept soaked in water in the refrigerator. For imaging of the fine root system, a part of the root that was not damaged during the sampling was selected, cut away from the remaining parts, and cleaned carefully with brush and tweezers. Cleaning of the root tips was checked under a dissecting microscope. With root originating from mineral layers of soil, brushing is very important as mineral particles may obscure the colour of the bark and root tips. Sometimes, for cleaning of very persistent organic particles attached to mycorrhizal root tips, cleaning in hot water was performed. However, hot water may change the colour of the bark. For this reason, cleaning with hot water was avoided as much as possible.

Imaging of the fine root system

For imaging of the fine root system, an Epson perfection V700 Photo Scanner (Seico Epson Corporation, Nagano, Japan) was used. Part of the fine root system was placed into a very clean and scratch-free Petri dish filled with water. As low a level of water as possible was used to keep as much of the root system as possible in the focus level of the scanner. To keep the root system under water, the water surface was covered by transparent plastic foil. The Petri dish with root was placed inside an additional, home-constructed LED-circle to provide additional light during imaging. The LED circle was always set to the same level of light intensity. Images of roots were taken in reflective mode of the scanning at 1200 dpi, with photo auto exposure type selected.

Imaging and observations of bark

Observations and imaging of the bark was performed under a Zeiss StereoLumar.V12 dissecting microscope (Carl Zeiss Microscopy GmbH, Jena, Germany). For imaging of bark, roots of 2-3 mm in diameter were mainly used and submerged in water in a Petri dish. Imaging inside water was selected as it gives better reproduction of colour. For imaging, a digital camera (Carl Zeiss AxioCam Icc 5, Carl Zeiss Microscopy GmbH, Jena, Germany) and ZEN software (Carl Zeiss Microscopy GmbH, Jena, Germany) were used. To avoid shading, reflective and transmitted light of the microscope were used at the same time. The light was always set to the same level of intensity and auto exposure was selected in ZEN software.

ANATOMY

Here we describe the procedures (Fig. 2) to obtain representative print-quality images for each selected species in the atlas. For routine use, these procedures are not necessary as they are too time-consuming. For this purpose, hand sectioning and immediate observation under the light microscope of a water-mounted sample is sufficient, preferably by using differential interference contrast. Staining is also not necessary. If cells are filled with starch grains that obscure the image then some drops of chloral-hydrate solution on one side of the coverslip can be added, and the sample observed after some time. The solution of chloral-hydrate (Gerlach 1977) is prepared by mixing:

chloral-hydrate 160 g
distilled water 100 ml
glycerol 50 ml

Sample preparation

After transfer to the lab, samples were immediately processed. In some cases they were stored in a refrigerator for a maximum of two days. Roots were soaked in water to prevent drying and to remove excess soil. With a calliper, parts of the roots of 5 mm, 3 mm and 1 mm in diameter, as well as the roots thinner than 1 mm, were selected and put into Petri dishes. Soil particles were cleaned away using a brush under a dissecting microscope.

Fixation

Roots were cut with a razor blade into small pieces of maximum thickness 5 mm in a Petri dish filled with water and transferred into tubes filled with formaldehyde-acetic acid-ethanol mixture (FAA). Samples for transversal and longitudinal sections were prepared separately. For longitudinal sections, roots of 5 and 3 mm in diameter were split longitudinally in half. The thinnest roots were left in bigger bunches to prevent their loss from embedding cassettes (Histosette, Simport) later during dehydration and paraffin infiltration. Tubes with samples were labelled with the tree species abbreviation, sample number, soil layer from which the sample was taken, thickness of the root, and an abbreviation for the sectioning direction (transversal or longitudinal). Samples were fixed in FAA, and left for at least one week, but not too long, in order to avoid degradation of softer tissues. A standard FAA mixture was used (Gerlach 1977), consisting of:

ethanol 70% 90 ml
glacial acetic acid 5 ml
formalin (40% formaldehyde) 5 ml

Dehydration

Dehydration of samples was performed using the following ethanol grades and times:

50% ethanol (min. 2 days)
70% ethanol (min. 1 day)
95% ethanol (3 h)
100% ethanol (2 h)

The first two steps of dehydration were performed in the tubes, while for the last two, selected samples for paraffin embedding were transferred into labelled embedding cassettes (Histosettes) and dehydrated inside 1 L plastic wide-neck bottles. Samples that were not chosen for paraffin embedding were left in 70% ethanol, which is appropriate for long-term storage.

Infiltration and paraffin embedding

From 100% ethanol, samples were transferred into UltraClear (J.T. Baker) for two hours, and then to melted paraffin where they remained overnight. The next day, they were embedded in paraffin. With heated forceps, the sample was oriented properly, depending on the kind of section preparation desired (transversal or longitudinal), inside the embedding mould, which was filled to one third with paraffin. After positioning of the sample, the embedding mould was filled to the top and left to solidify.

Trimming

The paraffin-embedded samples were trimmed into cut-topped pyramid shape with a heavy-duty utility cutter. The top of the pyramid was trimmed using a Leica RM2245 rotary microtome (Leica Microsystems, Wetzlar, Germany) in 10 µm steps until the surface of the sample was reached and even.

Sectioning

Before sectioning, the trimmed samples were soaked for 2-3 hours in a Petri dish filled with cold water. Soaking time can be adapted to tree species, and later for all tree species overnight soaking was used to avoid tearing of sections. Microscope slides were prepared by putting some drops of albumin (BioOptica, paraffin sections adhesive - in glycerol) on them and smearing it over the whole surface of the slide. However, albumin was not a perfect solution, as it often formed bubbles that remained on the slide and stained during the staining procedure. The problem of albumin bubbles was especially noticeable in slides of the thinnest roots. We also observed formation of wrinkles inside the phloem layer of roots, especially in samples that were collected during the growing season. Tests of commercially available adhesive microscope slides (Superfrost, and Poly-l-lysine, Thermo Scientific) in comparison to albumin slides and slides without any adhesive in six tree species did not show any improvement, but slides without any adhesive were advantageous in some species. From then on we started to prepare one albumin-covered slide and one slide without any adhesive for each sample. Before staining, slides were examined under a dissecting microscope and the best slide selected. Generally, albumin-covered slides performed better than slides without any adhesive for conifers.

Sectioning was performed by a Leica RM2245 rotary microtome, in 10 µm steps; however, for the most distal roots, 5 µm steps were the most appropriate. Paraffin ribbon was stretched inside a water bath set to 40 °C and then mounted onto a microscope slide. As mentioned above, two slides per sample were prepared. Slides with sections were transferred onto a flattening table set to 60 °C and left there for approximately half an hour.

Paraffin removal, staining and covering

For paraffin removal, slides were left in UltraClear for 45 minutes to one hour and then transferred to 96% ethanol two times. After that, they were stained in safranin-astra blue stain that was prepared according the following procedure: 100 ml of distilled water was mixed with 2 ml of acetic acid. Then 40 mg of safranine and 150 mg of astra blue were added. Staining time was approximately 10 minutes; after that, slides were washed in 96% ethanol, dried, and covered with coverslips.

Safranin stains lignins and polyphenols red, while astra-blue stains cellulose blue. In this way, lignified tissues are stained red and non-lignified parenchymatic tissues blue.

As a mounting medium, Euparal (Roth) was used. Slides were weighted down for one day to dry. However, as the drying time of Euparal is quite long (approx. 2 months), slides must be handled with care.

Observations under the microscope

For observation of slides, a light microscope was used (Zeiss Axio Imager Z2, Carl Zeiss Microscopy GmbH, Jena, Germany). Transmitted light was used for most of observations, while differential interference contrast was used for crystals. Images of slides were taken with a digital camera (Axio Cam Mrc 5, Carl Zeiss Microscopy, Jena, Germany) using ZEN software. For composing images of whole sections of the roots, the "panorama" function of the ZEN software was used. Images of 5 mm and 3 mm roots were taken under 100x magnification, while for 1 mm they were taken under 200x magnification. Images of roots, thinner than 1 mm were taken under 200x or 400x magnification. Anatomical features that are listed in the tables accompanying colour plates in Section 2 were observed.

Measuring of tangential vessel diameter in secondary xylem of roots of hardwood trees

Measuring of tangential vessel diameter was performed on composed images of the whole transversal section of the root using the "Analysis" function of the ZEN software. In species with discernible growth rings, tangential diameters of vessels were measured for each growth ring separately. As in tree roots, complete and incomplete, i.e. wedging, growth rings are present, only complete growth rings were taken into account during the measurements. For the species where growth rings were not evident, the root was separated into concentric zones from the centre outwards, with 500 µm distance between each zone, and tangential diameters measured for each zone separately. In cases where the frequency of vessels was very high, tangential diameters were measured only on half of the section in 3 mm roots or on one quarter of the section in 5 mm roots.

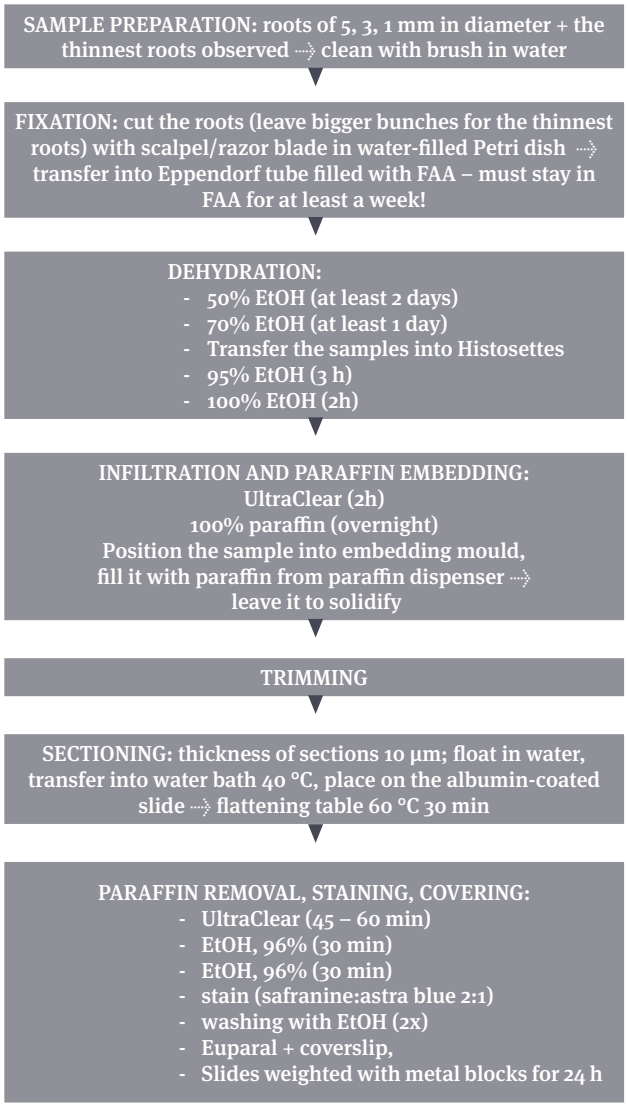


Figure 2: Graphical summary of paraffin embedding of root samples

1.MORPHOLOGY

1.1 General remarks on root morphology

Root morphology refers to the surface features of a root (Lynch 1995). Roots show few distinctive external features that would permit identification. The scarce variation in external features of roots is presumably related to the limited level of variation of the root environment (Fitter 2002).

Examination of root morphological characteristics is the first method to be chosen for root identification because of its low set-up costs and possibilities to perform it in the field. However, it requires time-consuming hand sorting and training of personnel (Rewald et al. 2012). As morphological determination keys are lacking or limited to a couple of species on a local level, there is not a clear consensus on which morphological features are the most reliable. According to Fitter (1987, 2002), the major morphological features in which differences can be discerned are root diameter, colour and surface texture. Root morphology may be subject to plasticity under changing environmental conditions and mycorrhizal symbiosis (Rewald et al. 2012). Morphological criteria used to identify tree roots (e.g. Hölscher et al. 2002, Korn 2004) may have some information on geometry included as well, such as ramification characteristics. Rewald et al. (2012) compiled morphological identification criteria for tree roots from different sources: root colour, odour, resilience to breakage, type of mycorrhiza, existence of root hairs, exodermal cell structure and periderm characteristics (furrows, dead periderm layers), root diameter, ramification pattern, root tip density, and morphotype of mycorrhizal root tips.

The selected morphological criteria used in this study are a subject of debate and further research.

ROOT COLOUR

Root colour is one of the first morphological characters to be used, although colour impression may change under different illumination conditions and differs between fresh (wet) and dried roots. The perception of colour is somewhat subjective and can pose a problem in determination keys.

Colour as the sole criterion should therefore be avoided (Rewald et al. 2012). The perception of root colour might also be obscured by the mineral particles adhering to the surface of the roots in samples obtained from mineral layers of soil and by the presence of fungi that grow on the periderm of roots, such as dark septate fungi. It is therefore advisable to observe roots in water under a dissecting microscope using always the same quality of light and to clean the surface of roots with a brush before observation, to reveal their true colour.

Even young roots can be coloured; a good example of this is *Salix purpurea* L., where root tips are red coloured due to the presence of anthocyanins. In *Juglans regia* L. the cell walls of rhizodermis contain juglandin that gives a dark brown colour to the roots. Yellow-brown, red, red-blue and black colours of the roots are caused by tannins and their derivatives (e.g. phlobaphene), anthocyanins and melanines. Occurrence of these substances is related to the age of the tissue and to the environmental conditions (Kutschera & Lichtenegger 2002).

Some pigments in young roots presumably serve as a defence against herbivory. Roots colonized by arbuscular mycorrhizal fungi are often yellow, but the significance of this pigmentation is unclear (Fitter 2002). Anthocyanins in roots are often a consequence of wet and nutrient-poor soil conditions, while roots may turn black due to melanine accumulation in the process of ageing, making them very resistant to decomposition, or due to drought. Cell walls of older bark parts are coloured due to the increasing quantity of phlobaphene (Kutschera & Lichtenegger 2002).

ROOT SURFACE STRUCTURE

Similarly to stem, root surface is covered by specific structures. Generally, the surface structure of the roots is less rugged and finer than the surface structure of the stem (Kutschera & Lichtenegger 2002), with structures becoming less prominent with diminishing diameter. For this reason, this feature is best applied on roots that are at least 2 mm in diameter.

Sloughing pattern is the pattern in which the bark exfoliates (bark = all tissues outside the vascular cambium). As bark remains about the same thickness all the time, surface sloughing must take place to maintain that thickness. Sloughing occurs in the form of powder or scales of different thicknesses, sizes and shapes; the dimensions and the relative arrangement of the pieces are usually controlled by the periderm(s), although sometimes external weathering is important. There are a limited number of periderm structures and arrangements and consequently a limited number of sloughing patterns. Functionally the periderm(s) usually delimits the living tissue from the dead or from the external environment (Whitmore 1962). Development and shedding characteristics of bark are related to the radial position of the initial periderm on the root, patterns of formation of subsequent periderms and arrangement of the cells in phloem (Borger 1973). When a plant forms successive phellogens, the bark produced by the first phellogen will usually contain epidermis

and cortex, whereas subsequent phellogens will contain only secondary phloem. Thus the nature of the very first bark on a young branch (or root) is often dramatically different from the later barks (Mauseth 1988). In tree roots with small diameter, only one periderm is typically observed, but in samples from colder environments, where small diameter roots could be several years old, the presence of subsequent periderms can also be expected.

In some tree species, e.g. *Fagus sylvatica* L. and *Populus tremuloides* Michx. periderm remains in a superficial position through the lifetime of the tree, increasing the circumference with anticlinal divisions of the cells. The bark of these tree species is regarded as smooth. In twigs, which contain juvenile tissues similar to roots, the number of layers of phellem cells usually increases for several years, then remains relatively constant (Borger 1973). Whether the same is true for roots still needs to be confirmed.

The development of the first periderm layer is affected by several environmental parameters, including temperature and soil moisture (Borger 1973).

Concomitantly with periderm formation or slightly before, **lenticels** are also formed. The activity of lenticel phellogen produces a large mass of complementary cells centrifugally and usually an equal number of phelloderm-like cells centripetally (Borger 1973). Primary lenticels on roots are located at the bases of root ramifications. In conditions of excessive soil moisture, secondary so-called hypertrophied lenticels, can form at the junction of lateral root with its parent root or at some other points as well (Hahn & Hartley 1920).

RAMIFICATION

Root systems grow by a simple ramification process, with laterals emerging from main roots some distance behind the tip. Normally, only a single lateral root emerges at any point. The ramification type of root systems is their most fundamental characteristic and can be shown to be central to their function. Root system can be described by several parameters: 1.) number of exterior (parts of the root that terminate in a meristem) and interior links (parts of the root that terminate in a ramification junction) in the system, 2.) the lengths of the links (distance between meristem and first ramification junction and between subsequent ramification junctions), 3.) the distribution of lateral roots within the system, 4.) ramification angles and 5.) relative diameter, which is the rate of increase of link diameter (Fitter 1987, 2002).

Ramification is key component of root system architecture (Fitter 1987). Root system architecture varies hugely among species and also shows extensive natural variation within species (Nibau et al. 2008). Ramification angle tends to be large, often between 60 and 90°. Even in narrowly conical root systems, the initial ramification angle is often high but later growth produces an effective ramification angle of 45° or less. Since lateral roots arise in the pericycle and must penetrate the cortex before emerging, it seems reasonable to expect them to take the shortest path, which would mean that they would normally emerge at a 90° ramification angle (Fitter 1987). Formation of lateral roots is controlled by endogeneous factors as well as many environmental parameters, such as nitrogen and phosphate availability, lack of sulphur and potassium, water and salt stress, light and biotic factors (Nibau et al. 2008).

As fine root lateral roots are deciduous, similarly to leaves and needles, they leave behind a distinct **root scar** after abscission (Pregitzer et al. 2002). It seems that the frequency of root scars varies among species, but this needs to be confirmed.

ROOT DIAMETER

Root diameter is important due to its effects on root function and the volume of soil that is available for exploitation and because of its influence on root costs (Fitter 1987). The diameter of individual roots varies widely both within and between species. Many trees that normally grow in association with ectomycorrhizal fungi (especially Pinaceae) have thick roots and very low root length densities. Species with thinner roots have a lesser tendency to be mycorrhizal (Fitter 2002). Thinner roots are produced as a response to low nutrient supply (Fitter 2002) and as a response to drought (Brunner et al. 2015).

MYCORRHIZAL STATUS AND MORPHOTYPE OF MYCORRHIZAL ROOT TIPS

Depending on mycorrhizal partner, root tips may appear very different (see Table 1.1.1 for characteristics of different mycorrhizas that occur in woody plants). In northern temperate and boreal climates ectomycorrhizae occur predominantly on plants from the families Pinaceae, Fagaceae, Betulaceae and Salicaceae (Smith & Read 2008). However, certain genera from other families can also be at least partly ectomycorrhizal (e.g. *Tilia* spp., *Sorbus* spp., *Ulmus* spp.,...) (Kraigher 1995).

Type of mycorrhiza	Characteristics	Fungal groups	Plant hosts
Ectomycorrhiza	Fungal mantle, Hartig net, emanating hyphae and rhizomorphs	*Glomeromycota*, *Basidiomycota*, *Ascomycota*, (*Deuteromycota*)	Pinaceae, Fagaceae, Betulaceae, Salicaceae (in northern temperate and boreal climate), Dipterocarpaceae (tropics), Myrtaceae, Fagaceae (southern hemisphere)
Endomycorrhiza, the most common arbuscular mycorrhiza	Arbuscules and vesicles inside the cells of primary cortex, root hairs preserved	*Glomeromycota* (*Endogone*, *Gigaspora*, *Acaulospora*, *Glomus*)	Approx. 90% of all plant species (spermatophytes, pteridophytes, some bryophytes)
Ectendomycorrhiza	Fungal mantle, Hartig net, intracellular hyphal growth	*Ascomycota*, *Basidiomycota*	Some normally ectomycorrhizal genera of spermatophytes
Ericoid mycorrhiza	Inter- and intracellular hyphal growth	*Ascomycota*	Ericaceae
Arbutoid mycorrhiza	Fungal mantle, Hartig net and intracellular hyphal growth	*Basidiomycota*	Ericaceae (*Arbutus*, *Arctostaphylos*)

Table 1.1.1: Types of mycorrhizal symbioses relevant for woody plants, their features and partners involved (Smith & Read 2008)

Most ectomycorrhizal plants have heterorhizic roots, with ectomycorrhizas forming on short, determinate roots. These mycorrhizas range from unramified (monopodial) to highly ramified structures, and even to compact, convoluted "tuberculate" forms with up to a thousand of root tips and where ramifications can no longer be clearly distinguished. The degree of ramification is determined by both plant and fungal identity. The formation of bifurcate, Y-shaped mycorrhizas is only observed in gymnosperms (McCormack et al. 2015).

1.2 Root morphological key

MORPHOLOGICAL KEY FOR DETERMINATION OF ROOTS OF TWELVE EUROPEAN TREE SPECIES

This key applies morphological characters that are based on empirical observations of tree roots from different climatic conditions and from different types of soil. The criteria refer mainly to roots of at least 2 mm in diameter with associated lateral roots of smaller diameters. The most stable criteria were compiled, and include root colour, surface structure with periderm characteristics, typical characteristics of distal roots, and type of mycorrhizal association. However, these criteria still need to be further evaluated and discussed to improve the performance of the key. Ramification patterns were generally avoided as much as possible as they are difficult to assess empirically, are subject to great variation and may not be easily observed in samples where roots occur in smaller fragments. As the key is empirical, the user should check the morphological identification at the beginning through colour plates with descriptions of root morphology for each species following the key and by means of root anatomy (Section 2).

1a Roots richly **dark red to reddish brown**, **ectomycorrhizal**

2a Surface of the root covered by a **firm structure of ridges** or completely **smooth**

3a Periderm forming a **mesh of alate anastomosing longitudinal ridges** or surface completely **smooth**. Cells of periderm of medium size*. Relatively thick and long laterals often with short lateral roots growing out (**thread-like appearance**) ..... ***Carpinus betulus***

3b Periderm forming a **mesh of longitudinal anastomosing longitudinal ridges**. **Periderm layers do not slough**. Cells of periderm **small**. Roots evenly and richly ramified ..... ***Fagus sylvatica***

3c Surface **smooth** to covered by **longitudinal parallel ridges with minor anastomosing**, sometimes **shiny**. Periderm peels off in **thin curly layers**, but occasionally forms a **thick layer** with brown surface and whitish colour underneath. Cells of periderm of medium size ..... ***Castanea sativa***

2b Surface covered by **loose longitudinal strips** of dead periderm that may reveal smooth whitish, slightly brown or reddish surface. Cells of periderm narrow and **elongated, with longer side along the axis**, sometimes arranged in **wavy patterns**, of medium size. **Distal roots thick**..... ***Abies alba***

1b Roots at **least partly dark brown**, with **arbuscular mycorrhiza or occasionally ectomycorrhiza**

4a Surface covered by **loose anastomosing longitudinal strips** of a dead periderm that reveal **pale brown surface** that is completely smooth or covered by a gentle mesh. Cells of periderm of medium size. **Ectomycorrhizal or with arbuscular mycorrhiza or combination of both**..... ***Populus nigra***

4b Completely dark brown or with dark brown ridges and paler furrows. Surface with **firm anastomosing parallel longitudinal ridges or smooth**. Periderm layers do not slough. Where periderm is damaged, **orange-brown** colour is revealed. Cells of periderm of medium size. **Lenticels** common, **oval-shaped. Vital root tips orange or yellow,** with arbuscular mycorrhiza**....** ***Prunus avium***

4c Surface covered by a **regular net** of densely parallel **longitudinal anastomosing ridges. Cells of periderm small. Ramifications to two**

**Cells of periderm can be tentatively divided into size classes (small, medium, large). Small cells are of size less than 30 µm and can be barely discernible under high magnification (40 x) by a dissecting microscope. The majority of observed roots had cells of medium size, approx. 30-50 µm. These cells can be easily discernible under 40x magnification by a dissecting microscope. Large cells (> 50 µm) were observed in Larix decidua and Pinus sylvestris. Large cells can already be discerned under low magnification by a dissecting microscope (10x). The sizes refer to the roots 2-3 mm in diameter. Generally the cells were of quadratic (isodiametric) to rectangular (narrow and elongated) shape. In Prunus avium, some cells were clearly hexagonal. If cells of the periderm are narrow and elongated, the longer axis of the cells is usually oriented perpendicularly to the root axis. However, in Abies alba, the longer axis of the cells is oriented along the axis of the root.*

or more equal laterals common, sometimes these ramifications appear **knot-like**. Lateral roots becoming paler towards the **root tips** that appear brownish-white to white or even **translucent and constricted** at the base or in the middle, with arbuscular mycorrhiza .....
Acer pseudoplatanus

1c Roots **pale brown or very lightly coloured**, ectomycorrhizal or with arbuscular mycorrhiza

5a Roots **smooth** or covered by a **rounded anastomosing longitudinal ridges**. Cells of periderm of medium size. **Root scars common**. **The most distal roots thick and often very long**, with **arbuscular** mycorrhiza .....
Fraxinus excelsior

5b Surface covered by a **regular net** of densely parallel **longitudinal anastomosing ridges. Cells of periderm small. Ramifications to two or more equal laterals** common, sometimes these ramifications appear **knot-like**. Lateral roots becoming paler towards the **root tips** that appear brownish-white to white or even **translucent and constricted** at the base or in the middle, with arbuscular mycorrhiza .....
Acer pseudoplatanus

5c Structure of the surface irregular, with some longitudinal waves or smooth. In areas where thick layer of periderm is accumulated the surface appears soft and **shiny** or dirty white. Periderm cells of medium size. Periderm sloughs off in **thin translucent pieces**. **Root scars abundant, tuberculate**. **Distal roots very fine, thin. Ectomycorrhizal** .....
Quercus petraea

1d Roots of **different shades of brown** as described above, ectomycorrhizal

6a Colour of the root orange-brown to pale brown, in some areas shiny or dirty white. Periderm cells of medium size. Periderm sloughs off in **thin translucent pieces**. **Root scars abundant, tuberculate**. Distal roots **very fine, thin**.....
Quercus petraea

6b Roots with odour of resin. Roots coloured in different shades of brown, commonly with white patches. Periderm sloughs off in large loose patches. **Cells of periderm medium to large, mainly isodiametric**. Root scars common. Distal roots thick.

7a Roots **sparsely ramified**, long sections without ramifications can be observed. **Cells of periderm large**. Distal roots with **dichotomous or corraloid ectomycorrhizas**.....
Pinus sylvestris

7b Roots **not sparsely ramified**. Cells of periderm medium to large. **Mycorrhizas not dichotomous or corraloid.**

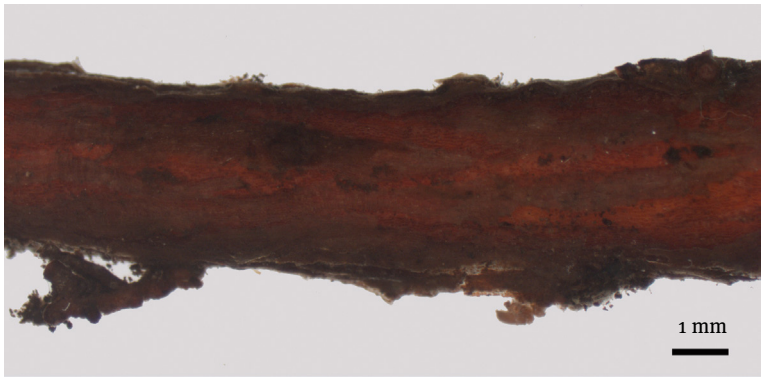
8a Periderm sheds in **large patches**, **very loose**. Below shedding layers there is a smooth surface of **reddish-orange-brown colour. Periderm cells large. Root scars prominent, tuberculate**. Roots **fragile**.....
Larix decidua

8b Periderm patches a bit smaller than in *Larix decidua* and not that loose. **Absence of reddish-orange tinges** below shedding layers of periderm. Periderm cells of medium size. Root scars less prominent. Roots less fragile.....
Picea abies

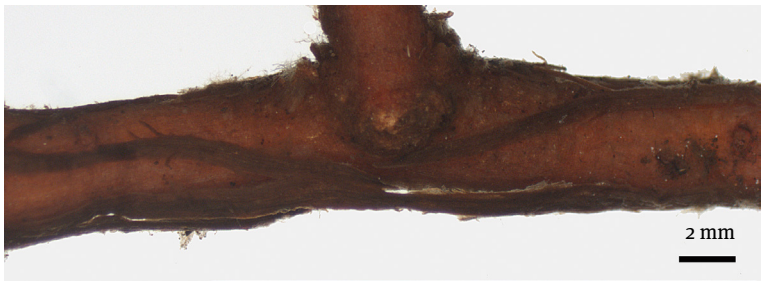
1.3 Plates with morphological descriptions

Abies alba Mill.

Lateral root of *Abies alba* with ectomycorrhiza. Roots of *A. alba* straight to sinuous. Distal roots thick.



Colour of the roots richly dark red.



In fine roots, the longitudinally cracking periderm layers reveal whitish to slightly brownish or reddish surface.

Surface of roots with loose longitudinal strips of periderm layers peeling off, below smooth surface is evident.

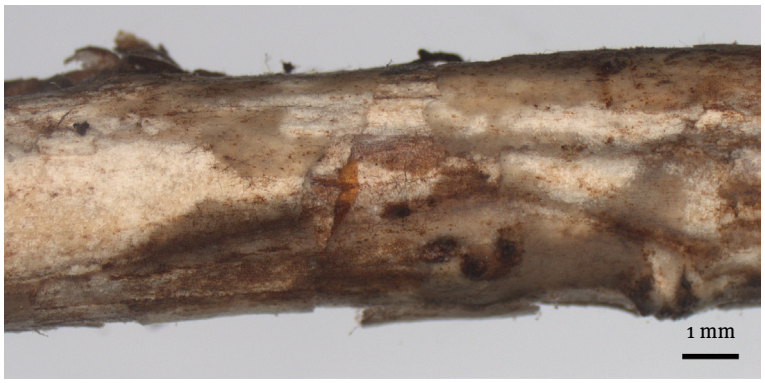
Cells of periderm of medium size, narrow and elongated, with longer axis oriented along the axis of the root. Usually they are arranged in longitudinal more or less wavy rows.

Picea abies (L.) Karsten

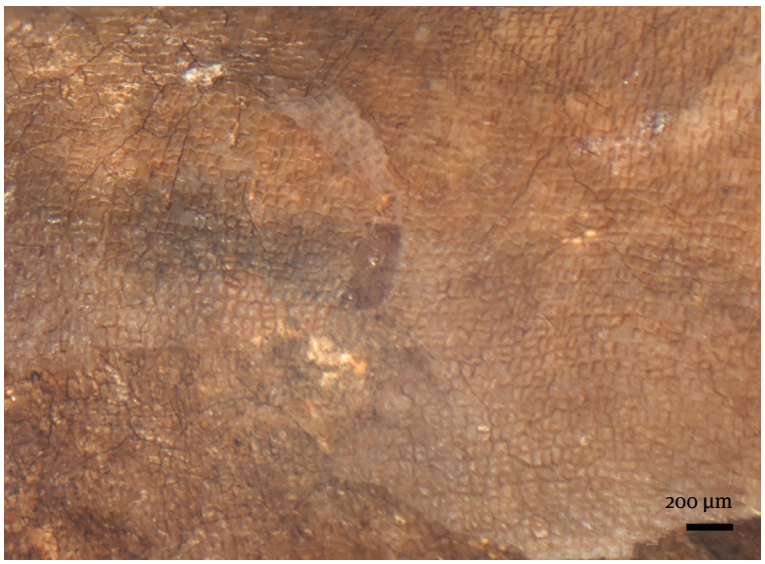
Lateral root of *Picea abies* with ectomycorrhiza. Roots of *P. abies* straight to slightly sinuous. Root scars abundant.

Roots coloured in different shades of brown with white patches that can be extensive. Colour more or less constant along the root up to mycorrhizal tips. Note root scars.

Surface of roots with large patches of shedding periderm layers. Below shedding layers there is a smooth surface of brown colour.



In this sample, large areas of periderm are white.



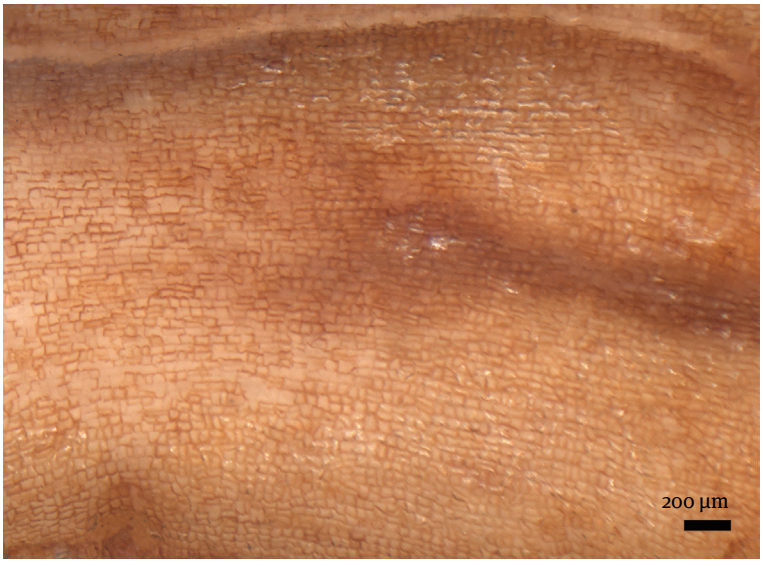
Cells of periderm of medium size, evident under high magnifications of dissecting microscope.

Larix decidua Mill.

Lateral root of *Larix decidua* with pioneer roots and abundant ectomycorrhizal roots. Roots of *L. decidua* straight to slightly sinuous. Root scars abundant, more prominent as in *P. abies*, tuberculate. Roots more fragile than in *P. abies*.

Roots coloured in different shades of brown, white patches can be present. Colour more or less constant along the root up to the mycorrhizal tips.

Surface of roots with large patches of shedding periderm layers. Periderm layers are looser than in *P. abies* and shed easily, the patches are bigger. Below shedding layers there is a smooth surface of reddish-orange-brown colour.



Cells of periderm large (but smaller than in *P. sylvestris*), evident under low magnifications of dissecting microscope.

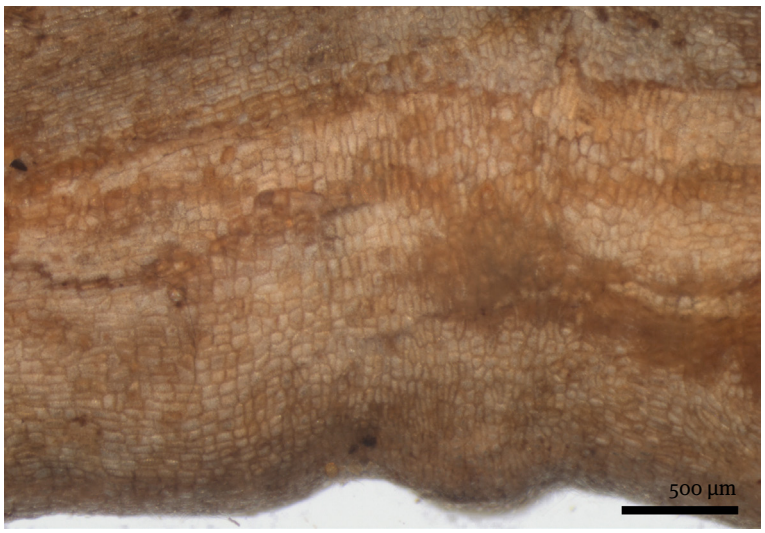
Pinus sylvestris L.

Lateral root of *Pinus sylvestris* with ectomycorrhiza. Roots of *P. sylvestris* straight to slightly sinuous, scarcely ramified, long sections without ramifications can be observed.

Typically, ectomycorrhiza is dichotomous, which can form, when ramifications are very frequent and root tips short, corraloid or tuberculate mycorrhiza. Tuberculate mycorrhiza forms when corraloid system is completely overgrown by mycorrhizal mycelium.

Colour of the roots orange-brown to ochre, more or less constant along the root up to the mycorrhizal tips. Shedding parts of the periderm give whitish appearance.

Surface of the roots smooth with large patches of shedding periderm layers. Root scars common.



Cells of periderm large, easily observed even under low magnification of dissecting microscope.

Prunus avium L.

Lateral root of *Prunus avium*. Roots of *P. avium* straight to sinuous. Lenticels observed, mainly located close to ramifications in roots thicker than 2 mm, oval-shaped. Mycorrhiza arbuscular.

Colour of the roots dark brown. Note oval-shaped lenticel to the left.

With diminishing diameter and in areas, where outer periderm layers are removed colour changes to orange-brown. Vital root tips orange and yellow.

Surface of the roots with anastomosing parallel longitudinal ridges, but can also be smooth.

Cells of periderm of medium size, evident under high magnifications of dissecting microscope.

Castanea sativa Mill.

Lateral root of *Castanea sativa* with ectomycorrhiza. Roots of *C. sativa* straight to sinuous. Distal roots very fine, thin. Lenticels not observed, root scars common.

Colour of the roots reddish-brown to brown with whitish and shiny parts, getting slightly paler with diminishing diameter.

Surface of the roots smooth or covered by parallel longitudinal periderm ridges with minor anastomosing. Periderm slough off in thin curly layers.

Root of *C. sativa* with smooth surface. Root scars evident as circles.

Cells of periderm of medium size, evident under high magnifications of dissecting microscope.

Fagus sylvatica L.

Lateral root of *Fagus sylvatica* with ectomycorrhiza. Roots of *F. sylvatica* straight to sinuous, densely ramified. Distal roots very fine, but may be thickened due to mycorrhiza. Lenticels not observed.

Colour of the roots reddish-brown, more or less constant along the root up to the mycorrhizal tips.

Surface of the roots covered by irregular net-like structure of the ridges, with diminishing diameter the structure of the ridges becomes more parallel and barely evident. Periderm layers do not shed.

Cells of periderm small, not discernible under dissecting microscope.

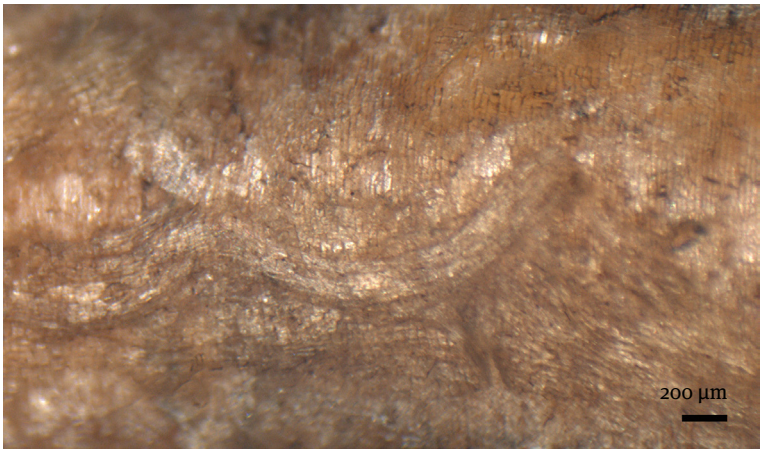
Quercus petraea (Matt.) Liebl.

Lateral root of *Quercus petraea* with ectomycorrhiza. Roots of *Q. petraea* straight to sinuous or even tortuous. Distal roots very fine, thin. Lenticels not observed, root scars abundant, tuberculate.

Colour of roots orange-brown to pale-brown, shiny and dirty white in areas where thicker layers of periderm are accumulated. With diminishing diameter, colour stays more or less the same.

Root scars evident as tubercles.

Structure of the surface irregular, appears soft in areas where thick layer of periderm is accumulated and with some longitudinal waves. Periderm sheds in thin transparent layers. Some areas appear very smooth.

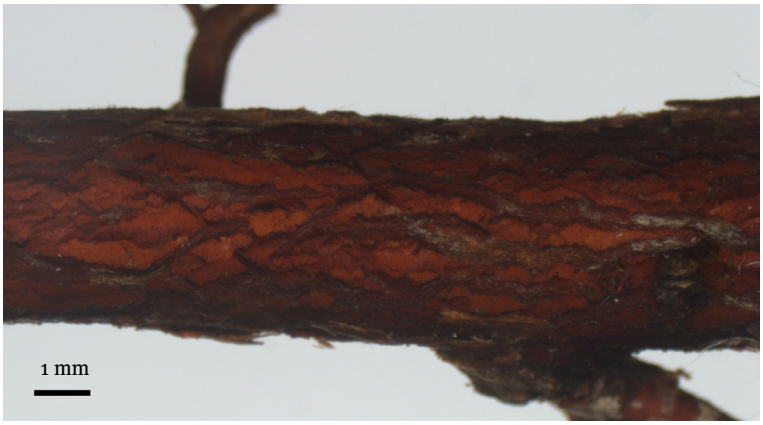


Cells of periderm of medium size, visible under higher magnifications of dissecting microscope.

Carpinus betulus L.

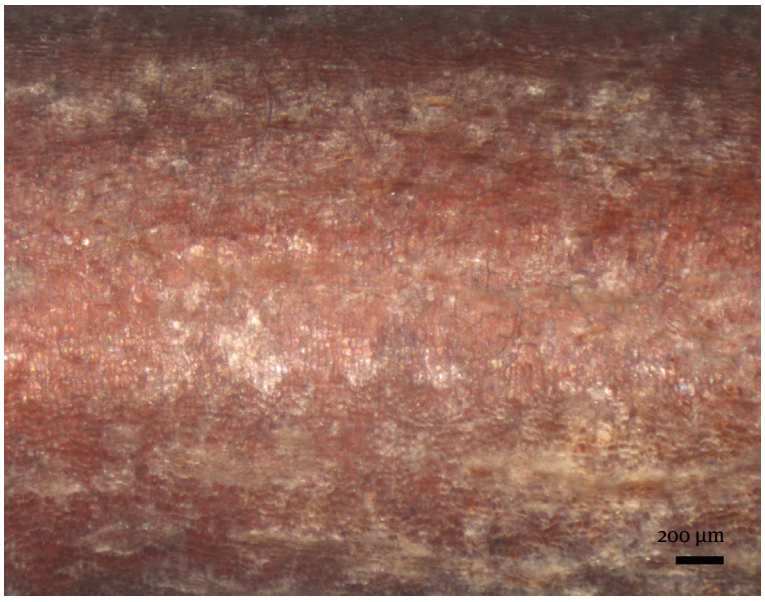
Lateral root of *Carpinus betulus* with ectomycorrhiza. Roots of *C. betulus* straight to slightly sinuous, regularly ramified, often with short fibrous roots growing out of relatively thick and long laterals (thread-like appearance). Lenticels not observed.

Colour of the roots reddish-brown, more or less constant along the root, getting slightly paler with decreasing diameter.



Surface of the roots with a mesh of alate longitudinal ridges, but can also be completely smooth.

Root of *C. betulus* with smooth surface.

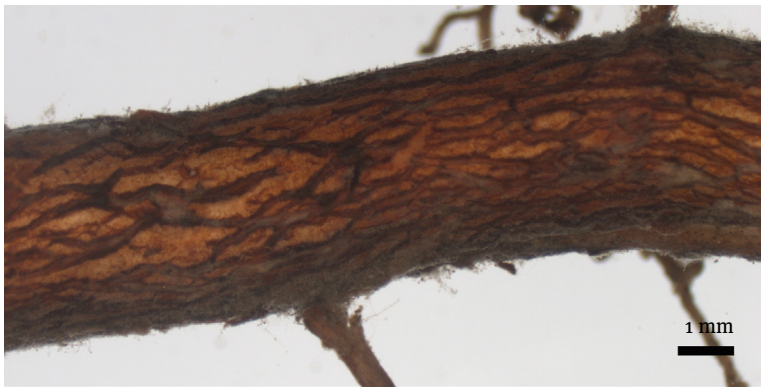


Cells of periderm of medium size, evident under high magnifications of dissecting microscope.

Acer pseudoplatanus L.

Lateral roots of *Acer pseudoplantanus*. Roots of *A. pseudoplatanus* straight to sinuous, ramifications to two or more equal laterals common, sometimes these ramifications appear knot-like (arrow). Root tips fine, commonly constricted at the base or in the middle. Lenticels not observed. Mycorrhiza arbuscular.

Colour of roots dark brown to bright brown, ridges darker. Lateral roots becoming paler towards root tips that appear brownish-white to white or even translucent.



Structure of periderm net-like, forming regular pattern with ridges along the root. In 1 mm root net-like structure not recognizable anymore, roots may appear paler due to phellem layers peeling off.

Cells of periderm small, barely or not discernible under higher magnifications of dissecting microscope.

Populus nigra L.

Lateral root of *Populus nigra*. Roots of *P. nigra* straight to sinuous. Lenticels observed close to ramifications, oval-shaped. Ectomycorrhiza and arbuscular mycorrhiza.

Colour of the roots dark brown with pale brown areas revealed below the sloughing periderm layers.

Surface of the roots with longitudinal strips of periderm tissue, that form a loose enveloping mesh, the surface below is smooth or covered by gentle mesh (see picture below).

Cells of periderm of medium size, evident under high magnifications of dissecting microscope.

Fraxinus excelsior L.

Lateral root of *Fraxinus excelsior.* Roots of *F. excelsior* sinuous to tortuous. Root tips thick, sometimes long and unramified. Root scars common. Lenticels, when observed, tubercle-like, roundish. Mycorrhiza arbuscular.

Roots very lightly coloured, pale brown. Colour of the tips of the same colour as the higher order roots.

Surface of the roots with anastomosing rounded longitudinal ridges, but may also appear completely smooth (see below). In 3 mm roots structure of the surface barely visible, covered by patches of shedding phellem layers. 1 mm roots smooth, structure not distinguishable, often covered by remnants of primary cortex that is sloughed off.

Cells of periderm of medium size, discernible under higher magnifications of dissecting microscope.

2.ANATOMY

2.1 Root Anatomy

The list of anatomical characteristics for species identification includes primary and secondary xylem and inner bark features of coniferous and broadleaved tree species with a special focus on young root structure (Fig. 2.1.1). Here we present the most relevant anatomical characteristics of these tissues for temperate tree species as well as differences between root and stem wood. The features are in accordance with the IAWA list of of microscopic features for hardwood, softwood and bark identification (IAWA Committee 1989, IAWA Committee 2004, IAWA Committee - 2016 - in preparation). It is not a complete list encompassing all the structural patterns that one can encounter in tree species, but it includes a list of features most useful for identification purposes. The list is combined with definitions of anatomical features. Identifying tree species relies on careful observation of a number of subtle features on micrographs of adequate quality. The list is based on root samples collected from living trees from different environments in Slovenia. Observations were performed on transverse and longitudinal sections stained with safranin and astra blue. We present a codification system for primary and secondary xylem and inner bark anatomy as seen in young roots.

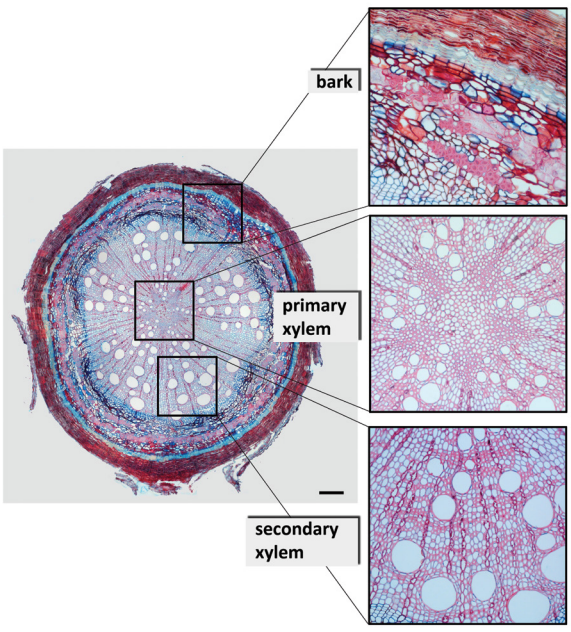


Fig. 2.1. 1: Anatomical structure of young root of *Quercus petraea*. Bar = 200 µm.

WOOD

1. Wood without vessels: CONIFERS
2. Wood with vessels: BROADLEAVED SPECIES

CONIFERS

Growth rings

Growth ring boundary

A boundary between two neighbouring annual increments (= annual rings).

Although trees from temperate regions usually have distinct growth ring boundaries in the stem, they often have indistinct growth ring boundaries in the roots. In *L. decidua*, it was observed that both juvenile and mature root wood possessed little or no latewood, growth rings were erratic or absent, and it was difficult to distinguish annual from false growth rings. Similar ob-

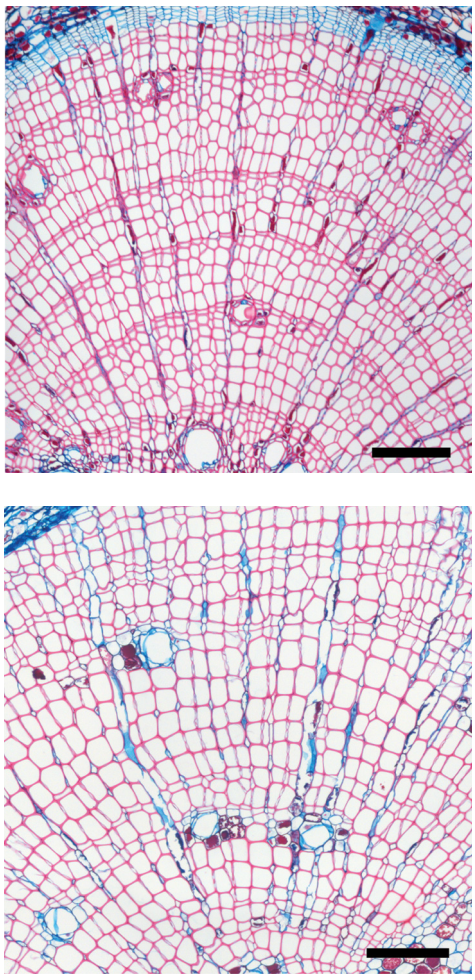


Fig. 2.1. 2: Growth ring boundary distinct (up, root of Picea abies) and growth ring boundary indistinct or absent (to bottom, root of P. sylvestris). Bar = 200 µm.

servations were recorded for roots of the investigated tree species. Root growth rings frequently have a narrow latewood part that often consists of a single row of cells and wedging (= partly missing) or missing rings, often interspersed with very wide rings.

3. Growth ring boundary distinct

Growth rings with an abrupt structural change at the boundaries between them, usually including a change in tracheid wall thickness and/or tracheid radial diameter. Macroscopically, such structural changes are accompanied by distinct differences in colour between earlywood (light) and latewood (dark).

4. Growth ring boundary indistinct or absent

Growth ring boundaries vague and with marked gradual structural changes, or not visible.

Tracheids

A tracheid is a dead imperforate wood cell, interconnected with congeneric elements by bordered pits. Communication between neighbouring tracheids occurs over pit pairs. A **pit** is a small opening in the secondary cell wall with a persisting middle lamella (a "membrane") that closes it towards the neighboring cell (Torelli 1990).

The **transition between earlywood and latewood** of the same growth ring is marked by structural changes, usually a change in tracheid wall thickness and radial diameter. In the beginning of the growth season, tracheids of **earlywood** with big lumina are formed, and at the end of the vegetation period tracheids of **latewood** with small lumina are formed. The radial diameter of tracheids decreases from earlywood towards latewood, while the thickness of cell walls increases. The tracheids of earlywood are important for conducting water because of their big lumina and the tracheids of latewood are more resistant to xylem cavitation and mechanical damage (Fengel & Wegener 1989, Pitterman and Sperry 2003).

TRACHEID PITTING IN RADIAL WALLS (IN EARLYWOOD ONLY)

It is important to consider the entire length of the tracheid. Occasional presence of locally biseriate pits should not be interpreted as a 'two or more seriate' condition. Uniseriate pitting in radial tracheid walls is the most common condition in coniferous woods. In *Larix* spp. (Pinaceae) pitting in earlywood is often biseriate.

5. Predominantly uniseriate

6. Predominantly two or more seriate

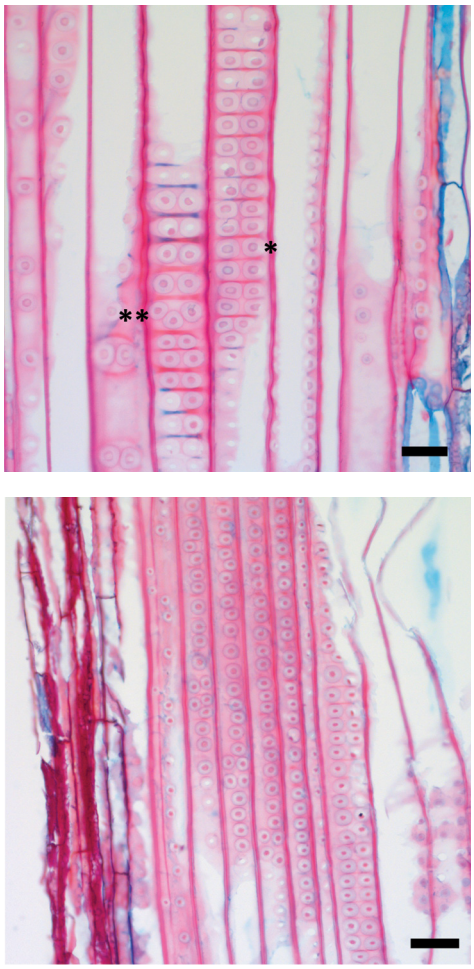


*Fig. 2.1. 3: Tracheid pitting in roots is not a very consistent character. In the upper picture, tracheids are mainly uniseriate (A. alba), while in the bottom (P. abies) two-seriate pits can be observed. Tracheid pits that are arranged oppositely are marked with *, while those marked with ** are arranged alternately. Bar = 50 µm.*

ARRANGEMENT OF (TWO OR MORE SERIATE) TRACHEID PITTING IN RADIAL WALLS (EARLYWOOD ONLY)

Pitting is usually opposite in all other taxa with multiseriate tracheid pits, e.g. in *Larix* spp. (Pinaceae).

7. Opposite

8. Alternate

LATEWOOD TRACHEID WALL THICKNESS

Double wall thickness and lumen diameter should always be measured in the radial direction.

9. Thin-walled

Double wall thickness less than radial lumen diameter.

10. Thick-walled

Double wall thickness larger than radial lumen diameter.

HELICAL THICKENINGS

Helical thickenings are ridges on the inner face of the tracheids. They may occur in both longitudinal as well as ray tracheids and usually extend over the entire body of the respective cell.

11. Present

12. Absent

HELICAL THICKENINGS IN RAY TRACHEIDS

Helical thickenings in ray tracheids have also been observed occasionally in the latewood of young stems and branches of *Larix* spp.

13. Present

14. Absent

Axial parenchyma

Axial parenchyma (excluding epithelial and subsidiary cells of intercellular canals) is responsible for storage of metabolites, and consists of cells with (usually) simple pits that have not undergone intrusive tip-growth during differentiation from the cambial cells.

PRESENCE AND ABUNDANCE OF AXIAL PARENCHYMA

Axial parenchyma is not as common in coniferous woods as in hardwoods. It may be present or absent and thus constitutes a valuable character for identification. Fusiform parenchyma (derived from fusiform cambial cells without subsequent transverse division) has been observed only in the wood of young stems and branches of several genera of Pinaceae, and may be diagnostically useful when differentiating *Larix* and *Picea* branch wood (Noshiro & Fujii 1994). Although axial parenchyma in coniferous woods can usually be recognized by the frequent presence of dark content, this may be removed during sample preparation.

15. Present

16. Absent

ARRANGEMENT OF AXIAL PARENCHYMA

17. Diffuse (evenly scattered throughout the entire growth increment)

Single parenchyma strands or pairs distributed evenly among the tracheids through the entire growth increment.

18. Marginal

Single cells along the growth ring boundaries in the first row of earlywood or the last row of latewood. It is more frequent in juvenile than in mature wood (Noshiro& Fujii 1994).

18.1. Only around resin ducts

TRANSVERSE END WALLS OF AXIAL PARENCHYMA

Markedly beaded or nodular end walls are commonly observed in many species of *Juniperus*, *Abies*, *Cedrus*, and *Tsuga*. Nodular end walls are generally more conspicuous in tangential sections where they commonly appear either singly or in a series of two or more nodules per end wall. The localized thickenings and pits or pit fields (in *Abies*, *Larix*, *Picea*, *Pseudotsuga*, and *Tsuga*) are so arranged on these walls that in radial sections only a single nodule is visible (Phillips 1948). Nodular or beaded walls are often obscured by resin.

19. Smooth

20. Irregularly thickened

21. Beaded or nodular

Rays

Ray parenchyma is present in all extant coniferous woods. Rays that contain radial intercellular canals are called fusiform because of their shape in a tangential plane.

RAY STRUCTURE

A **ray tracheid** is a tracheid forming part of a ray. Ray tracheids are a regular feature in stem wood of all Pinaceae that possess normal intercellular resin canals, excluding *Tsuga*, and in *Chamaecyparis nootkatensis*, in which some rays may consist entirely of tracheids, others only of parenchyma cells.

In stem wood, ray tracheids may form usually only

one (e.g. *Pseudotsuga*, *Tsuga*), one or occasionally two or three (e.g. *Larix*, *Picea*) or commonly several marginal cell rows (e.g. *Pinus* spp.). In *Pinus* spp., rows of ray tracheids may be located not only at the upper and lower margins but also in the interior of the ray (Core et al. 1979). However, in root wood ray tracheids occur in significantly lower numbers of rows (Bernabei & Bontadi 2011) or may be absent from the majority of rays (Denne & Gasson 2008). Ray tracheid rows are often interrupted or incomplete (Bernabei & Bontadi 2011), while ray tracheid cells are often distorted and oriented axially from the margin of the rays (Denne & Gasson 2008).

22. Homocellular rays

Rays composed solely of ray parenchyma cells.

23. Heterocellular rays

Rays composed of ray parenchyma and ray tracheids.

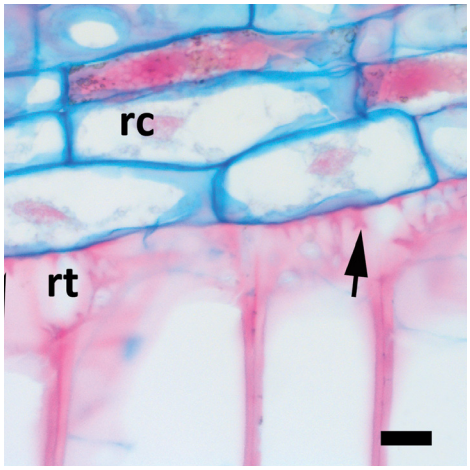


Fig. 2.1. 4: Heterocellullar ray (ray composed of ray parenchyma cells (rc) and ray tracheids (rt)) in root of P. sylvestris. Arrows show dentations on cell walls of ray tracheids that are characteristic of P. sylvestris. Ray tracheids can be generally observed in roots thicker than 5 mm in diameter. Bar = 20 µm.

RAY SIZE

All features referring to ray height and width exclude rays containing intercellular canals ('fusiform rays').

-Average ray height (number of cells)

The ray height (in number of cells) is determined from tangential planes. At least 25 randomly selected rays should be measured (counted) calculating the mean, standard deviation, and range.

24. Very low (up to 4 cells)

25. Medium (5 to 15 cells)

26. High (from 16 to 30 cells)

27. Very high (more than 30 cells)

-Ray width

28. Uniseriate

28.1. Exclusively uniseriate

Exclusively uniseriate including the very sporadic occurrence of partially biseriate rays.

29. 2–3 seriate in part

2-3 seriate in part = approximately 10% of the larger rays should be at least biseriate over nearly the full height.

Although rays in most coniferous woods are uniseriate (including the very sporadic occurrence of partially biseriate rays), some possess a fair number of bi- and triseriate rays (in addition to uniseriate ones).

CELL WALLS OF RAY TRACHEIDS

Dentations should not be confused with spiral thickenings, which may occur in species of *Larix*, *Picea* and *Pseudotsuga*.

30. Smooth

Ray tracheids smooth: walls with no ornamentation at all, and generally thin, e.g. in the 'soft pines' (*P. strobus*, *P. cembra*).

31. Dentate

Walls of variable thickness bearing pronounced internal tooth-like protrusions from the upper and lower cell wall. Generally more numerous in latewood. Very prominent in *Pinus sylvestris*, *P. nigra*, *P. pinaster*, *P. ponderosa*, *P. radiata*. Very small denticulations also occur in a few species of *Picea* (Phillips 1948).

32. Reticulate

Walls generally thin, bearing very numerous, narrow, pointed, internal tooth-like protrusions from the upper and lower cell wall, united by transverse ridges, which give a characteristic reticulate appearance, e.g. *Pinus palustris*, *P. taeda*, *P. banksiana*.

RAY TRACHEID PIT BORDERS ANGULAR OR WITH DENTATE THICKENING (RADIAL PLANE)

This character refers to the difference between *Larix* and *Picea* type bordered pits in tracheid cell walls.

Ray tracheid pit borders may be thickened and lined with small, irregular lumps, which make the pit opening appear like a narrow canal (*Picea*-1 type), or may feature additional dentate thickenings ("horns") on the pit borders (*Picea*-2 type) (Bartholin 1979). In *Picea abies* roots, ray tracheid borders of *Picea*-1 and *Picea*-2 types were observed (Bernabei & Bontadi 2011), which could help with distinguishing *Picea* from *Larix*. However, Denne & Gasson (2008) describe this character as difficult to apply in root wood as ray tracheids are rare or absent. The few bordered pits that they were able to observe in *Larix decidua* were of "*Larix*" or "intermediate" type.

33. Present

34. Absent

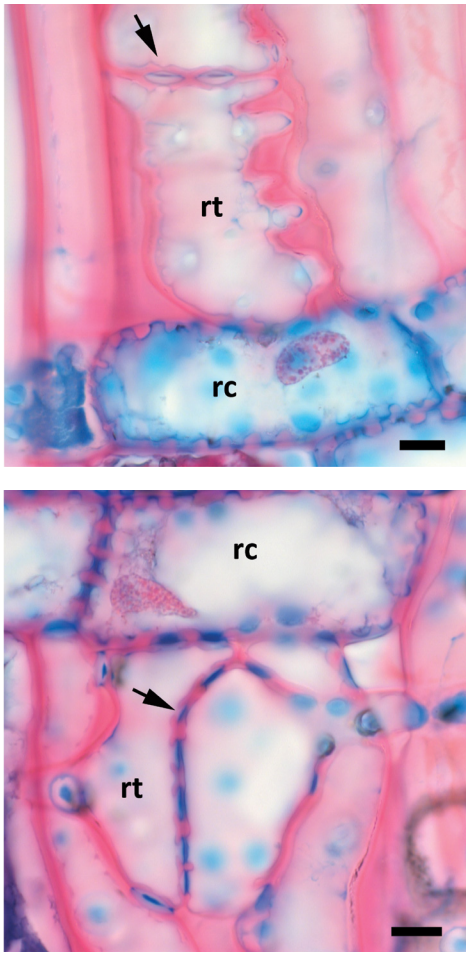


Fig. 2.1. 5: Ray tracheids (rt) in root of P. abies (up) and L. decidua (bottom). Rc = ray parenchyma cell. Arrows show tracheid pit borders. Here, ray tracheids are distorted and oriented axially from the margin of the ray. Bar = 10 µm.

END WALLS OF RAY PARENCHYMA CELLS

35. Smooth (unpitted)

Smooth end walls, which are relatively thin with few or no pits, are characteristic for most coniferous taxa.

36. Distinctly pitted (nodular)

Distinctly pitted (also referred to as nodular) end walls are characteristic of the genera *Abies*, *Larix*, *Picea*, *Tsuga* and *Pinus* of Pinaceae.

HORIZONTAL WALLS OF RAY PARENCHYMA CELLS

Upper and lower horizontal walls of ray parenchyma cells can be either smooth (unpitted) or distinctly pitted. Pitted horizontal walls of ray parenchyma cells appear to be restricted to a few genera of Pinaceace, e.g. *Abies*, *Cedrus*, *Larix*, *Pseudotsuga*, *Tsuga*. Most other coniferous taxa have smooth horizontal walls.

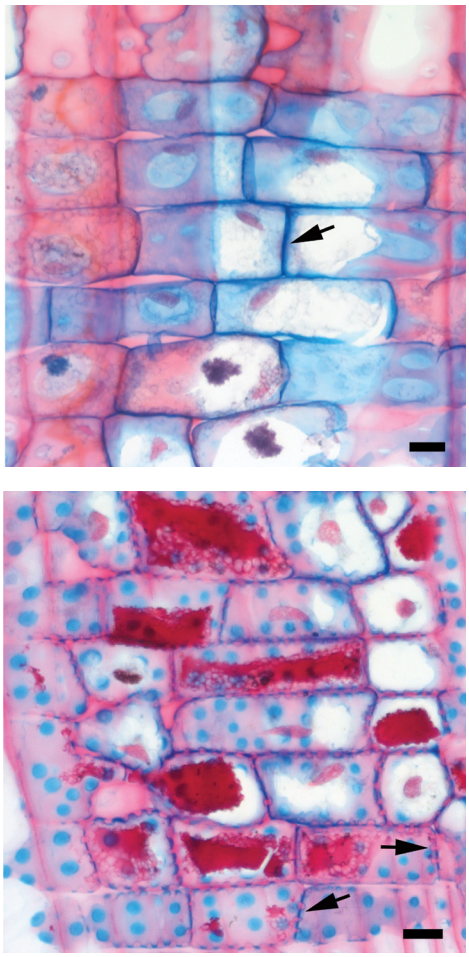


Fig. 2.1. 6: End walls and horizontal walls of ray parenchyma cells as seen in longitudinal section. Up: smooth horizontal and end walls (arrow) in root of P. sylvestris. Bottom: Pitted or nodular horizontal and end walls (arrows) in root of P. abies. Bar = 20 µm.

37. Smooth (unpitted)

38. Distinctly pitted

CROSS-FIELD PITTING

Cross-field is the area bounded by the intersecting walls of a single longitudinal tracheid and a single ray parenchyma cell. **Cross-field pitting** = pits occurring on the areas of contact between ray parenchyma cells and axial tracheids (cross-fields), to be observed only in earlywood and throughout the ray (body and marginal cells).

Pit apertures may be considerably modified in compression wood. Intergrading between pit types occurs especially between 'piceoid' and 'cupressoid' and also between 'cupressoid' and taxodioid' pits. The appearance of pits in radially oriented cells is influenced by how close to a perfect radial orientation the cut is. In root wood, perfect radial sections are difficult to obtain and this is especially true close to the centre of the root. In *Picea abies* roots, besides piceoid pits, which were in the majority, taxodioid and cupressoid pits were also observed (Bernabei & Bontadi 2011), while in *Larix decidua* roots, predominantly cupressoid or taxodioid pits with few piceoid pits were present, in contrast to stem wood where predominantly piceoid pits with cupressoid and taxodioid pits present were occasionally observed (Denne & Gasson 2008).

39. 'Window-like' (fenestriform)

With usually 1-2 large simple or apparently simple cross-field pits. Such large, square or rectangular pits occupying nearly the entire cross-field can be observed in *Pinus sylvestris* and *P. strobus*.

40. Pinoid

Cross-field pits 1-6 pinoid, 3 or more pits common. Such pits are small to fairly large depending on the number per cross-field, simple or with reduced borders, and often of irregular shape as opposed to the more or less rectangular 'window-like' pits. They can be found in all sections of *Pinus* except those with the large, 'window-like' type.

41. Piceoid

Cross-field pits piceoid. These pits have borders much wider than the narrow, slit-like and often extended apertures. As, for instance, in *Larix* spp., *Picea* spp., *Pseudotsuga* spp. and *Tsuga* spp. (Pinaceae).

42. Cupressoid

Cross-field pits cupressoid. They have elliptical apertures included within the limits of the pit border (contrary to the often extended piceoid pits); apertures are definitely narrower than the border. The long axis of the apertures varies in position from vertical to horizontal even within a single specimen. This type of pitting is characteristic of most Cupressaceae (*Thuja* is one exception) and also occurs in some Podocarpaceae and Taxaceae.

43. Taxodioid

Cross-field pits taxodioid. Taxodioid pits have large, oval to circular, included apertures; the aperture exceeds the width of the border at its widest point. Taxodioid pitting can be found in most taxa of former Taxodiaceae (now Cupressaceae), but also in the genera *Abies*, *Cedrus* (Pinaceae), *Thuja* (Cupressaceae) and in several species of Podocarpaceae.

44. Araucarioid

Cross-field pits araucarioid. The individual pits are predominantly cupressoid (pit aperture elliptical, included, definitely narrower than the border), but their arrangement in the cross-field is distinctive. The pits are arranged in alternate rows of usually three or more with a tendency for crowding; individual pits often have a polygonal outline similar to the alternate intertracheary pitting in Araucariaceae. Araucarioid cross-field pitting is restricted to Araucariaceae.

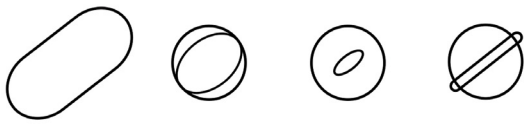


Fig. 2.1. 7: Cross-field pits at the contact of ray parenchyma with axial tracheid in conifers (from left to right): fenestriform, taxodioid, cupressoid, piceoid (adapted from Torelli 1986).

NUMBER OF PITS PER CROSS-FIELD (EARLYWOOD ONLY)

45. (Large, window-like) 1–2

46. 1–3

47. 3–5

48. 6 or more

Intercellular canals

The intercellular canal (synonyms: **resin duct, resin canal**) is a tubular intercellular duct lined by an epithelium, conducting secondary plant products secreted by the epithelial cells. The **epithelium** is the single layer of cells adjacent to the canal. The remaining parenchyma and included or strand tracheids outside the epithelium are **subsidiary cells**. The entity as a whole – canal, epithelium and subsidiary cells – is the resin canal complex.

Intercellular canals may be oriented axially (axial/vertical intercellular canal), or radially (radial /horizontal intercellular canal, within a ray). Axial and radial intercellular canals are usually interconnected in a three-dimensional network.

In conifers, the presence of normal intercellular canals (both radial and axial) is restricted to several genera of Pinaceae, i.e. *Larix*, *Picea*, *Pinus* and *Pseudotsuga*. Traumatic intercellular canals (axial and/or radial) may occur in these and in a number of other taxa of Pinaceae.

AXIAL INTERCELLULAR (RESIN) CANALS

In stem wood of Pinaceae from regions with a pronounced seasonal climate, axial canals are found mainly (but not exclusively) in the latewood. Axial canals are mostly single (or solitary) but occasionally also occur in pairs (e.g. in *Pseudotsuga* and in many species of *Larix*) or small tangential groups.

As regards the morphology of the epithelial cells, two types of canals are distinguished: narrow canals mainly with thick-walled epithelial cells, as in *Pseudotsuga*, *Picea*, and *Larix*, and wider canals with thin-walled epithelial cells, as in *Pinus* (Grosser 1977). Species with thick-walled epithelial cells in stem wood might have a certain proportion of thin -walled epithelial cells in root wood.

49. Present

50. Absent

RADIAL INTERCELLULAR (RESIN) CANALS

Radial canals are located exclusively within the rays. Rays containing intercellular canals are called fusiform rays because of their shape in tangential planes. In Pinaceae, the genera *Larix*, *Picea*, *Pinus* and *Pseudotsuga* possess radial intercellular canals in addition to axial canals. No coniferous taxon is known to have exclusively radial canals.

51. Present

52. Absent

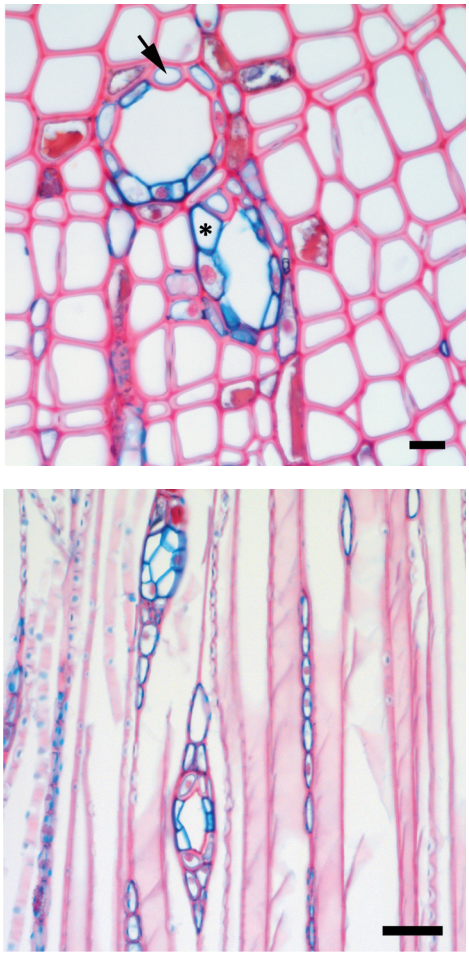


Fig. 2.1. 8: Axial intercellular canals in root of P. abies (up, bar = 20 µm) as seen in cross-section. In longitudinal section radial intercellular canals can be observed inside fusiform rays (bottom, bar = 50 µm). In adult wood, the majority of epithelial cells surrounding canals are thick-walled (arrow), but in juvenile wood of roots, a certain portion of epithelial cells can have thin walls (*).

TRAUMATIC INTERCELLULAR (RESIN) CANALS

Traumatic resin canals are usually larger in diameter, of irregular outline, and frequently tangentially fused. Traumatic resin canals are formed in taxa with normal resin canals as well as in many taxa in Pinaceae and other families (e.g. *Abies*, *Tsuga*) that normally do not have them.

53. Present

54. Absent

AVERAGE DIAMETER OF NORMAL AXIAL INTERCELLULAR (RESIN) CANALS

The diameter of axial intercellular canals is measured in transverse section. Canals are selected for measurement with care not to bias the selection towards the larger or smaller ones. At least 10 (preferably more) canals should be measured. It is recommended to enter the average and range of values, e.g. 30–**50**–70 µm.

-Tangential diameter, delimited by epithelial cells (in µm)

The tangential diameter of resin canal, including the epithelial cells, is measured at the widest part of the opening.

-Tangential diameter of entire resin canal complex (in µm)

The tangential diameter of the entire resin canal complex is measured at the widest point. The measurements include all components of the axial resin canal complex as differentiated from the axial tracheids.

-Radial diameter, delimited by epithelial cells (in µm)

The radial diameter of the resin complex, including the epithelial cells, is measured at the widest point.

AVERAGE DIAMETER OF NORMAL RADIAL INTERCELLULAR (RESIN) CANALS (IN µm)

Intercellular canals in fusiform rays tend to be smaller than corresponding axial canals. The diameter of radial intercellular canals is measured in tangential sections. Canals are selected for measurement with care not to bias the selection towards the larger or smaller ones. The diameter of the canal lumina plus the epithelial cells is measured at the widest part. At least 10 (preferably more) canals should be measured. It is recommended to enter the average and range of values, e.g. 25–**35**–60 µm.

EPITHELIAL CELLS (OF INTERCELLULAR CANALS)

Epithelial cells are specialized parenchyma cells that surround an intercellular canal. More specifically, the term 'epithelial cells' applies only to the cells facing the resin canals. It does not apply to other axial parenchyma cells forming part of a multi-layered sheath around the canals. Resin is produced in the epithelial cells and secreted into the canal.

Epithelial cells are square to sometimes rectangular in shape, forming a continuous interior lining of the canal (epithelium). They are usually thick-walled and rather rigid in *Larix*, *Picea* and *Pseudotsuga* and typically thin-walled in all species of *Pinus*. The clear division between thick- and thin-walled epithelial cells is occasionally obscured because the thick-walled epithelial cells, e.g. in *Larix* and *Picea*, may sometimes be mixed with thin-walled cells. Species with thick-walled epithelial cells in stem wood might have a certain proportion of thin-walled epithelial cells in root wood.

55. Thick-walled

56. Thin-walled

NUMBER OF EPITHELIAL CELLS IN NORMAL RADIAL CANALS

The number of epithelial cells in normal radial canals appears highly variable, and therefore has not been included in the IAWA character list.

57. ≤ 6

Characteristic of radial canals in *Pseudotsuga*.

58. 7–9

Characteristic of radial canals in *Picea*.

59. up to 12

Characteristic of radial canals in *Larix*.

Mineral inclusions

CRYSTALS

Crystals of calcium oxalate are rare in coniferous woods. Thus, their regular occurrence in species of *Abies*, *Picea* (prismatic crystals) and in *Ginkgo biloba* (druses) is of considerable diagnostic significance. Calcium oxalate crystals are birefringent and can be most readily observed under polarized light.

60. Present

61. Absent

TYPE OF CRYSTALS

62. Prismatic

Solitary rhombohedral or octahedral crystals composed of calcium oxalate.

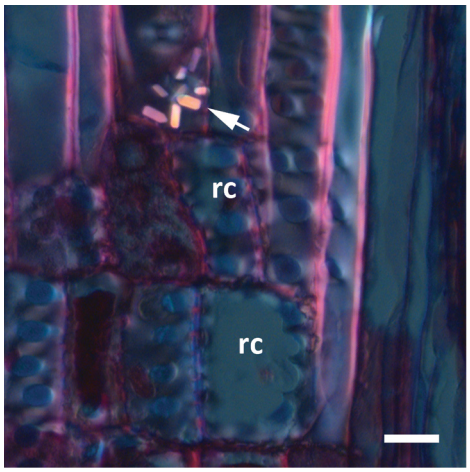


Fig. 2.1. 9: Prismatic crystals (arrow) in ray cells (rc) of A. alba root as seen under differentiation interference contrast (DIC). Bar = 20 µm.

63. Druses

A compound crystal of calcium oxalate, more or less spherical in shape, in which the many component crystals protrude from the surface giving the whole structure a star-shaped appearance (synonym = cluster crystal).

64. Other forms

Any type of crystal other than prismatic crystals and druses.

Crystals located in

Crystals in conifers appear to occur only in a single cell type in a given taxon. Prismatic crystals are more or less common in the marginal and submarginal ray cells of some species of *Abies*, *Cedrus* and some species of *Picea* (all Pinaceae). These cells are not subdivided and one or more crystals may be found in any single cell.

65. Rays

66. Axial parenchyma

67. Cells associated with intercellular canals

BROADLEAVED SPECIES

Growth rings

GROWTH RING BOUNDARY

68. Growth ring boundaries distinct

Growth rings with an abrupt structural change at boundaries between them, usually including a change in fibre wall thickness and/or fibre radial diameter.

69. Growth ring boundaries indistinct or absent

Growth rings vague and marked by more or less gradual structural changes at their poorly defined boundaries or not visible.

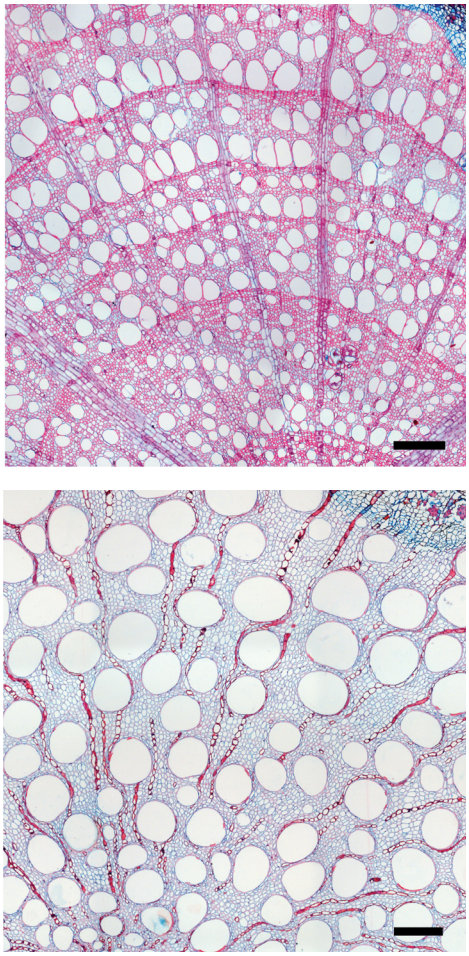


Fig. 2.1. 10: Distinct growth ring boundaries in root of F. sylvatica (up) and absent growth ring boundaries in root of C. sativa (bottom). In this sample of F. sylvatica, vessels are arranged in a semi-ring porous pattern, i.e. the size of the vessels gradually changes inside each growth ring. Bar = 200 µm.

Vessels

POROSITY

The three features for porosity form an integrating continuum, and many species range from diffuse-porous to semi-ring-porous, or from ring-porous to semi-ring-porous. In tree roots, the pattern of porosity may depend on the distance of the root from the stem. In the ring-porous species *Ulmus glabra*, roots in close proximity to the stem were semi-ring-porous, while more distal roots were diffuse-porous (Rewald et al. 2012).

70. Wood ring-porous

Wood in which the vessels in the earlywood are distinctly larger than those in the latewood. Earlywood vessels form a well-defined zone or ring. There is an abrupt transition to the latewood of the same growth ring.

71. Wood semi-ring -porous

1) Wood in which the vessels in the earlywood are distinctly larger than those in the latewood of the previous ring, but in which there is a gradual change to narrower vessels in the intermediate and latewood of the same growth ring; or
2) Wood with a distinct ring of closely spaced earlywood vessels that are not markedly larger than the latewood vessels of the preceding ring or the same growth ring.

72. Wood diffuse -porous

Wood in which the vessels have more or less the same diameter throughout the growth ring.

VESSEL ARRANGEMENT

73. Vessels in tangential bands

Vessels arranged perpendicular to the rays and forming short or long tangential bands. These bands can be straight or wavy.

74. Vessels in diagonal and/or radial patterns

Vessels arranged radially or intermediate between tangential and radial (i.e. oblique). Synonym for diagonal: 'in echelon'.

75. Vessels in dendritic patterns

Vessels arranged in a branching pattern, forming distinct tracts, separated by areas devoid of vessels. Synonym: flame-like.

VESSEL GROUPINGS

76. Vessels exclusively solitary (90% or more)

90% or more of the vessels are completely surrounded by other elements. Thus, 90% or more do not appear to contact another vessel, as viewed in cross-section.

77. Vessels in radial multiples of 4 or more common

Radial files of 4 or more adjacent vessels of common occurrence.

78. Vessel clusters common

Groups of 3 or more vessels having both radial and tangential contacts, and of common occurrence.

SOLITARY VESSEL OUTLINE

79. Solitary vessel outline angular

Shape of solitary vessel outline is angular as viewed in cross-section. In ring-porous woods, latewood solitary vessels should be examined. Earlywood vessels are usually circular to oval in outline.

PERFORATION PLATES

80. Simple perforation plates

A perforation plate with a single circular or elliptical opening.

80.1. Scalariform perforation plates

A perforation plate with elongated and parallel openings separated by one to many mainly unbranched bars.

81. Scalariform perforation plates with ≤ 10 bars
82. Scalariform perforation plates with 10–20 bars
83. Scalariform perforation plates with 20–40 bars
84. Scalariform perforation plates with ≥ 40 bars

85. Reticulate, foraminate, and/or other types of multiple perforation plates

Reticulate perforation plate = A plate with closely spaced openings separated by wall portions that are much narrower than the spaces between them, or with a profuse and irregular branching of wall portions resulting in a netlike appearance.

Foraminate perforation plate = A plate with circular or elliptical openings like a sieve; the remaining wall portions can be thicker than in the reticulate type.

Other types = for instance, complex or radiate perforation plates.

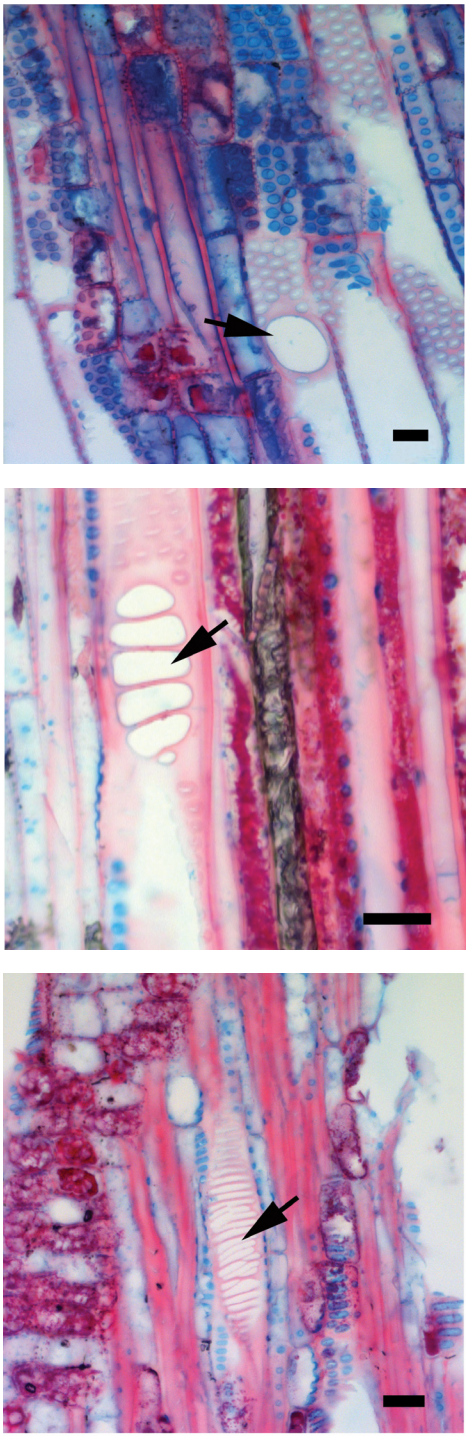


Fig. 2.1. 11: Perforation plates (arrow) in roots, from up to bottom: simple perforation plate in P. nigra, scalariform perforation plate with ≤ 10 bars in C. betulus, and scalariform perforation plate with 20-40 perforation plates in F. sylvatica. Bar = 20 µm.

INTERVESSEL PITS ARRANGEMENTS AND SIZE

Intervessel pits = pits between vessel elements.

86. Intervessel pits scalariform

Elongated or linear intervessel pits arranged in a ladder-like series.

87. Intervessel pits opposite

Intervessel pits arranged in short to long horizontal rows (rows orientated transversely across the length of the vessel).

88. Intervessel pits alternate

Intervessel pits arranged in diagonal rows.

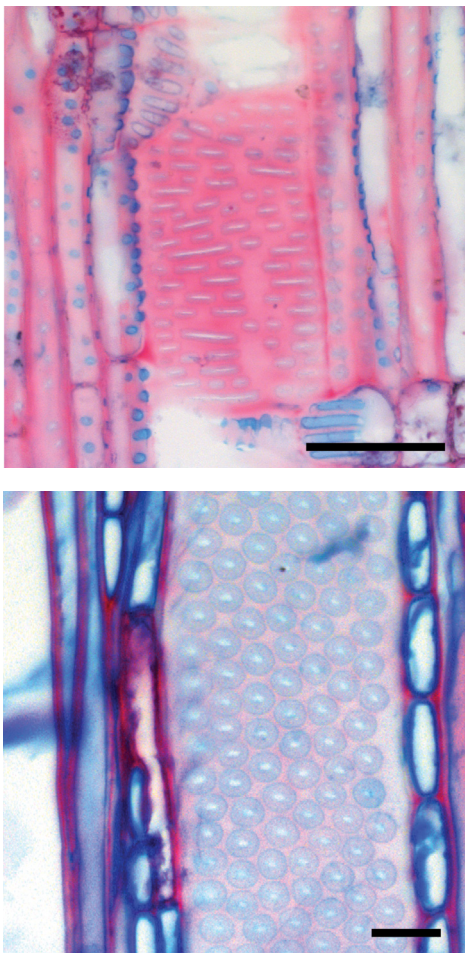


Fig. 2.1. 12: Intervessel pits scalariform (up, in root of F. sylvatica) and intervessel pits alternate (bottom, in root of P. nigra). Bar = 20 µm.

89. Shape of alternate pits polygonal

Outline of intervessel pits, as seen in surface view.

- Intervessel pit size (alternate and opposite)

Horizontal diameter of a pit chamber at the broadest point.

90. Minute ≤ 4 µm

91. Small 4–7 µm

92. Medium 7–10 µm

93. Large ≥ 10 µm

- Range of intervessel pit size (µm)

VESTURE PITS

Vesture pits = pits with the pit cavity and/or aperture wholly or partly lined with projections from the secondary cell wall.

94. Present

VESSEL-RAY PITTING

Vessel-ray pits = pits between a ray cell and a vessel element.

Unilaterally compound pits = pits in which one pit abuts two or more smaller pits on the adjacent cell.

95. Vessel-ray pitting with distinctive borders; similar to intervessel pits in size and shape throughout the ray cell

96. Vessel-ray pits with much reduced borders to apparently simple: pits rounded or angular

97. Vessel-ray pits with much reduced borders to apparently simple: pits horizontal (scalariform, gash-like) to vertical (palisade)

98. Vessel-ray pits of two distinct sizes or types in the same ray cell

99. Vessel-ray pits unilaterally compound and coarse (over 10 µm)

100. Vessel-ray pits restricted to marginal rows

HELICAL THICKENINGS

Helical thickenings in vessel elements = ridges on the inner face of the vessel element wall in a roughly helical pattern. Synonym: spiral thickenings.

101. Helical thickenings in vessel elements present
- *101.1. Helical thickenings throughout body of vessel element*
- *101.2. Helical thickenings only in vessel element tails*
- *101.3. Helical thickenings only in narrower vessel elements*

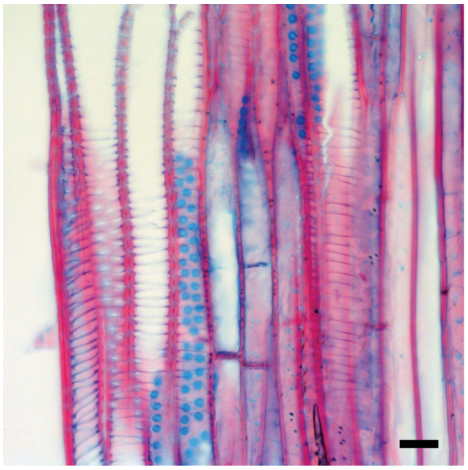


Fig. 2.1. 13: Helical thickenings in vessel elements of root of A. pseudoplatanus. Bar = 20 µm.

TANGENTIAL DIAMETER OF VESSEL LUMINA

In trees, mean tangential diameters of 100–200 µm are more common than mean tangential diameters greater than 200 µm or mean tangential diameters less than 50 µm. In shrubs, mean tangential diameters of less than 50 µm are common.

- Mean tangential diameter of vessel lumina

102. ≤ 50 µm

103. 50–100 µm

104. 100–200 µm

105. ≥ 200 µm

- Mean, +/- Standard Deviation, Range, n = x

106. Vessel of two distinct diameter classes, wood not ring-porous

Woods with a bimodal distribution of tangential diameters of vessel lumina.

TYLOSES AND DEPOSITS IN VESSELS

Tyloses = outgrowths from an adjacent ray or axial parenchyma cell through a pit in a vessel wall, partially or completely blocking the vessel lumen.

Sclerotic tyloses = tyloses with very thick, multi-layered, lignified walls. In ring-porous wood, it is best to examine earlywood vessels for tyloses because tyloses are often absent from small diameter latewood vessels.

Gums and other deposits includes a wide variety of chemical compounds, which are variously coloured (white, yellow, red, brown, black etc.).

107. Present

107.1. Tyloses

107.2. Deposits

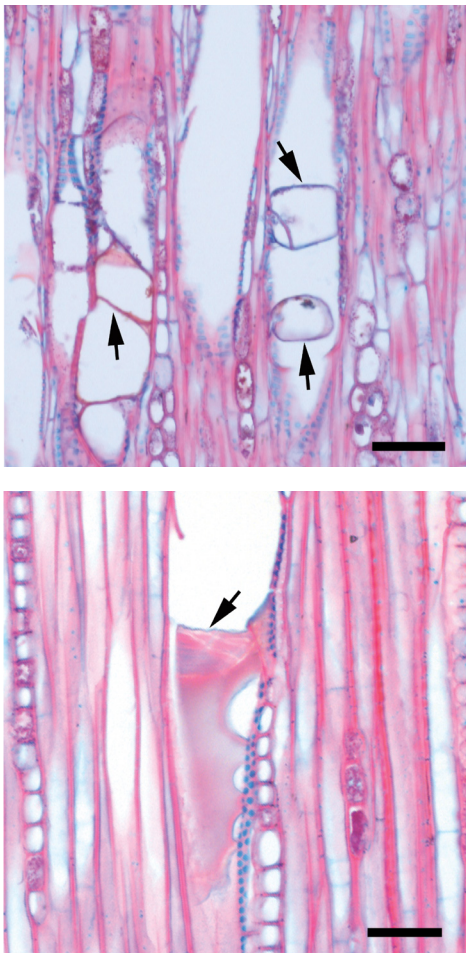


Fig. 2.1. 14: Tyloses (up, arrows) inside vessels in root of F. sylvatica and deposits inside vessels in root of A. pseudoplatanus (bottom). Bar = 50 µm.

Tracheids and fibers

VASCULAR/VASICENTRIC TRACHEIDS

Vascular tracheids = imperforate cells resembling in size, shape, pitting, and wall ornamentation narrow vessel elements and intergrading with the latter.

Vasicentric tracheids = imperforate cells with numerous distinctly bordered pits in their radial and tangential walls, present around the vessels, and different from ground tissue fibres, often of irregular shape.

110. Vascular/vasicentric tracheids present

GROUND TISSUE FIBRES

111. Fibres with simple to minutely bordered pits

Libriform fibres with simple pits or bordered pits with the chambers less than 3 µm in diameter.

112. Fibres with distinctly bordered pits

Fibre tracheids or ground tissue tracheids with border pits with chambers over 3 µm in diameter.

113. Fibre pits common in both radial and tangential walls

Fibre pits, either bordered or simple, common in radial and tangential walls.

114. Helical thickenings in ground tissue fibres

Usually occurs in woods that also have helical thickenings in the vessel elements. However, the opposite is not true. Helical thickenings are much more common in fibres with distinctly bordered pits than in fibres with simple to minutely bordered pits.

FIBRE WALL THICKNESS

In woods with distinct growth rings, fibre wall thickness changes throughout the growth ring, and may be particularly thick of the end at the growth ring. When describing fibre wall thickness, do not consider these last latewood fibres. In addition, do not describe gelatinous (tension wood fires), which usually have thick walls with an unlignified gelatinous layer.

115. Fibres very thin-walled

Fibre lumina 3 or more times wider than the double wall thickness.

116. Fibres thin to thick-walled

Fibre lumina less than 3 times the double wall thickness, and distinctly open.

117. Fibres very thick-walled

Fibre lumina almost completely closed.

Axial parenchyma

118. Axial parenchyma absent or extremely rare

APOTRACHEAL AXIAL PARENCHYMA

Axial parenchyma not associated with the vessels. Although by definition apotracheal parenchyma is not associated with vessels, woods with abundant diffuse or diffuse-in-aggregates parenchyma may exhibit several strands touching the vessels. Such random contacts should not be recorded as paratracheal parenchyma.

119. Axial parenchyma diffuse

Single parenchyma strands or pairs of strands distributed irregularly among the fibrous elements of the wood.

120. Axial parenchyma diffuse-in-aggregates

Parenchyma strands grouped into short discontinuous tangential or oblique lines.

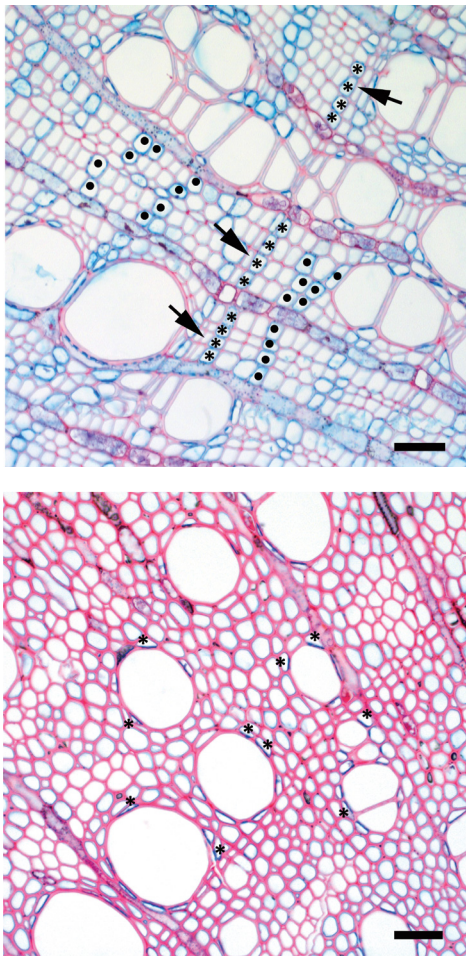


Fig. 2.1. 15: Axial parenchyma in secondary xylem of roots. Diffuse-in-aggregates (dots) and marginal (asterisks) in root of C. betulus (up), arrow marks growth ring. Scanty paratracheal (asterisks) in A. pseudoplatanus (bottom). Bar = 50 µm.

PARATRACHEAL AXIAL PARENCHYMA

Axial parenchyma associated with the vessels or vascular tracheids, types of paratracheal parenchyma cells are scanty paratracheal, vasicentric, aliform, confluent and unilateral paratracheal.

121. Axial parenchyma scanty paratracheal

Occasional parenchyma cells associated with the vessels or an incomplete sheath of parenchyma around the vessels.

122. Axial parenchyma vasicentric

Parenchyma cells forming a complete circular to oval sheath around a solitary vessel or vessel multiple.

123. Axial parenchyma aliform

Parenchyma surrounding or to one side of the vessel and with lateral extensions.

124. Axial parenchyma confluent

Coalescing vasicentric or aliform parenchyma surrounding or to one side of two or more vessels, and often forming irregular bands.

125. Axial parenchyma unilateral paratracheal

Paratracheal parenchyma forming semi-circular hoods or caps only on one side of the vessels, and which can extend tangentially or obliquely in an aliform or confluent or banded pattern.

BANDED PARENCHYMA

Parenchyma bands may be mainly independent of the vessel (apotracheal), definitely associated with the vessels (paratracheal), or both. Bands may be wavy, diagonal, straight, continuous, or discontinuous.

126. Axial parenchyma bands more than three cells wide

127. Axial parenchyma in narrow bands or lines up to three cells wide

128. Axial parenchyma reticulate

Parenchyma in continuous tangential lines of approximately the same width as rays, regularly spaced and forming a network with them, the distance between the rays is approximately equal to the distance between the parenchyma bands.

129. Axial parenchyma scalariform

Parenchyma in regularly spaced fine lines or bands, arranged horizontally or in arcs, appreciably narrower than the rays and with them producing a ladder-like appearance in cross-section. The distance between the rays is greater than the distance between parenchyma bands.

130. Axial parenchyma in marginal or in seemingly marginal bands

Parenchyma bands which form a more or less continuous layer of variable width at the margins of a growth ring or are irregularly zonate. Marginal parenchyma includes terminal and initial parenchyma; seemingly marginal includes what has been called irregular zonate bands.

AXIAL PARENCHYMA CELL TYPE/ STRAND LENGTH

131. Fusiform parenchyma cells

Parenchyma cells derived from fusiform cambial cells without subdivision or tip growth. In shape they resemble a short fibre.

132. Two cells per parenchyma strand

A series of axial parenchyma cells formed through transverse(s) of a single fusiform cambial cell. Type of parenchyma, fusiform vs. strand, is determined from tangential sections. Fusiform parenchyma cells are relatively uncommon and generally occur in woods with storied structure and short axial elements.

133. Four (3–4) cells per parenchyma strand

134. Eight (5–8) cells per parenchyma strand

135. Over eight cells per parenchyma strand

136. Unlignified parenchyma

Unlignified parenchyma usually occurs in broad bands, and is restricted to a small number of taxa.

Rays

RAY WIDTH

Ray width should be determined on the tangential sections by counting the number of cells in the widest part of the rays, perpendicular to the ray axis. When rays are of two distinct sizes, record the width of the larger size class in the database. Exclusively uniseriate rays and rays > 10-seriate are the least common of the ray width features.

137. Rays exclusively uniseriate

138. Ray width 1 to 3 cells

139. Larger rays commonly 4- to 10-seriate

140. Larger rays commonly > 10-seriate

141. Rays with multiseriate portion(s) as wide as uniseriate portions

AGGREGATE RAYS

A number of individual rays so closely associated with one another that they appear macroscopically as a single large ray. The individual rays are separated by axial elements, e.g. many species of *Alnus* (Betulaceae), *Carpinus*, *Corylus* (Fagaceae), *Quercus* – evergreen species (Fagaceae).

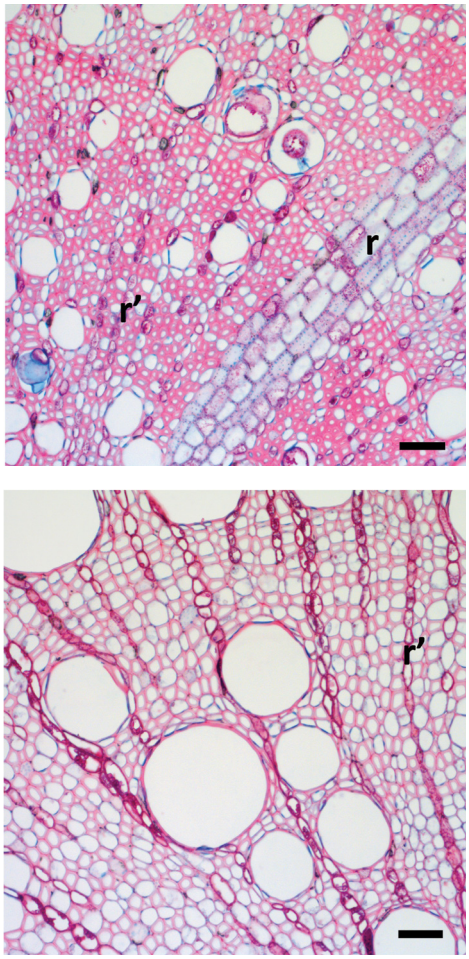


Fig. 2.1. 16: Wide rays (r) in root of F. sylvatica are accompanied by uniseriate rays (r'). In the upper figure, a uniseriate ray is shown in the root of C. sativa. In contrast to the stem, in the roots of C. sativa, rays are not exclusively uniseriate, but can be 1-3 cells wide (bottom). Bar = 50 µm.

142. Aggregate rays

RAY HEIGHT

Ray height is quite variable in some woods (particularly woods with markedly heterocellular rays), but quite uniform in others (particularly woods with storied structure).

143. Rays height > 1 mm

RAYS OF TWO DISTINCT SIZES

When viewed in tangential section, rays form two distinct populations by their width and usually also by their height. There are no limits for the size classes;

the smaller rays may be 1- or 2- or 3-seriate, the larger rays may be less than 5-seriate. Generally, to fit the feature definition, intermediate rays should not exist between the two populations or be quite rare. Thus, when very large rays occur with a few medium-sized and more numerous small rays (e.g. *Fagus*), this feature may still be applied. Aggregate rays *per se* should not be considered as a separate ray size class.

144. Rays of two distinct sizes

SHEATH CELLS

Ray cells that are located along the sides of broad rays (>3-seriate) as viewed in tangential section and are larger (generally taller than broad) than the central ray cells. Presence of sheath cells should be determined from tangential sections. Do not confuse sheath cells with tile cells, which are always found in the body of the ray as well as the edges and are visible in both tangential and radial sections.

145. Present

TILE CELLS

A special type of apparently empty upright (rarely square) ray cells occurring in intermediate horizontal series usually interspersed among the procumbent cells. Tile cells do not occur in uniseriate rays.

146. Present

PERFORATED RAY CELLS

Ray cells of the same dimensions or larger than the adjacent cells, but with perforations, which generally are on the side walls connecting two vessels on either side of the ray. The type of perforation in a perforated ray cell may be simple, scalariform, reticulate or foraminate, and does not necessarily coincide with the type of perforation plate occurring in the vessel elements of the same wood. Perforated ray cells have bordered pits similar to the intervessel pits. They can occur individually or in radial or tangential rows.

147. Present

DISJUNCTIVE RAY PARENCHYMA CELLS WALLS

Ray parenchyma cells partially disjoined but with contact maintained through tubular or complex wall processes. Axial parenchyma may also be disjunctive.

148. Present

RAYS PER MILLIMETRE

For stem wood, the feature 'rays 4-12 per mm' is more common than the features 'rays ≤ 4 per mm' or '≥ 12 per mm'.

149. ≤ 4/mm

150. 4–12/mm

151. ≥ 12/mm

Secretory elements and cambial variants

OIL AND MUCILAGE CELLS

An oil cell is a parenchymatous idioblast filled with oil; mostly, but not always, enlarged and rounded in outline, occasionally of considerable axial extension. A **mucilage cell** is a parenchymatous idioblast filled with mucilage; typically enlarged and rounded in outline; occasionally of considerable axial extension (resembling fibres). Both oil and mucilage cells are commonly associated with axial/and or ray parenchyma, but may also occur among fibres.

152. Oil and/or mucilage cells associated with ray parenchyma

153. Oil and/or mucilage cells associated with axial parenchyma

154. Oil and/or mucilage cells associated present among fibres

INTERCELLULAR CANALS

Intercellular canal = a tubular intercellular duct surrounded by an epithelium, generally containing secondary plant products such as resins, gums, etc., secreted by the epithelial cells. Intercellular canals may be orientated axially (axial/vertical intercellular canal) or radially (radial/horizontal intercellular canal, within a ray). It is possible to have a mixture of these features in one wood.

155. Axial canals in long tangential lines
More than five canals in a line.

156. Axial canals in short tangential lines
Two to five axial canals in a line.

157. Axial canals diffuse
Randomly distributed solitary canals.

158. Radial canals
Canals present in rays.

159. Intercellular canals of traumatic origin
Canals formed in response to injury, arranged in tangential bands, generally irregular in outline and closely spaced.

TUBES/TUBULES

Tubes/tubules = cells or series of cells of indeterminate length, extending radially or vertically (among fibres); two types can be distinguished, based on specific contents.

Laticifers = tubes containing latex, the latex may be colourless or light yellow to brown; laticifers may extend either radially or axially.

Tanniniferous tubes = tubes containing tannins, which are reddish-brown, in rays.

160. Laticifers or tanniniferous tubes

CAMBIAL VARIANTS

161. Included phloem, concentric
Phloem strands in tangential bands alternating with zones of xylem and/or conjunctive tissues.

162. Included phloem, diffuse
Scattered, isolated phloem strands. The phloem strands may be surrounded by parenchyma or imperforate tracheary elements.

163. Other cambial variants
Category for a variety of cambial variants including axes elliptical, flattened, and furrowed in cross-section; axes with lobed or furrowed xylem; fissured xylem; compound, divided corded and cleft xylem masses. The features for included phloem type are based on the appearance of the wood, and do not have developmental inferences – they are not defined on the basis of whether there is a single permanent cambium or successive cambia, or whether the tissue surrounding the phloem strands is xylem or conjunctive tissue.

Mineral inclusions

Generally, there is one crystal per cell or chamber. However, two or more similar-sized crystals, especially acicular and/or navicular, and cubic and/or rectangular crystals, may occur in the same cell or chamber. It is rare that there are two distinct sizes of crystals in the same cell or chamber.

PRISMATIC CRYSTALS

Solitary rhombohedral or octahedral crystals composed of calcium oxalate, which are birefringent under polarized light. Prismatic crystals are the most common type of crystal in wood. The relative abundance of prismatic crystals is variable.

164. Prismatic crystals present
- *164.1. Prismatic crystals in ray cells*
- *164.2. Prismatic crystals in parenchyma cells*
- *164.3. Prismatic crystals in fibres*

DRUSES

A compound crystal, more or less spherical in shape, in which many component crystals protrude from the surface, giving the whole structure a star-shaped appearance.

165. Druses present
- *165.1. Prismatic crystals in ray cells*
- *165.2. Prismatic crystals in parenchyma cells*
- *165.3. Prismatic crystals in fibres*

OTHER CRYSTAL TYPES

166. Raphides
A bundle of long needle-like crystals.

167. Acicular crystals
Small needle-like crystals, not occurring in bundles.

168. Styloids and/or elongate crystals
Styloids = large crystals at least four times as long as broad with pointed or square ends.

Elongate crystals = crystals two to four times as long as broad with pointed ends.

169. Crystals of other shapes (mostly small)
Includes all other shapes of crystals, e.g. cubic, spindle-shaped, navicular, pyramidal, tabular, twinned.

170. Crystal sand
A granular mass composed of very small crystals.

OTHER DIAGNOSTIC CRYSTAL FEATURES

171. More than one crystal of about the same size per cell or chamber

172. Two distinct sizes of crystals per cell or chamber

173. Crystals in enlarged cells

174. Crystals in tyloses

175. Cystoliths

Internal stalked outgrowths of the cell wall that project into the cell lumen and are composed of cellulose impregnated with calcium carbonate. They are irregular in shape and sometimes completely fill a cell.

BARK

Sieve elements

The conducting cell in the phloem tissue concerned with longitudinal transport of photosynthates throughout the plant body, classified into **gymnosperm sieve cells** and **angiosperm sieve-tube elements.**

SIEVE-TUBE ELEMENT

In the phloem of angiosperms, one of the series of cellular components of a sieve tube characterized by the presence of sieve plates with wide pores and lateral sieve areas with narrow pores. **Sieve tubes:** A series of sieve-tube elements arranged end-to-end and interconnected by sieve plates.

176. Sieve tube elements present (BROADLEAVED TREE SPECIES)

SIEVE CELL

The type of **sieve element** found in the phloem of gymnosperms with sieve areas of uniform structure on all walls; lack of sieve plates.

177. Sieve cells present (CONIFERS)

Companion cells and Strasburger cells

COMPANION CELLS

Companion cells are specialized parenchyma cells that are ontogenetically related to the sieve-tube element in angiosperms. In the conducting phloem the companion cells are turgid and, in transverse section, typically appear in the corners of the sieve-tube elements. The companion cells in nonconducting phloem typically collapse when their associated sieve-tube elements cease to function and therefore are difficult to discern.

There is an integration between companion cells and parenchyma cells, and their morphological similarity may make it difficult to distinguish between them (Evert 2006).

Sclerification of companion cells in old phloem has been reported in *Carpodetus* and in *Tilia*.

178. Companion cells present (BROADLEAVED TREE SPECIES)

STRASBURGER CELLS

Strasburger cells are the counterparts of the companion cells in gymnosperms, and are distinguished from other parenchymatous elements of the phloem by their symplastic connections with the sieve cells. They frequently have more densely staining protoplasts than others parenchymatous elements of the phloem. Unlike companion cells, Strasburger cells are not ontogenetically related to their associated sieve cell (Trockenbrodt 1990), although rare exceptions occur (Evert 2006). Like companion cells, Strasburger cells die when their associated sieve cells die. Presumably, the Strasburger cell plays a role similar to that of the companion cell: maintenance of its associated (enucleate) sieve element. Depending on the taxon, Strasburger cells may be found in the rays, the axial system, or in both rays and axial system.

179. Strasburger cells present (CONIFERS)

Axial parenchyma

Parenchyma cells derived from the fusiform initials of the cambium in the secondary phloem, orientated with their longest diameter parallel with the main axis of stem or root; as opposed to ray parenchyma cells (adapted from Evert 2006). Parenchyma cells are also characteristic for retaining the protoplast at maturity, being more or less isodiametric, capable of dividing and growing.

TYPES (AS SEEN IN TRANSVERSE SECTION)

180. Diffuse

Axial parenchyma cells sparsely distributed among other cells of the secondary phloem.

181. In interrupted tangential bands

Axial parenchyma cells distributed in interrupted tangential bands alternating with other cells of the secondary phloem.

182. In continuous tangential bands

Axial parenchyma cells distributed in continuous tangential bands alternating with other cells of the secondary phloem.

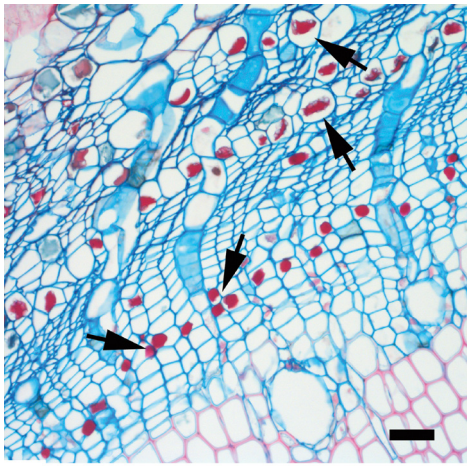


Fig. 2.1. 17: Axial parenchyma (arrows) in interrupted tangential bands in secondary phloem of root of P. abies. In nonconducting phloem axial parenchyma cells become enlarged. Bar = 50 µm.

183. In radial rows

Axial parenchyma cells forming radial rows of 3 or more cells.

184. In clusters

Axial parenchyma in groups of more than 3 cells, having both radial and tangential contact.

185. Sievecentric

Axial parenchyma cells distributed always around the sieve elements, typically found in phloems where the fibres are very abundant, forming a ground tissue where the other cells are embedded.

AXIAL PARENCHYMA MORPHOLOGICAL CHANGES

All changes undergone by the phloem axial parenchyma from the conducting to the non-conducting phloem.

186. Cell enlargement

Axial parenchyma cells become enlarged/swallowed.

187. Collapse

Axial parenchyma cells collapse.

188. Sclerification

= the thickening and lignification of the walls of plant cells and the subsequent dying off of the protoplasts. Sclerification increases the solidity of the plant's organs, as well as their resistance to disease agents. Parenchyma cells are most often subjected to sclerification and turned into sclereids; however, epidermal cells are often sclerified as well. Axial parenchyma cells sclerify.

Phloem rays

The **phloem rays** are continuous with the xylem rays, since both arise from common ray cambial cells. Near the cambium the phloem and xylem rays of common origin are usually identical in height and width. The older part of the phloem rays, which is displaced outward by the expansion of the stem, may increase in width (**ray dilatation**), sometimes to a considerable extent (e.g. Malvaceae).

Phloem ray width, the presence of rays of two distinct sizes and ray height of more than 1 millimetre can be classified following the ray classification in xylem proposed by the IAWA list of microscopic features for hardwood identification. Ray width must be determined on the tangential section by counting the number of cells in the widest part of the ray. The phloem rays may be composed of one cell type (homocellular), or they may contain procumbent, square, and upright cells (heterocellular). Rays in conifer phloem may contain Strasburger cells, if these cells are present in the species. In non-conducting phloem ray cells sclerification occurs in some species. Sclereids in rays may or may not form a continuous band with axial sclereids.

RAY WIDTH IN CELL NUMBER (TO BE ANALYZED IN THE CONDUCTING PHLOEM)

189. Rays exclusively uniseriate

190. Ray width 1 to 3

191. Larger rays commonly 4-to-10-seriate

192. Larger rays commonly > 10-seriate

AGGREGATE RAYS

– Similar to IAWA Hardwood List (IAWA Committee 1989)

193. Aggregate rays present

COURSE OF RAYS IN THE NONCONDUCTING PHLOEM

194. Straight

195. Undulated or wavy

Sclerenchyma

Sclerenchyma cell = Cell variable in form and size and having more or less thick secondary walls that are often lignified. Belongs to the category of supporting cells and may or may not be devoid of protoplast at maturity (from Evert 2006).

TYPES OF SCLERENCHYMA CELLS

Fibre = An axially oriented elongated sclerenchyma cell developing either from procambium **(primary phloem fibres)**, or from fusiform initials of vascular cambium **(secondary phloem fibres)**, may or may not undergo apical intrusive growth during its development. Intrusive elongation of fibres can be recognized by tapered tips, and by their longer length in comparison with sieve tube elements and axial parenchyma strands. In secondary phloem true phloem fibres reach maturity in the conducting phloem; typically chambered crystalliferous cells occur along the margins of fibre bands.

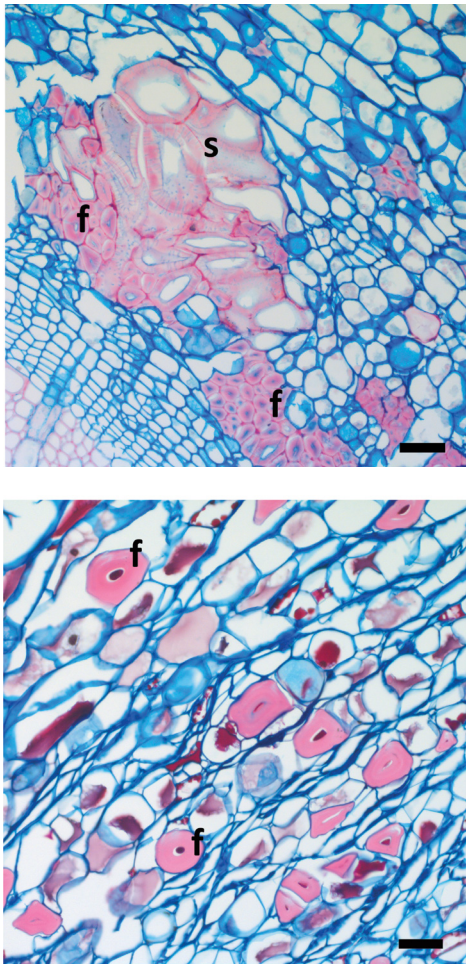


Fig. 2.1. 18: Sclerenchyma in secondary phloem of roots: clusters of sclereids (s) and fibres (f) in secondary phloem of F. excelsior (up) and diffuse arrangement of single fibres in secondary phloem of L. decidua (bottom). Bar = 50 µm.

Sclerotic fibre = same as fibre, but with polylamellate wall.

Fibre-sclereid = A sclereid with characteristics intermediate between those of a fibre and sclereid. Fibre-sclereids originate from axial parenchyma cells in the non-conducting phloem. These cells undergo intrusive growth, so at maturity they may be indistinguishable from true phloem fibres.

Sclereid = A sclerenchyma cell of any orientation and origin, varied in form, but typically not much elongated, and showing no traits of apical intrusive growth. Sclereids develop mainly in the non-conducting phloem by modification of already differentiated axial or ray parenchyma cells.

ABUNDANCE OF FIBRES IN THE CONDUCTING SECONDARY PHLOEM

196. Fibres absent

197. Phloem scarcely fibrous

Fibres present in low abundance.

198. Phloem semi-fibrous

Fibre bands alternating regularly with other axial cells of the phloem.

199. Phloem fibrous

The sclerenchyma is the main background tissue where all other cells of the phloem are found embedded.

FIBRE SHAPE IN THE CONDUCTING SECONDARY PHLOEM

200. Square

201. Rectangular

202. Radially elongated

FIBRE BANDS IN THE CONDUCTING SECONDARY PHLOEM

203. Thin fibre bands (1-2)

204. Medium thick fibre bands (3-5)

205. Thick fibre bands (> 5)

FIBRE LIGNIFICATION IN THE CONDUCTING SECONDARY PHLOEM

206. Lignified

207. Non-lignified

FIBRE PITTING IN THE CONDUCTING SECONDARY PHLOEM

208. Simple to minute bordered

209. Distinctly bordered

ARRANGEMENT OF THE SCLERENCHYMA IN THE SECONDARY PHLOEM

210. Diffuse

Sclerenchyma cells scattered among the other cells of the phloem.

211. Diffuse-in-aggregates

Forming scattered aggregates of loosely arranged elements.

212. Discontinuous tangential bands

Sclerenchyma cells present in tangential bands, alternating with other cells of the secondary phloem. This arrangement is most common in fibres, but may incorporate sclereids or fibre sclereids.

213. Continuous concentric rings

Sclerenchyma cells forming concentric rings on the organ circumference. Only for narrow stems or forming concentric rings because they join with highly lignified ray cells in radial pattern.

214. Radial rows

Sclerenchyma cells in radial disposition.

215. Clusters

Sclerenchyma cells present in clusters intermingling other cells of the secondary phloem.

LAYERING OF SCLERENCHYMA CELL WALLS

216. No layering

Cell walls with even or gradual pattern showing no layers that can be distinguished by light microscopy.

217. Polylamellate cell walls

Cell walls show two to several layers with distinctly marked boundaries.

218. Gelatinous layer (G-layer)

Innermost secondary wall layer that can be distinguished from the outer secondary wall layer(s) by its high cellulose content and lack of lignin.

PITS IN THE SCLERENCHYMA PIT WALLS

219. No pits

220. Pits with unbranched canals

221. Pits with branched canals

THICKNESS OF SCLERENCHYMA CELL WALLS

222. Very thin-walled

Lumina of sclerenchyma cells 3 or more times wider than double wall thickeness.

223. Thin- to thick-walled

Lumina of sclerenchyma cells less than 3 times double wall thickness, and distinctly open.

224. Very thick-walled

Lumina of sclerenchyma cells almost completely closed.

LIVING PROTOPLAST IN SCLERENCHYMA CELLS

225. Absent

226. Present

Living protoplast persists in the sclerenchyma cell lumina (distinguished by the occurrence of cell nuclei, positive staining by Alcian Blue, etc.).

SEPTATE SCLERENCHYMA CELLS

227. Septate

Sclerenchyma cells with thin unpitted walls that do not extend to the compound middle lamella between adjacent sclerenchyma cells.

228. Nonseptate

Sclerenchyma cells without septa.

SCLERIFICATION OF NONCONDUCTING SECONDARY PHLOEM

229. Absent

230. Present

Secretory structures

231. Secretory cells

=Idioblastic (more rarely groups of parenchymatous cells accumulating secretory substances such as oil, mucilage, tannin, myrosin or proteins (not including epithelial cells, which secrete resins or gums into an intercellular duct or cavity). The general term secretory cell is recommended in all cases when their contents have not been tested histochemically.

232. Oil cells

Secretory cell filled with oil, usually idioblastic, mostly enlarged and rounded in outline, often axially extended. The oil drops, completely filling the lumen at maturity, are commonly attached to wall protruberances, often in the shape of a cupule.

233. Mucilage cells

Secretory cells filled with mucilage, usually idioblastic, mostly enlarged and rounded in outline, often axially extended. Mucilage-containing cells often include raphide crystals.

234. Tannin cells

Parenchyma cells filled with tannin, usually idioblastic. Tannins are a broad category of phenolic substances that are usually brown in colour and stain dark brown with ferric chloride and potassium dichromate. When phloem or cortex cells mature or senesce they may accumulate phenolic substances resulting in dark colouring of the contents throughout the parenchyma tissue. In such cases the term tannin cells is not applied.

Tubes/tubules

Very strongly elongated secretory cells or cell series, extending vertically or radially, containing latex (laticifers) or tannin (tanniniferous tubules).

235. Laticifers

Cells or series of connected cells filled with latex – a watery suspension or emulsion of particles of diverse chemical composition. A single-celled laticifer can be qualified, on the basis of origin, as a simple laticifer, and the structure derived from union of cells as a compound laticifer.

236. Non-articulated laticifers (or latex cells)

Unicellular, multinucleate laticifers that may extend throughout the plant body, and originate from initial cells in the embryo.

237. Articulated laticifers (or latex vessels)

Single or branched and anastomosing longitudinal series of laticiferous cells. The end walls of these cells may persist or become porous and disappear completely.

238. Tanniniferous tubes/tubules

Tubes or tubules containing tannins.

SECRETORY INTERCELLULAR SPACES (DUCTS/CANALS)

Secretory cavities and ducts (canals) differ from secretory cells in that they secrete substances (resins or gums) into intercellular spaces. They are glands consisting of relatively large **intercellular spaces** commonly lined by specialized secretory (epithelial) cells. Axial parenchyma may also surround canals. Sheath of parenchyma around the canal may be of various forms: aliform, aliform confluent and in concentric rings. Secretory cavities are short secretory spaces and secretory ducts are long secretory spaces. The development of secretory intercellular spaces may be lysigenous (originating after dissolution of cells), schizogenous (originating from an expanding intercellular space by further separation along the compound middle lamella) or a mixture of both processes (schizo-lysigenous). At maturity, when an epithelium has differentiated along the cavity, it is often impossible to deduce the precise development, and we therefore refrain from categorizing ducts according to their ontogeny.

239. Epithelium

A layer of secretory cells lining an intercellular cavity or duct.

240. Resin ducts

Axial or radial intercellular canals containing resin – a lipophilic substance of great chemical diversity.

241. Gum ducts

Axial or radial intercellular canals containing gums – a hydrophilic material of great chemical diversity.

MUCILAGE CAVITIES OR CANALS

Cavities (isodiametric structures) or ducts/canals (elongated structures) of varying size, containing mucilage or gum (mainly polysaccharides).

242. Mucilage cavities or canals

Crystals

A body that is formed by the solidification of a chemical element, a compound, or a mixture and has a regularly repeating internal arrangement of its atoms and often external plane faces. Often, crystals in plants are made of calcium oxalate and are birefringent under polarized light. All crystals described here are visible under polarized light or DIC, but brightness can vary.

CRYSTAL SHAPE

243. Prismatic crystals

Prismatic crystals (synonym rhomboidal crystal) = prisms of various shapes, mainly made of calcium oxalate (prismatic crystals made of calcium sulphate, magnesium oxalate and silica also exist).

244. Druses or druse crystals

IAWA Committee 1989 = Compound crystal, more or less spherical in shape, in which the many component crystals protrude from the surface giving the whole structure a star-shaped appearance (synonym cluster crystal). Druses are composed of calcium oxalate.

245. Raphides:

Bundles of needle-shaped (acicular) crystals, grouped in bundles.

246. Acicular crystals

Small needle-like crystals, not occurring in bundles (IAWA Committee 1989).

247. Elongated crystals

Crystals two to four times as long as broad with pointed ends (IAWA Committee 1989).

248. Crystal sand

A granular mass composed of very small crystals (IAWA Committee 1989). Synonym: microcrystals.

249. Navicular crystals

Boat-shaped crystals.

LOCATION

Crystals present in:

250. Epidermis (epidermal cells)

251. Pericycle (pericyclic collenchyma cells, pericyclic parenchyma cells, sclereids)

252. Periderm (phelloderm cells, phellem cells)

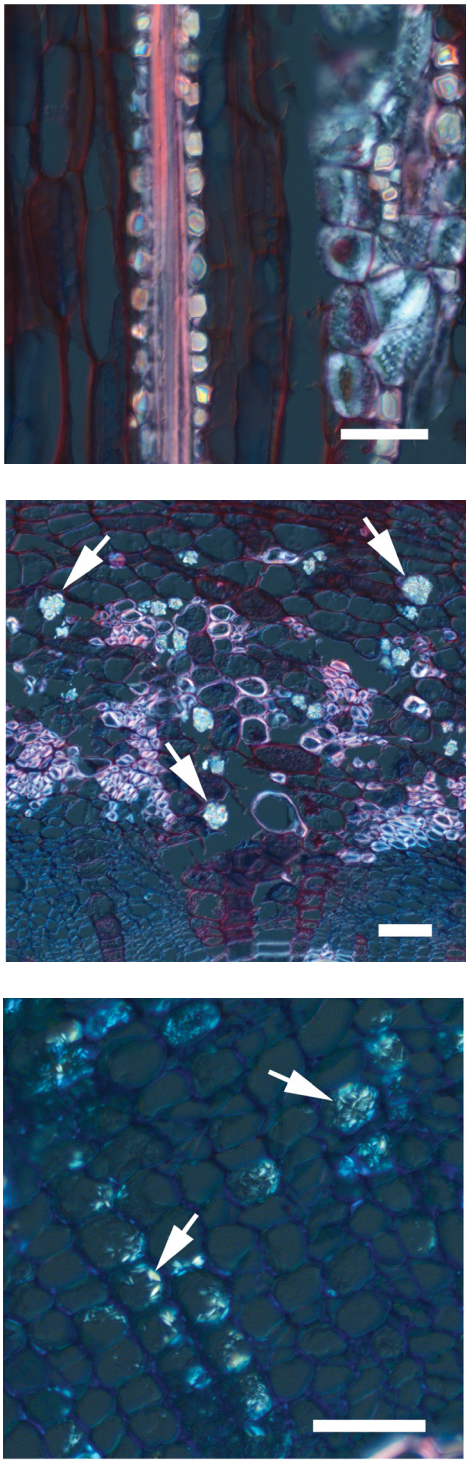


Fig. 2.1. 19: Crystals in secondary phloem in roots of Q. petraea – prismatic, located in chamber cells (up), P. avium – druses (in the middle) and F. excelsior – navicular crystals. Bar = 50 µm.

253. Secondary phloem (axial parenchyma cells, fibres, ray cells)

Dilatation tissue

Dilatation is growth of parenchyma cells by tangential extension with or without subsequent anticlinal divisions. The dilatation occurs in the non-conductive secondary phloem, mainly in the ray cells but also in the axial parenchyma, and in the cortex if present. Dilatation growth is a process that increases the circumference of the bark in stem and root (adapted from Trockenbrodt 1990 and Evert 2006).

Both axial and radial parenchyma undergo sclerification in the non-conducting phloem. Sclerification of non-conducting phloem is almost always associated with dilatation growth.

254. Absent or scanty

Absent or extremely rare.

255. Present

DILATATION DISTRIBUTION

Localization of the differentiation of the dilatation:

256. Only in the rays

The cells can extend tangentially or, more commonly, divide anticlinally. Sometimes these divisions are restricted to the median region of the rays forming a wedge shape, and sometimes restricted to its margins. In some species, such as *Tilia americana* (Malvaceae) and *Cordia trichotoma* (Boraginaceae), these median ray cells are similar to meristematic cells, with very thin primary walls, that divide anticlinally. These groups of cells are called "dilatation meristem". Where **dilatated rays** occur, not all rays are dilatated. In some genera, all the rays remain similar as they were originated by the cambium.

257. Only in axial parenchyma

Less common than in rays. The cells enlarge and expand, as in conifers, or subsequently also divide and proliferate forming wedges, similar to the ray wedges.

258. Axial parenchyma and rays

The participation of dilatation in both systems of cells together is rare.

259. Also in the cortex

Sometimes the primary tissue stays on the organ and undergoes the dilatation process; in this case the name secondary cortex is used.

DILATATION ARRANGEMENT

Arrangement of the dilatation cells and in which type of cells it occurs:

260. Irregular

Normally axial parenchyma, but also radial parenchyma, in small groups of cells.

261. Continuous lines or bands

Axial parenchyma, alternating with the other secondary phloem cells. Line: up to three cells wide. Band: more than three cells wide.

262. Dilatated, wedge-shaped

Normally radial, but also axial parenchyma.

263. Dilatated cortex bands or lines

Expanded and/or divided cortex cells.

DILATATION MERISTEM

Well-defined meristem located on the median region of the ray with very thin primary wall cells, which divide anticlinally.

264. Absent

265. Present

Periderm

FIRST FORMED PERIDERM

Periderm: Secondary protective tissue that replaces the epidermis in stems and roots, rarely in other organs. Consists of **phellem (cork)**, **phellogen (cork cambium)**, and **phelloderm** (Evert 2006).

ORIGIN OF THE PERIDERM

Periderm is formed by phellogen. The phellogen of the first formed periderm may be initiated at different depths outside the vascular cambium: subepidermal layer, epidermal cells, second or third cortical layer, near vascular region, pericycle or directly within the phloem. For more information on the origin, see Evert (2006).

In most roots the first periderm originates deep in the axis, usually in the pericycle, but it may appear near the surface as, for example, in some trees and perennial herbaceous plants in which the root cortex serves for food storage. The first phellogen is initiated either uniformly around the circumference of the axis or in localized areas and becomes continuous by a lateral spread of meristematic activity.

In older trees the last periderm separates the dead outer bark from the living inner bark, which consists of secondary phloem (Esau 1960). The arrangement of periderm layers may vary with the species and/or dif-

ferent parts of the stem, when seen in cross-section. Thickness of periderm is variable within and among tree species.

COURSE

266. Straight

267. Undulated

268. Ramified

ARRANGEMENT OF PERIDERM

(after Roth 1981)

269. Stratified tangentially

270. Stratified radially

271. With U-thickenings

272. With reverse U-thickenings

273. With regular stone cells

CORK AERENCHYMA

Parenchyma tissue containing particularly large intercellular spaces. It may occur in some trees of tropical humid forests, in which intercellular spaces arise between radial files of phellem cells, forming cork aerenchyma (Roth 1981). Flooding may result in increased phellogen activity and the production of loosely arranged radial files of phellem cells. In flooded *Ulmus americana* stems, the system of intercellular spaces of the phellem was continuous with that of the cortex via intercellular spaces in the phellogen (Angeles et al. 1986).

274. Absent

275. Present

PHELLEM

276. Thick-walled cells

277. Thin-walled cells

GROWTH INCREMENTS IN PHELLEM

In *Pseudotsuga menziesii*, growth increments are discernible because of the presence of denser and darker appearing zones of phellem cells at the end of the increments, resulting from severe folding and crushing of their radial walls. In *Picea glauca*, each growth increment, which consists of bands of thick- and thin-walled cells, ends with one or more layers of crystal-containing cells. Cork used commercially as bottle cork comes from the cork oak, *Quercus suber*, which is native to the Mediterranean region. Consisting of thin-walled cells with air-filled lumina, it is highly impervious to water and gases and resistant to oil. It is light in weight and has thermal insulating qualities.

278. Indistinguishable

279. Distinguishable

PHELLEM CELLS SHAPE

These are usually compactly arranged. Phellem cells are nonliving at maturity. They are then filled with air, fluid, or solid contents; some are colourless and others pigmented. Phellem cells may have either thick or thin walls. In thick-walled cells a lignified cellulose layer occurs on the inner surface of the suberin lamella, which thus is embedded between two cellulose layers. Phellem cells may have evenly or unevenly thickened walls. Some have U-shaped wall thickenings, with either the inner or outer tangential wall together with adjoining parts of the radial walls being thickened. In many *Pinus* species the thick-walled cells develop into heavily lignified stone cells. The distinctly lamellate walls contain numerous ramiform (branched simple) pits and possess many irregular projections along their margins. In tangential sections these sclereids resemble irregularly rounded, interlocked cogwheels (Howard 1971). Phellem cell walls may be brown or yellow, or they may remain colourless. The suberized cells are characterized by the presence of Casparian strips in their anticlinal walls. In some plants the phellem consists of thin-walled cells and thick-walled cells, often arranged in alternating tangential bands of one or more cell layers (species of *Pinus*, *Picea*, *Larix*, *Betula populifolia*, *Robinia pseudoacacia*). There are many examples of layered phellem among tropical trees (Roth 1981). In some, the layers may simply be distinguished by their cell content.

280. Prismatic

Phellem cells approximately prismatic in shape.

281. Irregular

Phellem cells may be rather irregular in the tangential plane.

282. Elongated

Phellem cells may be elongated vertically, radially, or tangentially.

PHELLEM STRATIFICATION

284. Absent

285. Present
285.1. Stratified tangentially
285.2. Stratified radially

PHELLODERM

Phelloderm can have one to three or more cell layers. The number of phelloderm cells in the radial file may change somewhat as the stem ages. In *Tilia*, for example, the phelloderm may consist of one cell layer in the first year, two in the second, and three or four later. In some gymnosperms the phelloderm can be very wide (IAWA Committee 2016 - in preparation, Roth 1981).

286. Absent

287. Present

PHELLODERM WIDTHS

288. Thin 1-4 cells in radial file

289. Thick > 4 cells

PHELLODERM SHAPE OF CELLS

The phelloderm is commonly depicted as consisting of cells resembling cortical or phloem parenchyma cells and distinguishable from the latter only by their position in the same radial files as the phellem cells. In fact, cells similar in appearance to those of the phellem may be found in the phelloderm, although those of the phelloderm do not have suberized walls. Unlike the typical compact arrangement of the phellem cells, the phelloderm cells have numerous intercellular spaces among them.

PHELLODERM SCLERIFICATION

290. Absent

291. Present

Many conifers have phelloderms consisting of both parenchymatous and sclerenchymatous elements. Sclerification of all or part of the phelloderm is common in barks of tropical trees. The sclereids may have evenly thickened walls or U-shaped wall thickenings, and layers of thin-walled unlignified cells may alternate with layers of lignified sclerenchyma cells.

LENTICELS

A limited part of the periderm in which the phellogen is more active than elsewhere and produces a tissue that, in contrast to the phellem, has numerous intercellular spaces. Because of this relatively open arrangement of cells, the lenticels are regarded as structures permitting the entry of air though the periderm (IAWA Committee 2016 - in preparation). Lenticels are usual components of periderm of stems and roots (Groh et al. 2002).

292. Absent

293. Present

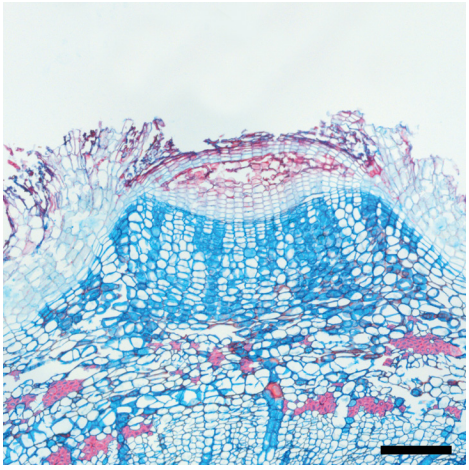


Fig. 2.1. 20: Lenticel in root of F. excelsior as seen in cross-section. Bar = 200 µm.

LENTICELS DISTRIBUTION

294. Completely irregular

No apparent order at all.

295. Disposed in vertical rows

296. Disposed in tangential rows

297. Stratified lenticels

Common in tropical trees (Roth 1981).

LENTICELS SHAPE

298. Elliptic

299. Roundish or circular

300. Rhomboid

301. Tangentially elongated

302. Vertically elongated (resulting linear)

(Roth 1981).

PRIMARY TISSUES

The root in its primary stage consists of three tissue systems: epidermis, the cortex and the primary vascular tissues. In most roots, primary vascular tissues form a solid cylinder, but many roots have a pith or pith-like region in the centre.

Epidermis (Rhizodermis)

The root epidermis consists of closely packed elongated cells with thin walls that lack a cuticle. In young roots epidermis is specialized as an absorbing tissue. The uptake of water and minerals is facilitated by **root hairs,** which greatly increase the absorptive surface of the root (Evert & Eichhorn 2013). In woody plants with ectomycorrhiza, fungal hyphae penetrate between the epidermal cells and then ramify in the intercellular spaces of the outer part of the cortex, forming a Hartig net. Roots with ectomycorrhiza lack root hairs. In plants with endomycorrhiza, fungal hyphae penetrate into the cells of the epidermis or between the cells, and grow into the cortical cells and between them, forming arbuscules (tree-like structures) and vesicles (Mauseth 1988).

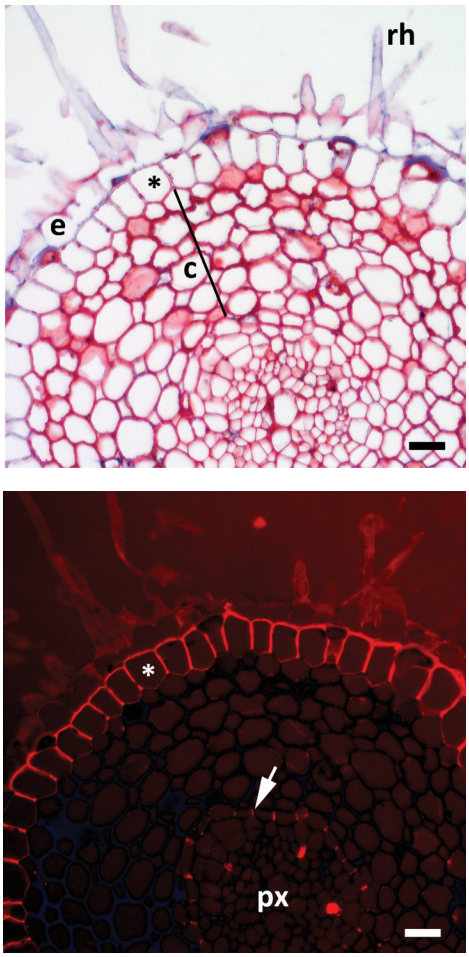


*Fig. 2.1. 21: Primary root of F. excelsior – as seen in bright-field and in fluorescence, where suberized and lignified cell walls are visible (bottom). Rh: root hairs, e: epidermis, *: exodermis, c: cortex, arrow: endodermis with Casparian strips, px: primary xylem. Bar = 20 µm.*

Cortex

Cortex occupies the greatest area of the primary body of most roots. Gymnosperm and angiosperm roots that undergo secondary growth shed their cortex, together with its innermost layer, the endodermis, early. In such roots, the cortical cells remain parenchymatous. Cortical tissue contains numerous intercellular spaces essential for aeration of the root cells. In many aquatic and wetland plants, the intercellular spaces become large and form aerenchyma (=parenchyma tissue with large and abundant intercellular spaces) (Evert & Eichhorn 2013).

The cortex is the outermost layer of cells, and it can be detected in young bark. Unlike the phloem, the cortex does not contain rays. It is composed mostly of parenchyma cells and ground tissue cells, including collenchyma. Lignification can occur in all parenchyma cell walls or in part of them. Parenchyma cell size can be very large or small in all the cells, or large and small cells can be mixed as seen in cross-section. The shape of parenchyma cells range from round to oval. Ducts, laticifers or aerenchyma occur in some species. Fibres and sclereids are typical of some species; arrangement description (single cells, small groups, bands, belt) seems to have a taxonomical significance.

In herbaceous plants, no secondary vascular tissues and periderm are developed, and the cortex is retained for the life of the plant. In roots of woody plants, as secondary phloem and xylem are produced, the primary phloem is compressed and obliterated. Furthermore, a phellogen differentiates within the outer pericyclic parenchyma shortly after the beginning of cambial activity. Cut off from a source of water and photosynthate, the cortex and epidermis die and slough off (Beck 2010).

Unlike the rest of the cortex, the innermost layer is compactly arranged and lacks air spaces. This layer, the **endodermis**, is characterized by the presence

of **Casparian strips** in its anticlinal walls (the radial and transverse walls, which are perpendicular to the surface of the root). A Casparian strip is a bandlike region of primary wall containing suberin and lignin. It is found in anticlinal walls of endodermal and exodermal cells. Some of the endodermal cells may remain thin-walled and retain their Casparian strips for a prolonged period. Such cells are called **passage cells**. In some species these endodermal cells remain as passage cells, whereas in others they eventually become suberized and deposit additional cellulose. The roots of most angiosperms also have **exodermis**, which develops from the outermost layer of layers of cortex cells.

Primary vascular tissues

The vascular tissues of the root consist of primary vascular tissues and one or more layers of nonvascular cells that constitute **the pericycle**, which completely surrounds the vascular tissues.

Pericycle = a tissue characteristic of roots that is bounded externally by the endodermis and internally by the phloem. The pericycle is considered part of the vascular cylinder because, like the vascular tissues, it originates from the procambium. In the young root, the pericycle is composed of parenchyma cells with primary walls, but as the root ages, the cells of the pericycle may develop secondary walls.

In most seed plants, lateral roots arise in the pericycle. In plants undergoing secondary growth, the pericycle contributes to the vascular cambium opposite the protoxylem and generally gives rise to the first cork cambium. Pericycle often proliferates (= give rise to more pericycle). Divisions of pericycle cells cause an increase in the number of layers of pericycle cells in the radial direction. The outer part of proliferated pericycle gives rise to phellogen (cork cambium). The remaining cells of the proliferated pericycle may form tissue that resembles a cortex (Evert & Eichhorn 2013).

The centre of the vascular cylinder of most roots is occupied by a solid core of primary xylem, from which ridge-like projections extend toward the pericycle. Nestled between the ridges of xylem are strands of primary phloem. Lacking a pith, the vascular cylinder in such roots is a **protostele**, a solid cylinder of vascular tissue.

The number of ridges of primary xylem differs from species to species, sometimes even varying along the axis of a given root:

303. Diarch: Two ridges are present.

304. Triarch: Three ridges are present.

305. Tetrarch: Four ridges are present.

306. Pentarch: Five ridges are present.

307. Polyarch: Many ridges are present.

RESIN DUCT IN THE PRIMARY XYLEM

308. Present

309. Absent

POSITION OF RESIN DUCT IN THE PRIMARY XYLEM

310. Central

311. Peripheral

NUMBER OF RESIN DUCTS IN THE PRIMARY XYLEM

312. No.: 1

313. No.: 2

314. No.: 3

315. No.: 4

316. More than 4

SIZE OF CELLS OF THE PRIMARY XYLEM

317. Of one size

318. Of various size

PRIMARY XYLEM

Primary xylem is differentiated from the procambium in the primary plant body, and is spatially associated with the primary phloem in the vascular system. The first (proto-) primary xylem elements to mature in roots are located next to the pericycle, and the tips of the ridges are commonly referred to as **protoxylem** poles. Thus, the protoxylem is the first part of the primary xylem, which matures during elongation of the plant part in which it is found. The **metaxylem** parts (the part of the primary xylem that differentiates after the protoxylem and before the secondary xylem) occupy the inner portions of the ridges and the cente of the vascular cylinder. The metaxylem reaches maturity after the portion of the plant part in which it is located had finished elongating. The roots of some angiosperms have a pith or pith-like region, which some

botanists regards as part of the vascular cylinder because they consider it to be of procambial origin (Evert & Eichhorn 2013).

PRIMARY PHLOEM

Primary phloem is differentiated from the procambium in the primary plant body, and is spatially associated with the primary xylem in the vascular system. It is composed of sieve elements, parenchyma cells, and fibres. The primary phloem may be divided into **protophloem** and **metaphloem**. Axial and ray (radial) systems are not characteristic of primary phloem.
Protophloem is the first formed part of the primary phloem. It matures in plant parts that are still undergoing extension growth. Consequently, its sieve elements are stretched, soon become non-functional, and eventually completely obliterated. In many eudicots elongated fibre primordia occur among the sieve elements. While the sieve elements cease to function and undergo obliteration, the fibre primordia increase in length, develop secondary walls and mature as fibres called primary phloem fibres, or protophloem fibres.

Metaphloem differentiates after the protophloem. In plants without secondary growth it constitutes the only conducting phloem in adult plant parts. In woody and herbaceous species having cambial secondary growth, the metaphloem sieve elements become inactive after the secondary phloem sieve elements mature. In such plants the metaphloem sieve elements may be partly crushed or completely obliterated.

Perivasular fibres are fibres located on the periphery of the vascular cylinder inside the innermost cortical layer (endodermis) and outside the phloem. Perivascular fibres are commonly referred as pericyclic fibres. The designation pericyclic is often used with reference to primary phloem fibres, which have their origin from the procambium (Blyth 1958). Inasmuch as a developmental study often would be required to distinguish between true perivascular/pericyclic fibres and primary phloem fibres, systematic anatomists long have designated both fibre groups perycicliclic for purely descriptive purposes. Esau (1979) noted that since the structure of the peripheral part of the vascular region is of taxonomic value, a simple topographic designation for the region should be available. She suggested continued use of the familiar “pericycle” and “pericyclic” for that purpose.

PERICYCLIC FIBRES

319. Present

320. Absent

2.2 Coded description of anatomical structure of the selected tree species

Numbers of general anatomical features for given tree species are written with regular font, numbers of anatomical features characteristic for species are in bold, and numbers of rarely present anatomical features are in parentheses.

CONIFERS

Abies alba Mill.

1, 3, 5, (6), 7, 8, **12**, **15**, (16), **18**, **22**, 25, 26, (27), **28.1.**, (35), 36, (37), 38, 40, 43, **50, 52**, 53, 60, 62, 64, 65, 177, 179, 180, 181, 186, 188, **189**, 195, **196**, 210, 211, 230, **233**, 243, 251, 253, 255, 256, 264, 277, 278, 287, 288, 303, **308, 310**

Pinus sylvestris L.

1, 4, (5), 6, 7, 9, 12, 15, **18.1.**, 22, 23, 25, 28, 29, **31**, 35, 37, **39**, **49, 51**, 53, **56,** 57, 58, 177, 179, 180, 181, 186, 189, 190, 195, **196**, 254, **255**, 276, 277, 287, 288, **304, 308,** 311, (313), **314**, (315)

Picea abies (L.) Karsten

1, 4, 5, 6, 7, 8, 9, **12**, **15**, 17, 18, 18.1., 22, 23, 26, 28, 29, **33**, **36, 38**, 40, 41, **49, 51**, 53, **55, 56**, 58, 59, 177, 179, 180, 181, 186, 188, 189, 190, 195, **196**, 210, 215, **240, 255,** 264, 276, 277, 287, 288, **303, 308,** 311, **313**

Larix decidua Mill.

1, 3, (4), 5, 6, 7, 8, 9, **12**, **15**, 17, 18, 18.1., 22, 23, 26, 28, 29, **33**, **36, 38**, 40, 41, **49, 51**, 53, **55, 56**, 58, 59, 177, 179, 180, 181, 186, 188, 189, 190, 195, **196,** 210, **240,** 243, 251, 253, **255,** 264, 276, 277, 287, 288, **303, 308,** 311, **313**

BROADLEAVED SPECIES

Acer pseudoplatanus L.

2, 68, 72, **77**, 78, **80**, **88**, 96, **101**, 102, 103, 111, 116, **121, 138**, 176, 178, 180, 186, **190,** 195, **212**, **230**, **235**, **243**, 251, (253), **255**, 277, 278, 287, 288, **(293)**, **303**, **318**

Carpinus betulus L.

2, 68, 72, **77**, 78, **80, (80.1.)**, **88**, 96, **(101)**, **102**, (107), (107.1), 111, **120, 130, 138**, (143), **164, 164.1.**, 176, 178, 180, **190**, 195, **206**, **211**, 212, **243, 244**, 251 253, **255**, 256, **277**, 278, 287, 288, **307, 318**

Castanea sativa Mill.

2, **69, 72**, **76**, **80, 88, 91, 97, 103, (107)**, **(107.1),** 112, **116, 120**, 138, 176, 178, 180, 186, 190, 195, 198, 204, 206, **211, 212**, **243, 244**, 251, 253, 255, 256, 264, 277, 278, 287, 288, **307**

Fagus sylvatica L.

2, 68, (69), 72, **73**, **80, 80.1.**, **86**, **97**, 102, **(107)**, **(107.1),** 112**,** 116, 119, 120, 129, **138, 140, 143**, **144**, 145, **164, 164.1**, 176, 178, 180, 186, **188**, **190, 192**, **212**, **230, 243, 244**, 251, 253, 255, 264, 277, 278, 287, 288, **307**

Fraxinus excelsior L.

2, **68**, **77**, **80**, **90**, 96, **102**, 111, **121, 130**, **138**, 176, 178, 180, 186, **188**, **190**, **197**, 204, **212**, **249**, 251, 253, 255, 264, **277**, 278, 287, 288, **307**

Prunus avium L.

2, 68, 72, 76, 78, **80, 88, 90**, 96, 102/103, **(107), (107.2)**, 112, **119, 138, 139**, **143**, 176, 178, 180, **188**, **190, 191**, 195, 211, **214, 230, 244**, 251, 253, 255, 264, 277, 278, 287, 288, **(293)**, **307**

Populus nigra L.

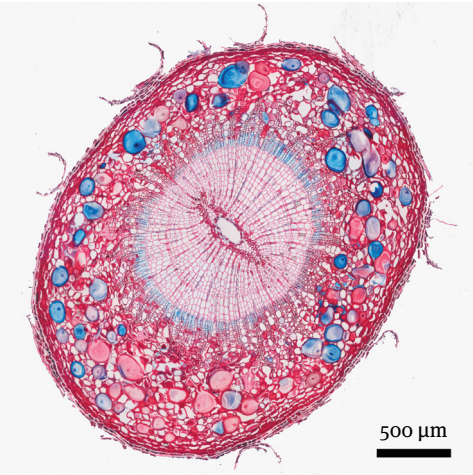
2, 69, 72, 77, 78, **80, 88**, 92, 96, 102/103, 111, 115, **121, 137**, 176, 178, 180, **189**, 195, 197, 204, 206, 211, **243**, **244**, 251, 253, 277, 278, 287, 288, **305**

Quercus petraea (Matt.) Liebl.

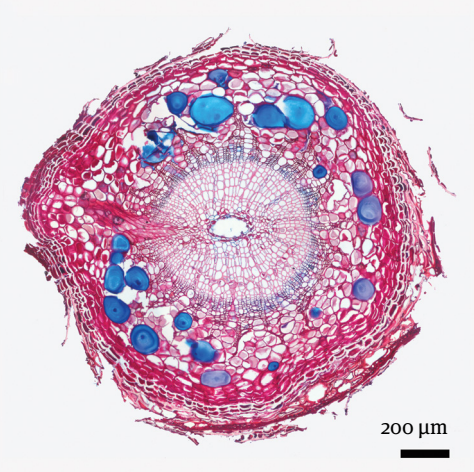
2, 69, **71, 72**, **74**, **76**, **80, 88, 91, 97**, 103, 112, 116, **119, 120, 137, 142,** 176, 178, 180, 186, 188, **189, 193**, 195, **197**, 204, 206, 212, **230**, **243, 244**, 251, 253, 277, 278, 287, 288, **307**

2.3 Plates with anatomical descriptions

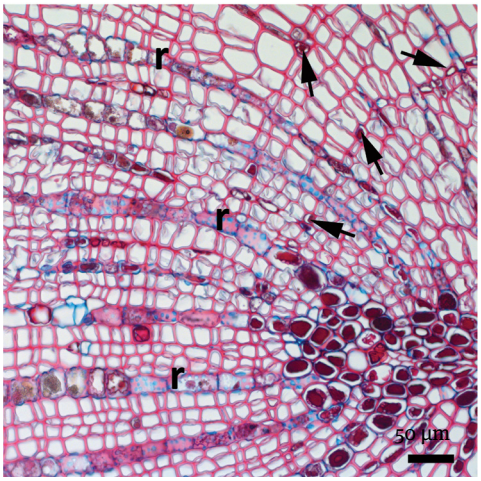
Abies alba Mill.



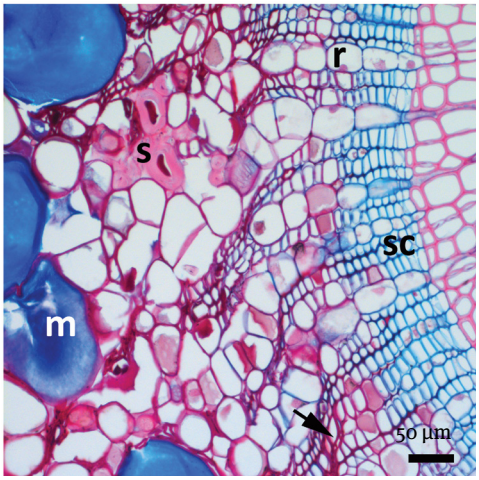
3 mm root, cross-section, note central resin duct and large mucilage cells in bark.



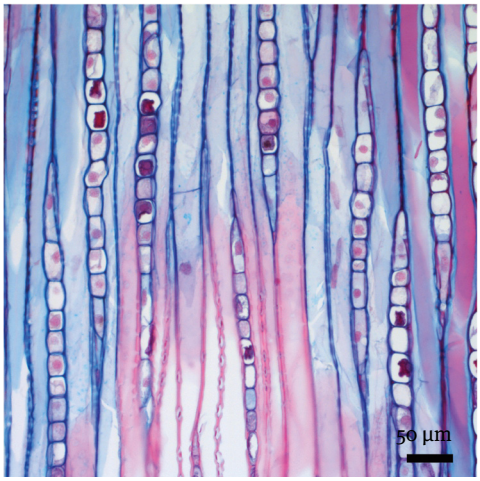
1 mm root: cross-section, note central resin duct and large mucilage cells in bark.



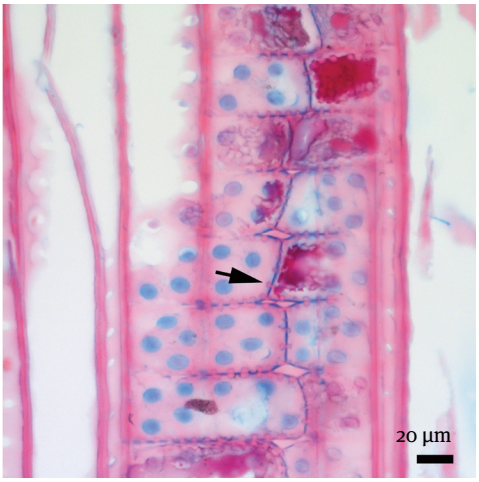
Secondary xylem with uniseriate rays (r) and axial parenchyma cells (arrows).



External tissues, cross-section (sc: sieve cells, arrow: collapsed sieve cells, r: ray, mc: mucilage cell).



Rays on transition between secondary xylem and phloem, tangential view.



Cross-field pits, longitudinal section: horizontal and end cell walls of ray cells nodular (marked by arrow).

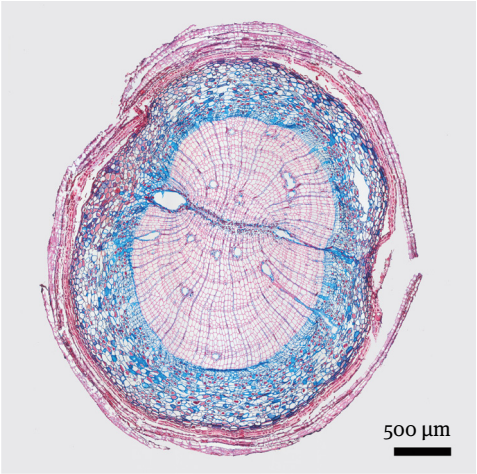
Characteristics of root tissues:

SECONDARY XYLEM		
Growth rings		Present
Tracheids	Bordered pits	Mainly 1 seriate, but also 2-3 seriate, in this case opposite to alternate
	Spiral thickenings	Absent
	Other characteristics	-
Axial parenchyma	Presence and abundance	Marginal, presence varies, very rare to absent
	Other characteristics	-
Rays	Ray width	Uniseriate
	Ray height	7-20 (up to 50) cells high
	Ray tracheids – presence and type	**Absent**
	Horizontal walls	Nodular, in thinner roots or close to phloem also smooth
	End walls	Nodular, in thinner roots or close to phloem also smooth
	Cross-field pits	Taxodioid to pinoid
	Other characteristics	-
Resin ducts	Presence	**Absent**
	Type (axial/radial)	-
	Epithelial cells - type	-
	Epithelial cells - number	-
Miscellaneous features		-
Crystals and other inorganic inclusions		Present occasionally in tracheids and ray cells, prismatic - elongated, in groups

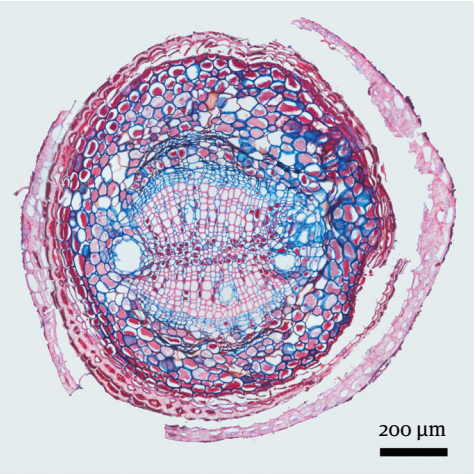
BARK	
Phloem	Sieve cells in radial rows, non-conducting phloem undergoes secondary changes, collapsed or non-collapsed
Ray course	Straight to bent
Ray dilatations	**All rays dilatated**
Fibres	**Absent**
Ray dilatations	Marginal, presence varies, very rare to absent
Sclereids	Groups of sclereids and solitary sclereids present in non-conducting phloem and to some extent in pericycle (may be absent from pericycle), not observed in 1 mm roots
Pericycle	Cells spherical to oval, cell walls secondarily changed, outer cells of pericycle elongated and compressed against periderm
Resin ducts	**Absent**
Crystals	**Prismatic**, mainly in groups, in non-conducting phloem and to lesser extent in pericycle, abundance varies from very low to abundant
Periderm	Thin to very thick (up to 20 layers), sclerotized, cell walls thin to thick
Other features	**Mucilage cells** present in pericycle and rarely in non-conducting phloem

PRIMARY TISSUES	
Shape	Mainly **diarch** with **central resin duct**
Miscellaneous features	Some cells filled with contents

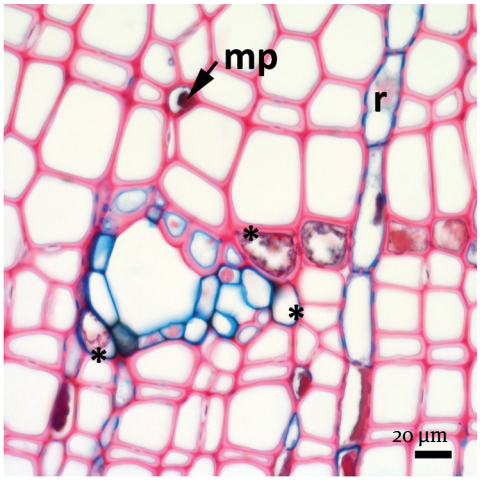
Picea abies (L.) Karsten



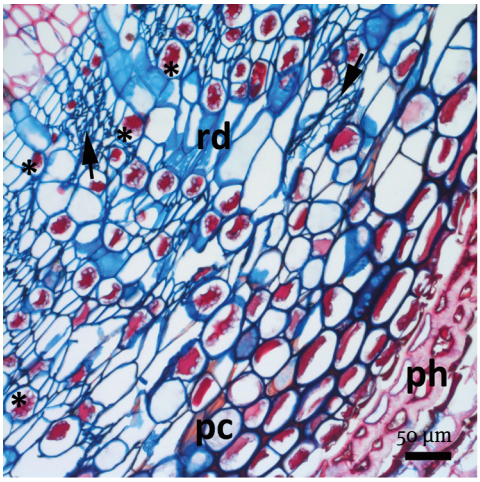
3 mm root, cross-section.



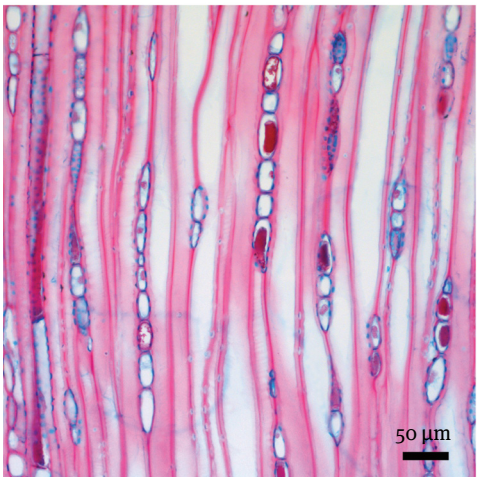
1 mm root, cross-section.



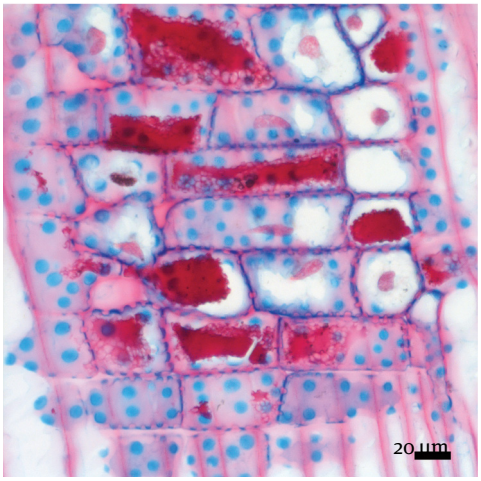
Resin duct, cross-section: unlignified epithelial cells intermixed with lignified, surrounded by axial parenchyma cells (asterisks); mp: marginal parenchyma; r: ray.



External tissues, cross-section (arrows: collapsed sieve cells, rd: resin duct, pc: pericycle, ph: phellem).



Rays, tangential section.



Cross-field pits, longitudinal section: horizontal and end cell walls of ray cells nodular.

Characteristics of root tissues:

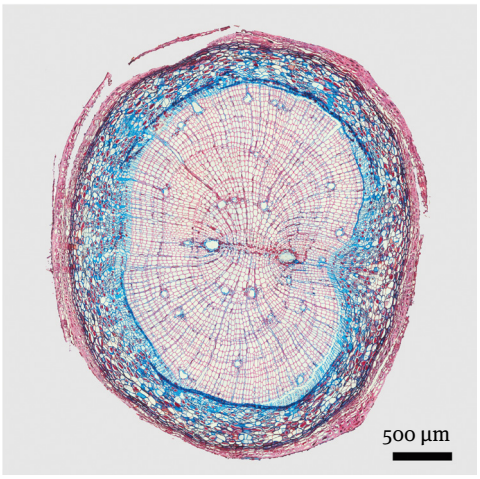
SECONDARY XYLEM		
Growth rings		Present, but inconspicuous (late wood often consisting of a single row of cells), wedging
Tracheids	Bordered pits	1-2 seriate, in later case alternate to opposite
	Spiral thickenings	May be present in narrower tracheids
	Other characteristics	-
Axial parenchyma	Presence and abundance	Axial parenchyma cells **around resin ducts, marginal and fusiform, occasionally filled with contents**
	Other characteristics	-
Rays	Ray width	**Uniseriate and fusiform**
	Ray height	Up to 16(28) cells high
	Ray tracheids – presence and type	Observed only in thicker (>=5 mm) roots, ray tracheid pit border may help to distinguish *Picea* from *Larix* in thicker roots (Bartholin 1979).
	Horizontal walls	**Nodular**
	End walls	**Nodular**
	Cross-field pits	**Piceoid to pinoid**
	Other characteristics	-
Resin ducts	Presence	**Present**
	Type (axial/radial)	**Axial and radial**
	Epithelial cells - type	**Thin, unlignified and thick, lignified***
	Epithelial cells - number	**6-18****
Miscellaneous features		-
Crystals and other inorganic inclusions		Not observed

BARK	
Phloem	Sieve cells in radial rows, collapsed sieve cells present, axial parenchyma cells in tangential rows, filled with contents
Ray course	Bent to straight
Ray dilatations	**Cells of rays dilatated**
Fibres	Absent or present in small quantities
Sclereids	Present (in small clusters or solitary) or absent
Pericycle	Cells undergo secondary changes and become collenchyma-like
Resin ducts	**Present** in phloem
Crystals	**Prismatic**, mainly in **groups**, in non-conducting phloem and pericycle, presence varies
Periderm	Cells in radial rows with **tangential cell walls thickened**, sometimes appear confluent, **shed in tangential layers**

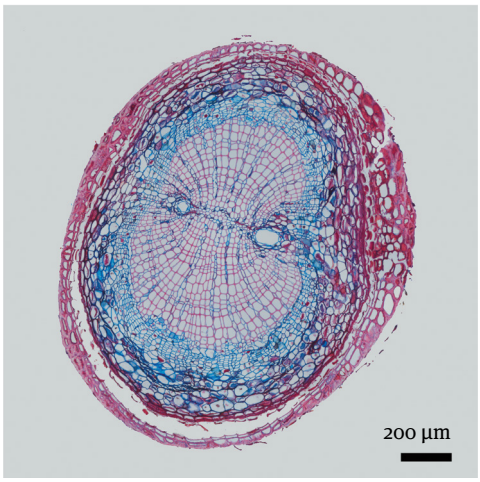
PRIMARY TISSUES	
Shape	**Diarch**
Miscellaneous features	**Two resin ducts** associated with primary xylem

*in stem wood epithelial cells of resin ducts are thick and lignified
**not valid for resin ducts that occur in connection with primary xylem

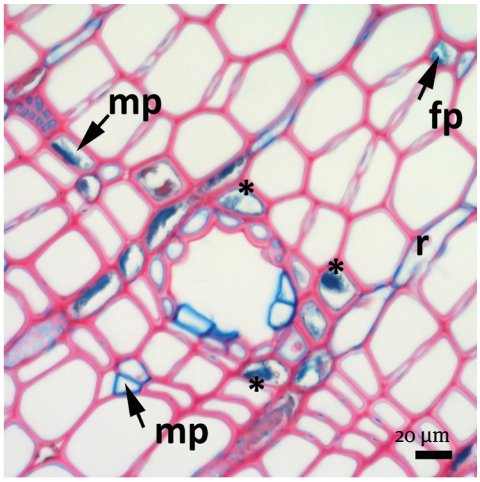
Larix decidua Mill.



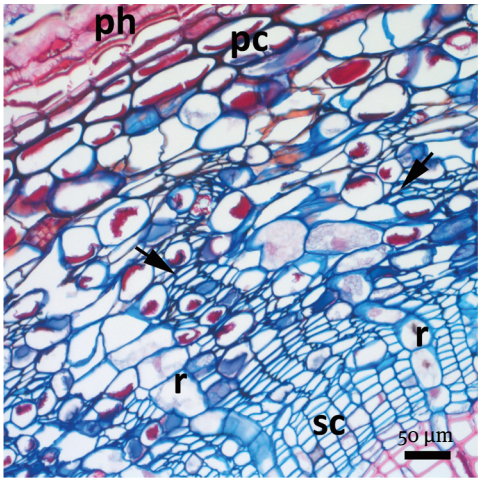
3 mm root, cross-section.



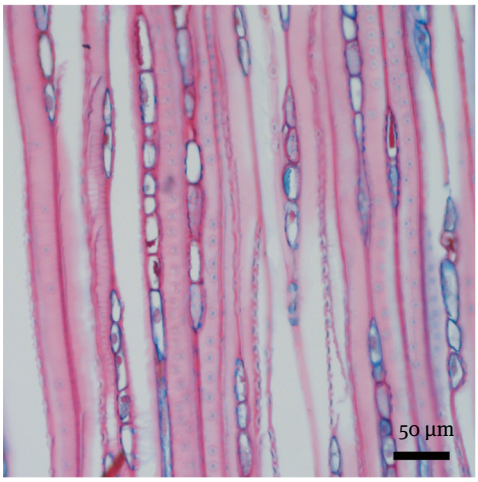
1 mm root, cross-section.



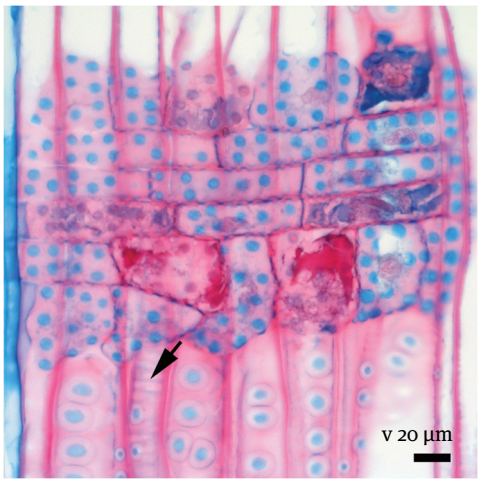
Resin duct, cross-section: unlignified epithelial cells intermixed with lignified, surrounded by axial parenchyma cells (asterisks); mp: marginal parenchyma, fp: fusiform parenchyma, r: ray.



External tissues, cross-section (arrows: collapsed sc: sieve cells, r: rays, pc: pericycle, ph: phellem).



Rays, tangential section: helical thickenings visible.



Cross-field pits, longitudinal section: horizontal and end cell walls of ray cells nodular. Helical thickenings in tracheid marked by arrow.

Characteristics of root tissues:

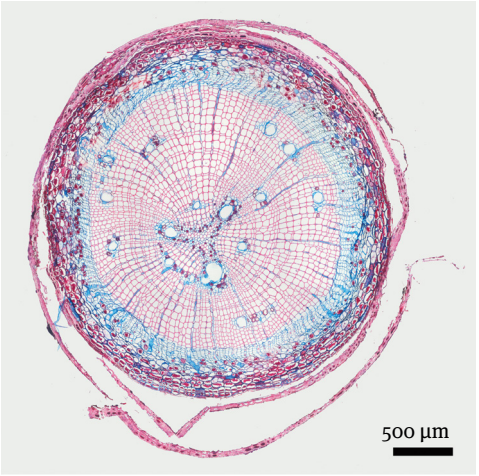
SECONDARY XYLEM		
Growth rings		Present, but sometimes inconspicuous (late wood often consisting of a single row of cells), wedging
Tracheids	Bordered pits	1-2 seriate, in later case alternate to opposite
	Spiral thickenings	Often present
	Other characteristics	-
Axial parenchyma	Presence and abundance	Axial parenchyma cells **around resin ducts, marginal and fusiform, filled with contents**
	Other characteristics	-
Rays	Ray width	**Uniseriate and fusiform**
	Ray height	Up to 24 cells high
	Ray tracheids – presence and type	Observed in 3 and 5 mm roots, ray tracheid pit border may help to distinguish *Picea* from *Larix* in thicker roots (Bartholin 1979).
	Horizontal walls	**Nodular**
	End walls	**Nodular**
	Cross-field pits	**Piceoid to pinoid**
	Other characteristics	-
Resin ducts	Presence	**Present**
	Type (axial/radial)	Axial and radial
	Epithelial cells - type	Thin, unlignified and thick, lignified*
	Epithelial cells - number	6-20**
Miscellaneous features		-
Crystals and other inorganic inclusions		Not observed

BARK	
Phloem	Sieve cells in radial rows, collapsed sieve cells present, axial parenchyma cells in tangential rows, filled with contents
Ray course	Straight to bent
Ray dilatations	**Cells of rays dilatated**
Fibres	**May contain numerous single fibres**
Sclereids	Absent or present in small amounts
Pericycle	Cells walls undergo secondary changes and appear collenchyma-like
Resin ducts	**-**
Crystals	**Prismatic, in groups**, in non-conducting phloem and pericycle, presence varies
Periderm	Cells in radial rows with **tangential cell walls thickened**, sometimes appear confluent, **shed in tangential layers**

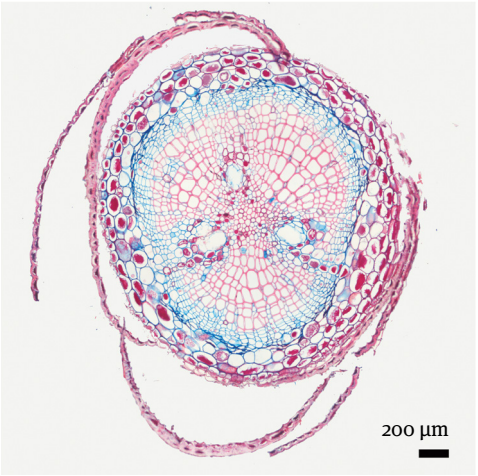
PRIMARY TISSUES	
Shape	**Diarch**
Miscellaneous features	**Two resin ducts** associated with primary xylem

*in stem wood epithelial cells of resin ducts are thick and lignified
**not valid for resin ducts that occur in connection with primary xylem

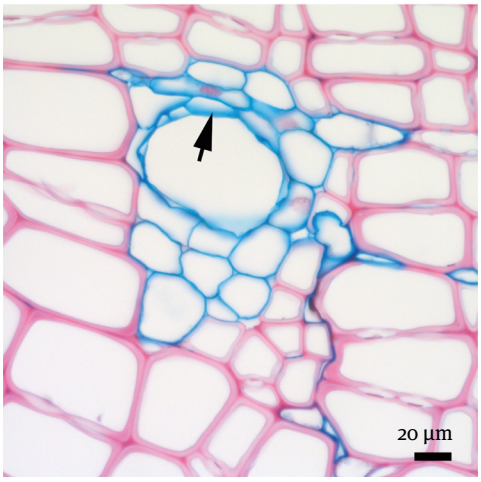
Pinus sylvestris L.



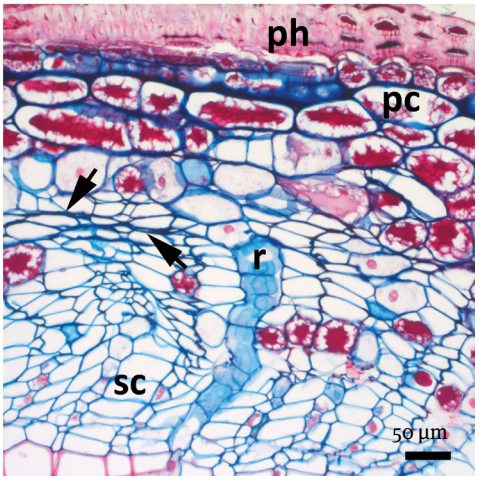
3 mm root, cross-section.



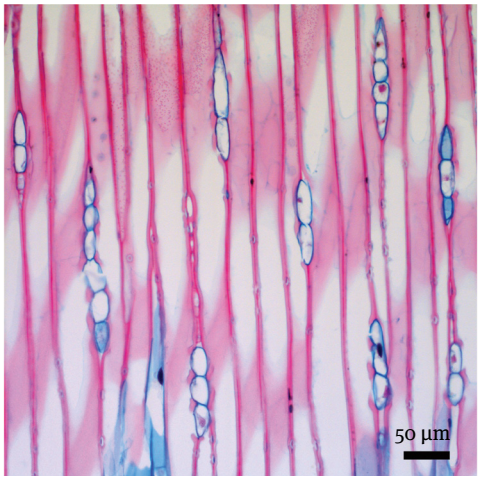
1 mm root, cross-section.



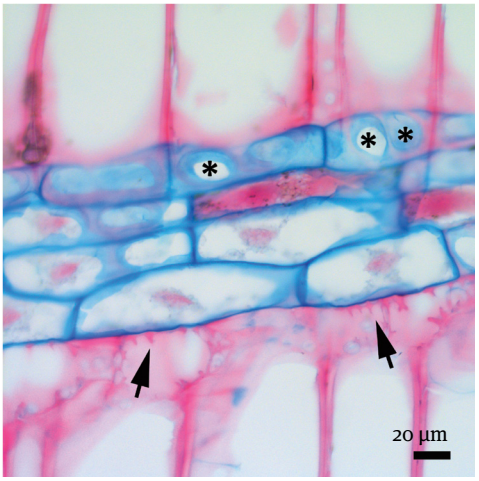
Resin duct, cross-section: epithelial cells thin walled (arrow), surrounded by parenchyma cells.



External tissues, cross-section (sc: sieve cells, arrows: collapsed sieve cells, r: ray, pc: pericycle, ph: phellem).



Rays, tangential section.



Cross-field pits (asterisks) and ray tracheids (arrows), radial section: Cross-field pits large; end cell walls of ray cells thin and smooth; ray tracheids dentate.

Characteristics of root tissues:

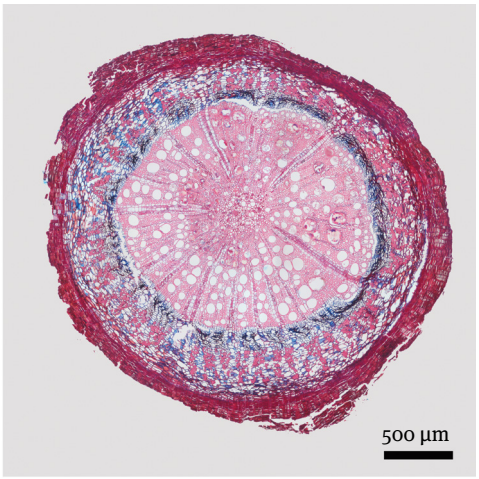
SECONDARY XYLEM		
Growth rings		Present, but inconspicuous, late wood inconspicuous due to the thin cell walls
Tracheids	Bordered pits	(1)-2 seriate, opposite
	Spiral thickenings	Absent
	Other characteristics	-
Axial parenchyma	Presence and abundance	Parenchyma cells **only around resin ducts**
	Other characteristics	-
Rays	Ray width	**Uniseriate and fusiform**
	Ray height	2-10 cells high
	Ray tracheids – presence and type	Present (but not observed in 1 mm roots), **dentate**, radial and vertical (connecting two rays)
	Horizontal walls	**Thin, smooth**
	End walls	**Thin, smooth**
	Cross-field pits	**Large, fenestriform**
	Other characteristics	-
Resin ducts	Presence	**Present**
	Type (axial/radial)	**Axial and radial**
	Epithelial cells - type	**Thin, unlignified**
	Epithelial cells - number	5-7*
Miscellaneous features		-
Crystals and other inorganic inclusions		Not observed

Cells undergo secondary changes and appear collenchyma-like	
Phloem	Sieve cells in radial rows, collapsed sieve cells present
Ray course	Straight to bent
Ray dilatations	**Some rays in older phloem dilatated**
Fibres	**Absent**
Sclereids	**Absent**
Pericycle	Cells undergo secondary changes and appear collenchyma-like
Resin ducts	**Present** in phloem and pericycle
Crystals	Very infrequent, **prismatic**, solitary or in small groups, in non-conducting phloem and pericycle
Periderm	With **thick (dentate) cell walls**, that sometimes appear confluent, easily **shedded in tangential layers**

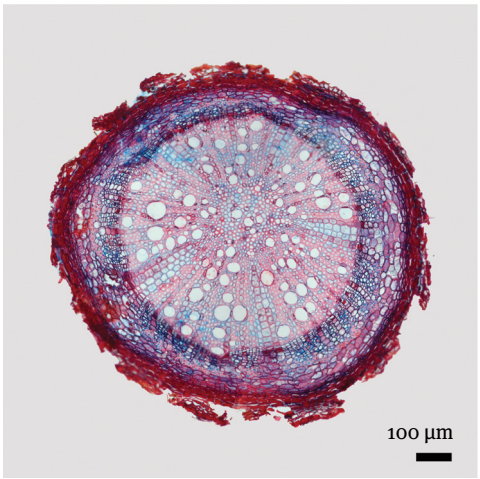
PRIMARY TISSUES	
Shape	Mainly **triarch** (occasionally diarch to tetrarch)
Miscellaneous features	**Three** (occasionally 2 or 4) **resin** ducts associated with primary xylem

*not valid for resin ducts that occur in connection with primary xylem

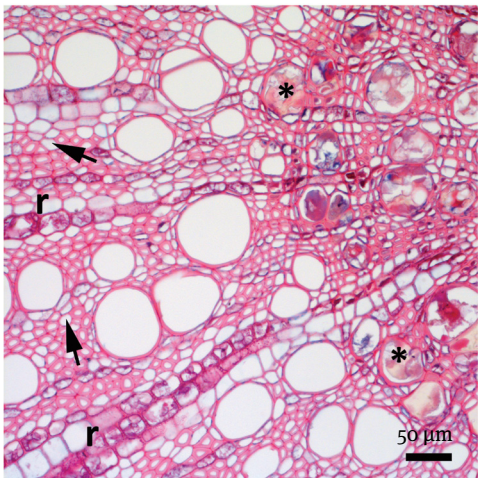
Prunus avium L.



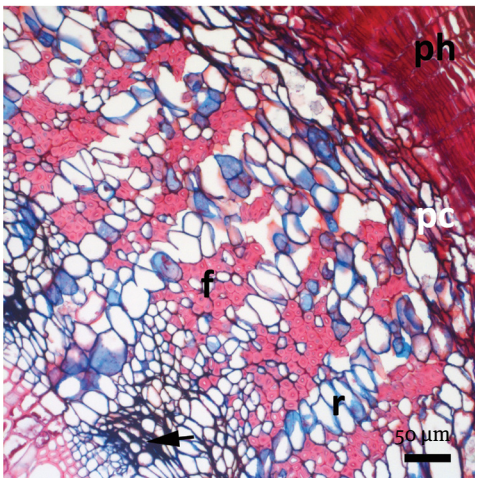
3 mm root, cross-section.



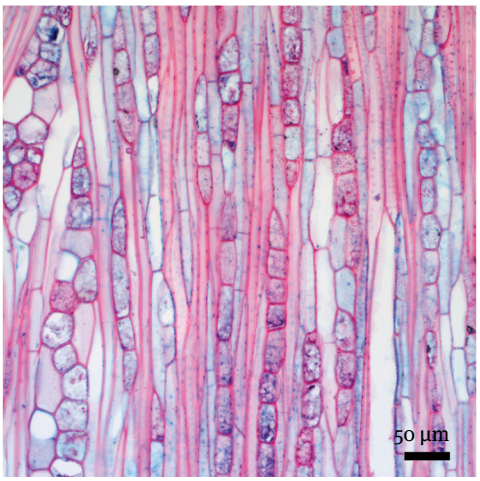
1 mm root, cross-section.



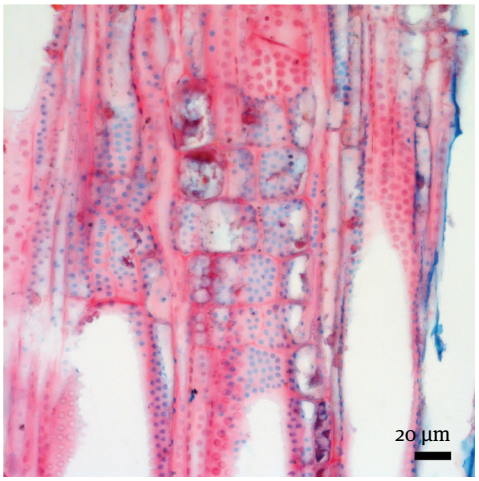
Axial parenchyma, cross-section: apotracheal, diffuse (arrows), r: ray, *: deposits inside vessels.



External tissues, cross-section (f: fibres, pc: pericycle, ph: phellem, arrow: compressed non-conducting phloem).



Rays, tangential view.



Cross-field pits (pits to vessels) , longitudinal section.

Characteristics of root tissues:

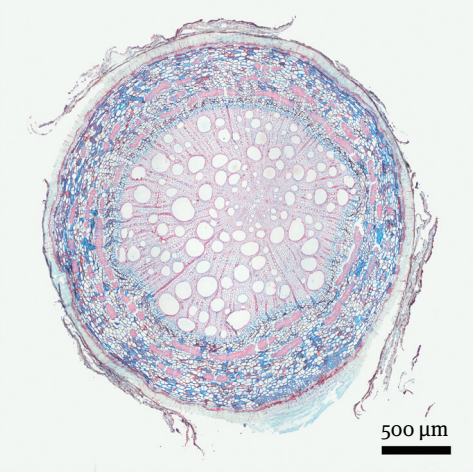
SECONDARY XYLEM		
Growth rings		More or less evident
Porosity pattern	Bordered pits	Diffuse porous
Vessels	Arrangement and groupings	Solitary, in tangential and radial pairs
	Size	*Growth ring (GR) number / No. of vessels measured / Mean tangential diameter ± stderr. (µm) GR1 391 36.0±0.69 GR2 342 55.2±1.03 GR3 197 62.0±1.54 GR4 197 45.8±1.42 GR5 92 53.6±1.74 GR6 130 53.6±1.74
	Perforations	Simple
	Spiral thickenings	Not observed
	Intervascular pits	**Alternate, minute (less than 4 µm)**
	Tyloses	Absent
	Deposits	**May be present**
	Other characteristics	Walls of vessels partly thickened
Libriform fibres and fibre tracheids	Type	Fibre tracheids
	Other characteristics	-
Rays	Size in height	May be more than 1 mm high
	Width	**From 1 to 6 cells wide**
	Pits to vessels	**Minute (less than 4 µm), round**, without border
	Other characteristics	-
Axial parenchyma	Presence	Present
	Type	**Apotracheal-diffuse**
Miscellaneous features		-
Crystals and other inorganic inclusions		-

BARK	
Phloem	Non-conducting phloem compressed, secondarily changed
Ray dilatations	Cells of wider rays dilatated
Fibres	Present, **in radially oriented groups in non-conducting phloem and pericycle**, radial orientation may not be discernible in early stages or later due to growth pattern
Sclereids	Absent
Pericycle	Cells of pericycle elongated and compressed against the periderm
Crystals	**Druses** in phloem rays, non-conducting phloem and pericycle
Periderm	Phellem filled with polyphenolic contents, thickness varies

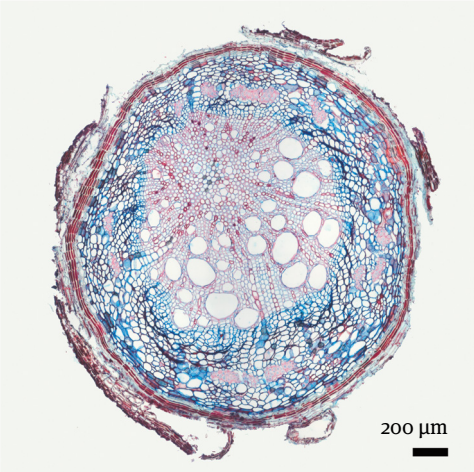
PRIMARY TISSUES	
Shape	Polyarch, unremarkable
Miscellaneous features	-

*Growth ring number corresponds to position of the growth ring from the primary xylem towards outside. The smallest growth ring number corresponds to the position just outside of the primary xylem.

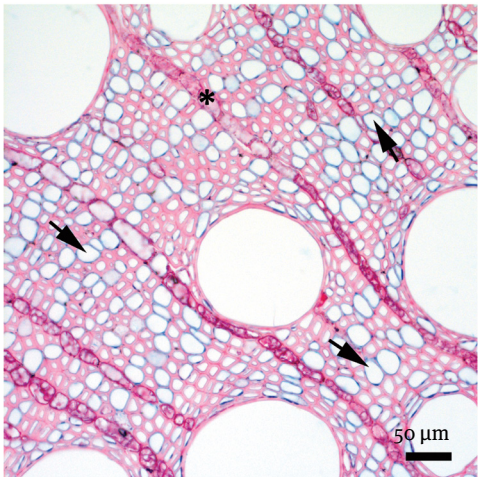
Castanea sativa Mill.



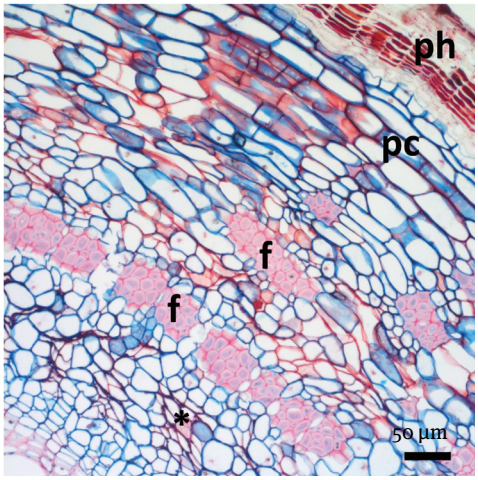
3 mm root, cross-section.



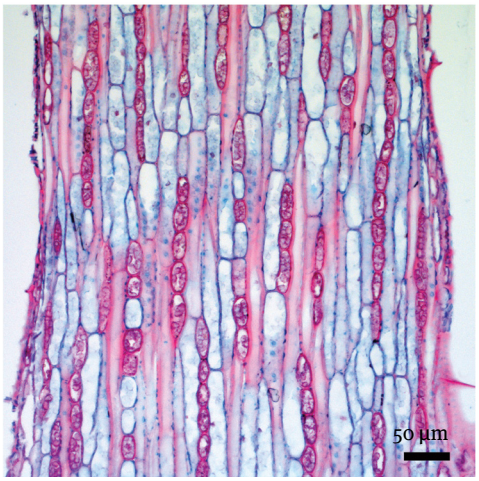
1 mm root, cross-section.



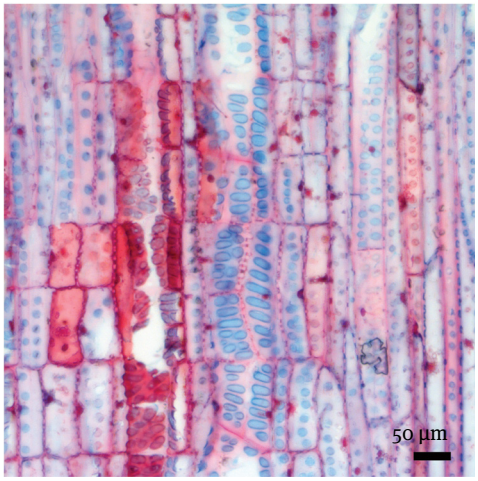
Axial parenchyma, cross-section: apotracheal, diffuse-in-aggregates (arrows), *: ray.



External tissues, cross-section (f: fibres, pc: pericycle, ph: phellem, asterisk: collapsed non-conducting phloem).



Rays, tangential view.



Cross-field pits (pits to vessels), longitudinal section.

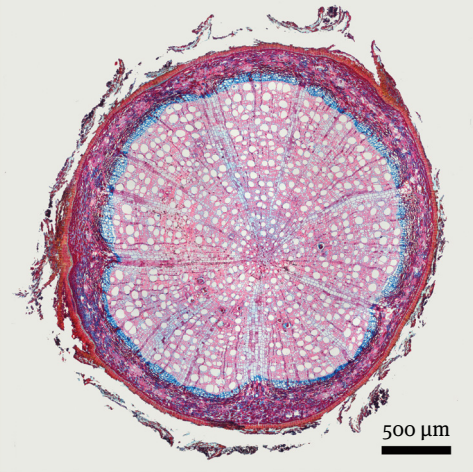
Characteristics of root tissues:

SECONDARY XYLEM		
Growth rings		Not discernible
Porosity pattern	Bordered pits	Diffuse porous
Vessels	Arrangement and groupings	**Solitary, occasionally in pairs**, cell walls partially thickened
	Size	Distance from the centre of the root (mm) / No. of vessels measured / Mean tangential diameter ± stderr. (µm) 0.00-0.49 / 724 / 57.1±8.20 0.50-0.99 / 627 / 70.5±1.35 1.00-1.49 / 390 / 79.0±2.21 1.50-1.99 / 251 / 93.2±3.33 2.00-2.49 / 96 / 94.4±5.43 2.50-2.99 / 55 / 54.3±3.49
	Perforations	**Simple**
	Spiral thickenings	Absent
	Intervascular pits	**Alternate, small (6.0-7.5 µm)**
	Tyloses	-
	Deposits	-
	Other characteristics	-
Libriform fibres and fibre tracheids	Type	Fibre tracheids
	Other characteristics	**Cell walls thick**
Rays	Size in height	**Less than 1 mm**
	Width	**1-2 (3) cells wide (in stem wood, rays are strictly one cell wide), filled with contents**
	Pits to vessels	**Scalariform (vessel-ray pits with large horizontal apertures)**
	Other characteristics	-
Axial parenchyma	Presence	Present
	Type	**Apotracheal – diffuse-in-aggregates, abundant**
Miscellaneous features		-
Crystals and other inorganic inclusions		Absent

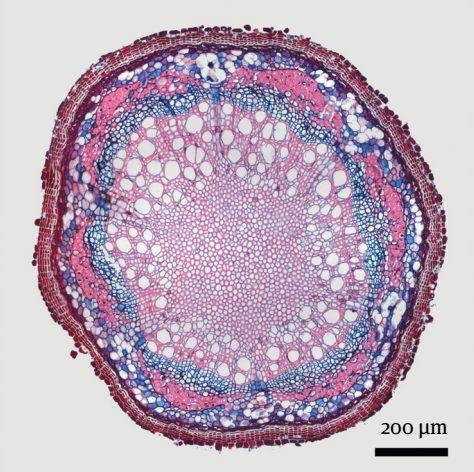
BARK	
Phloem	Sieve elements of non-conducting phloem collapsed and undergo secondary changes
Ray dilatations	Cells of phloem rays are dilatated
Fibres	In **tangential groups** in phloem and pericycle, groups getting smaller with distance from cambium
Sclereids	Absent
Pericycle	**Cells around tangential groups of fibres small and spherical**, the remaining cells large and elongated
Crystals	Present around tangential groups of fibres, **prismatic, of more or less homogeneous size**, common, in chamber cells; **druses** occur in small amounts in pericycle and occasionally in non-conducting phloem
Periderm	**Central layers of phellem cells filled with polyphenolics**, cells of periderm occur in radial rows

PRIMARY TISSUES	
Shape	**Polyarch**
Miscellaneous features	-

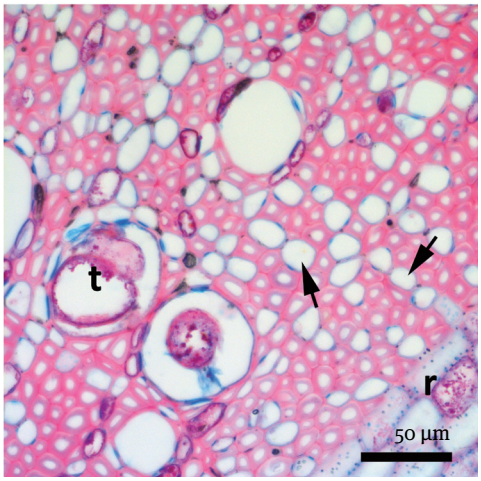
Fagus sylvatica L.



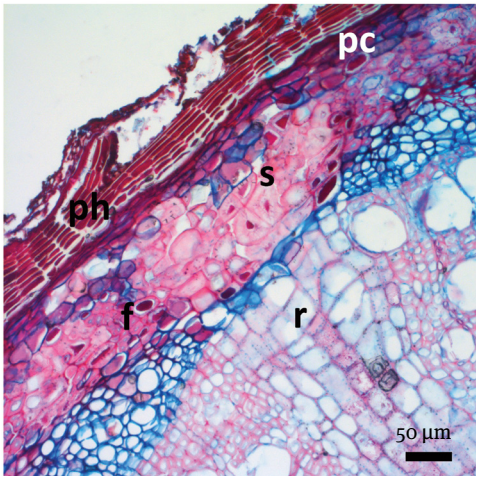
3 mm root, cross-section.



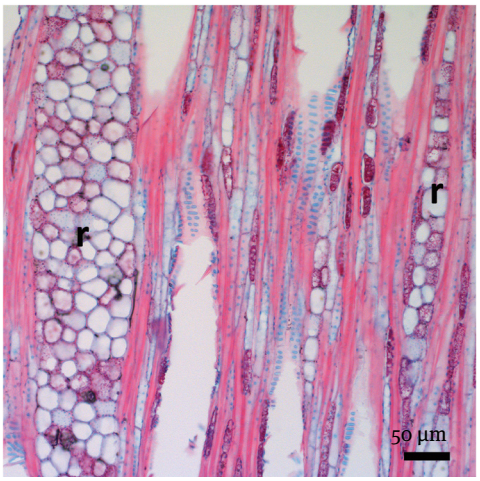
1 mm root, cross-section.



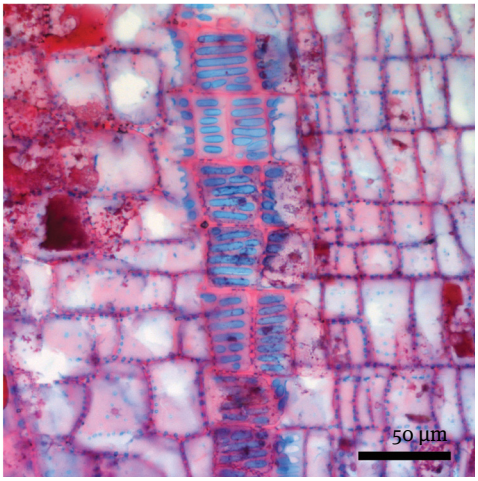
Axial parenchyma, cross-section,: apotracheal, diffuse-in-aggregates (arrows), r: ray, t: vessel with tylose.



External tissues, cross-section (s: sclereids, f: fibres, pc: pericycle, ph: phellem, r: ray).



Rays, tangential view.



Cross-field pits (pits to vessels), longitudinal section.

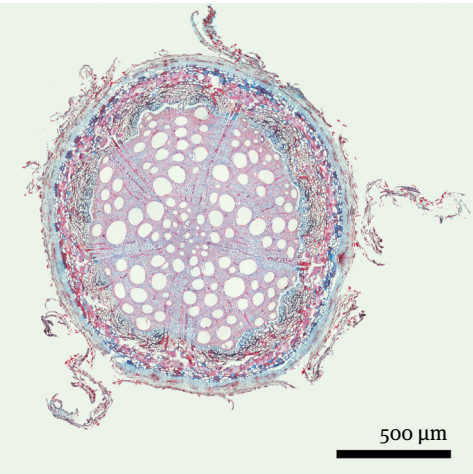
Characteristics of root tissues:

SECONDARY XYLEM		
Growth rings		Present, but occasionally very narrow and inconspicuous, wedging growth rings present
Porosity pattern	Bordered pits	Diffuse porous to semi-ring porous (in wider growth rings there is a trend of decreasing vessel size in late wood)
Vessels	Arrangement and groupings	**In tangential bands, solitary and in groups of 2 (up to 4) with tangential contacts**
	Size	Growth ring (GR) number / No. of vessels measured / Mean tangential diameter ± stderr. (µm) GR1 / 707 / 23.5±0.31 GR2 / 601 / 32.6±0.41 GR3 / 771 / 36.7±0.45 GR4 / 531 / 43.1±0.69 GR5 / 375 / 44.8±0.98 GR6 / 324 / 47.3±1.08
	Perforations	**Simple to scalariform**
	Spiral thickenings	Absent
	Intervascular pits	**Scalariform**
	Tyloses	**Common**
	Deposits	-
	Other characteristics	-
Libriform fibres and fibre tracheids	Type	Fibre tracheids
	Other characteristics	**Cell walls thick**
Rays	Size in height	**More than 1 mm**
	Width	**From 1 to 12 cells wide**
	Pits to vessels	**Scalariform to opposite**
	Other characteristics	-
Axial parenchyma	Presence	Present
	Type	**Apotracheal – diffuse-in-aggregates**
Miscellaneous features		-
Crystals and other inorganic inclusions		Present **in cells of wider rays, prismatic**, large

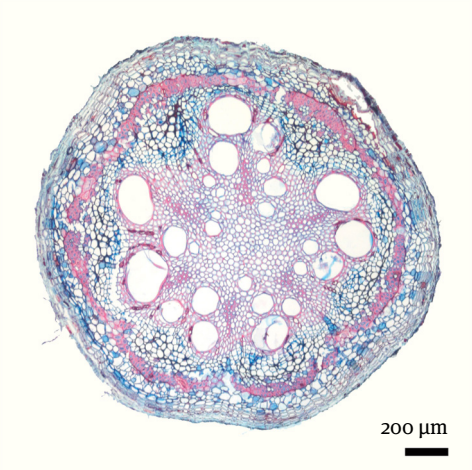
BARK	
Phloem	Sieve elements of non-conducting phloem collapsed and undergo secondary changes
Ray dilatations	Present in **wider rays**
Fibres	In **tangential groups** in phloem
Sclereids	Present in phloem and forming a **sclerenchymatous band together with fibres**, sometimes extending into pericycle, in 1 mm roots not very abundant
Pericycle	First with spherical cells that are soon **compressed against the periderm, filled with polyphenolics**
Crystals	Present in phloem rays and accompanying tangential sclerenchymatous band, sometimes extending into pericycle, **prismatic**, large, common; **druses** occur in small amounts
Periderm	**Phellem cells filled with polyphenolics**, occur in radial rows

PRIMARY TISSUES	
Shape	**Polyarch**, sometimes inconspicious
Miscellaneous features	-

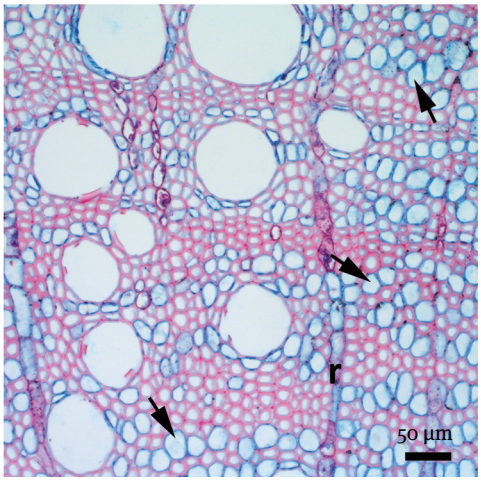
Quercus petraea (Matt.) Liebl.



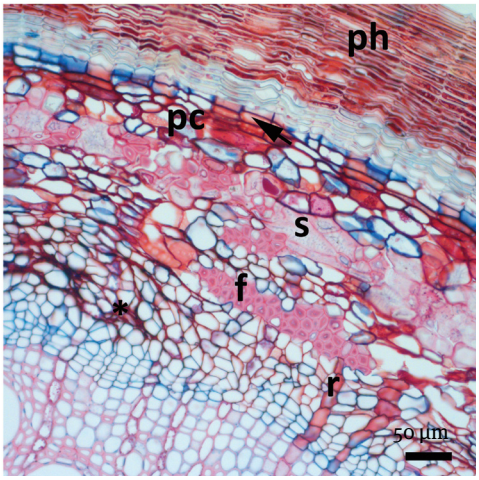
3 mm root, cross-section, typical (for explanation, see table).



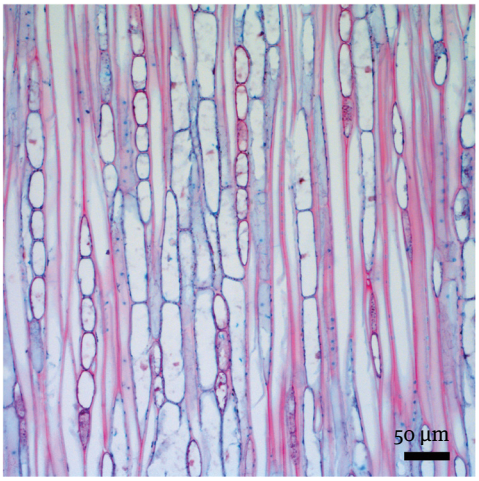
1 mm root, cross-section, typical.



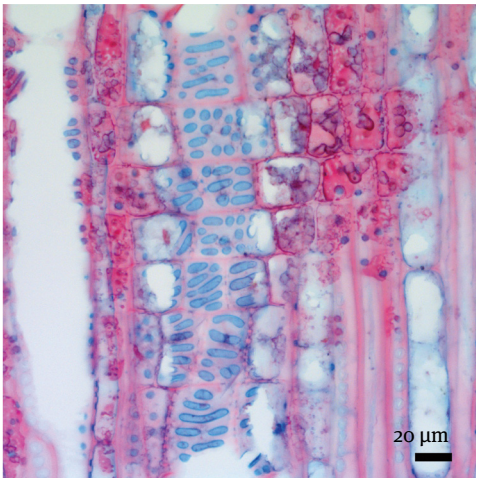
Axial parenchyma, cross-section: apotracheal, diffuse-in-aggregates (arrows), r: ray.



External tissues, cross-section (s: sclereids, f: fibres, pc: pericycle, ph: phellem, r: ray, arrow: phelloderm).



Rays, tangential view.



Cross-field pits (pits to vessels), longitudinal section.

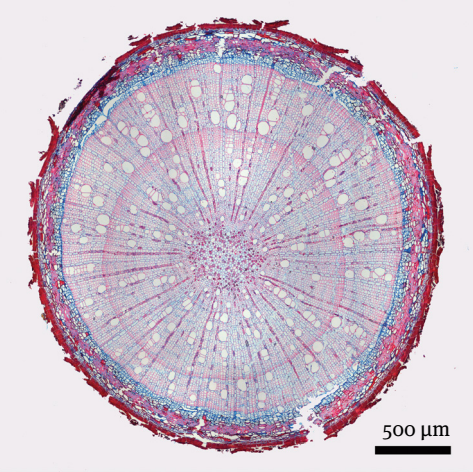
Characteristics of root tissues:

SECONDARY XYLEM		
Growth rings		Not discernible
Porosity pattern	Bordered pits	Diffuse porous to semi-ring porous
Vessels	Arrangement and groupings	**Solitary, typically in diagonal pattern**
	Size	Distance from the centre of the root (mm) / No. of vessels measured / Mean tangential diameter ± stderr. (µm) 0.00-0.49 / 761 / 38.2±0.92 0.50-0.99 / 682 / 66.8±1.57 1.00-1.49 / 279 / 76.6±2.32 1.50-1.99 / 183 / 68.8±2.56 2.00-2.49 / 105 / 62.7±2.90 2.50-2.99 / 59 / 54.5±3.56
	Perforations	**Simple**
	Spiral thickenings	Absent
	Intervascular pits	**Alternate, small (4-7 µm)**
	Tyloses	**Not observed**
	Deposits	-
	Other characteristics	-
Libriform fibres and fibre tracheids	Type	Libriform fibers and fibre tracheids
	Other characteristics	-
Rays	Size in height	**Mainly less than 1 mm**
	Width	**Mainly 1 cell wide, filled with contents, typical samples possess wide areas devoted of vessels where parenchymatic cells might occur in larger quantities. In these areas, wider rays, typical of oak stems, are expected to develop. However, it seems that roots of oak are a subject to dimorphism. In some roots ("atypical") wide areas devoted of vessels are not observed, as well as vessels are of smaller diameter.**
	Pits to vessels	**Scalariform (vessel-ray pits with large horizontal apertures)**
	Other characteristics	-
Axial parenchyma	Presence	Present
	Type	**Apotracheal – diffuse-in-aggregates, abundant**
Miscellaneous features		-
Crystals and other inorganic inclusions		Absent

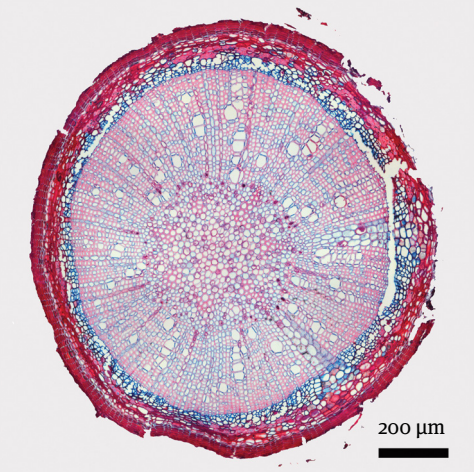
BARK	
Phloem	Sieve elements of non-conducting phloem collapsed and undergo secondary changes
Ray dilatations	Absent
Fibres	In **tangential groups** in phloem and pericycle
Sclereids	Forming a **sclerenchymatous band together with fibres**, sometimes extending into pericycle
Pericycle	Mainly with isodiametric cells that can be peripherally **compressed against the periderm**
Crystals	Present around tangential sclerenchymatous groups, **prismatic, of different sizes**, common, in chamber cells; **druses** occur in small amounts in pericycle and occasionally in non-conducting phloem
Periderm	**Phellem cells occur in radial rows, outer phellem cells filled with polyphenolics**

PRIMARY TISSUES	
Shape	**Polyarch**, sometimes inconspicious
Miscellaneous features	-

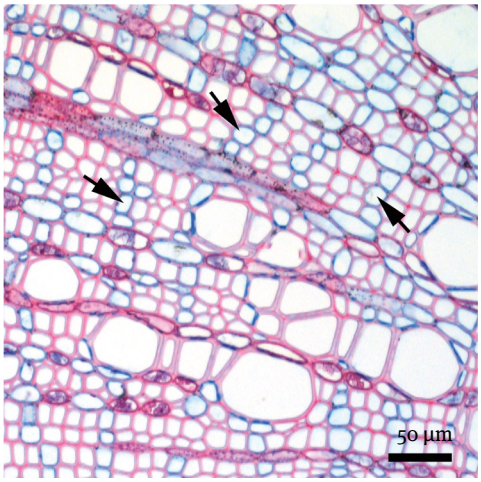
Carpinus betulus L.



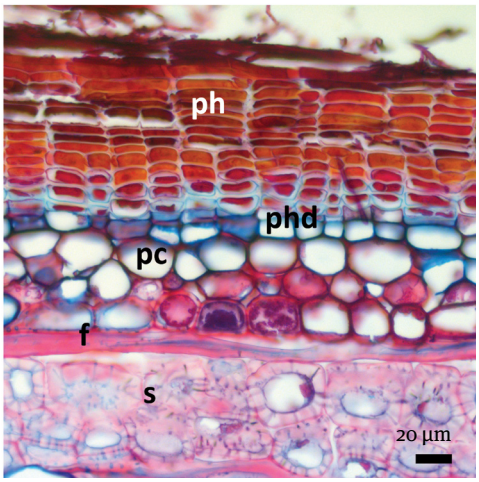
3 mm root, cross-section.



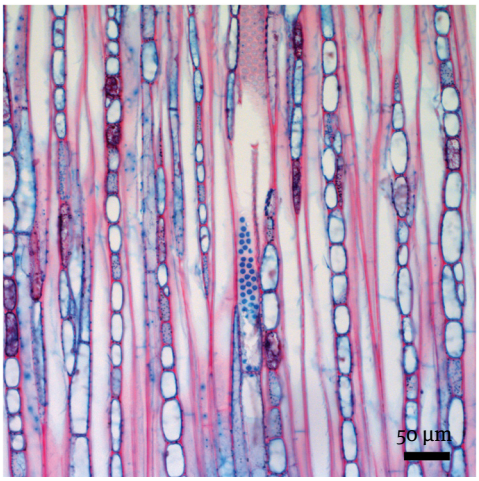
1 mm root, cross-section.



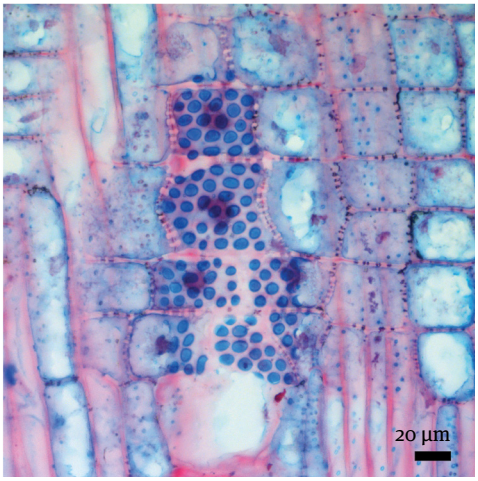
Axial parenchyma: diffuse-in-aggregates.



External tissues, longitudinal section (s: sclereids, f: fibres, pc: pericycle, phd: phellodерm, ph: phellem).



Rays, tangential view.



Cross-field pits (pits to vessels), longitudinal section.

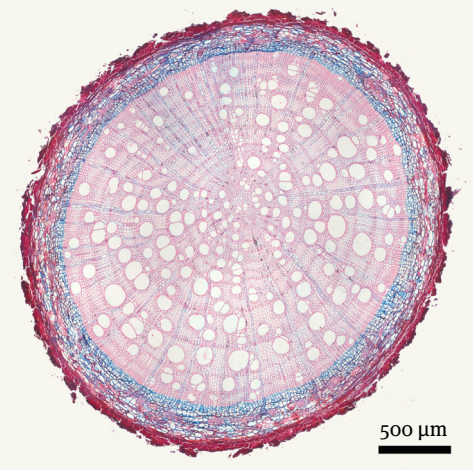
Characteristics of root tissues:

SECONDARY XYLEM		
Growth rings		Distinct, wedging growth rings present
Porosity pattern	Bordered pits	Diffuse porous, no special age trend in vessel size
Vessels	Arrangement	**Solitary, in clusters and radial multiples (mainly 2-4, but also up to 8-9)**
	Size	Growth ring (GR) number / No. of vessels measured / Mean tangential diameter ± stderr. (µm) GR1 574 24.7 ± 0.44 GR2 789 34.4 ± 0.56 GR3 618 43.2 ± 0.82 GR4 313 47.2 ± 1.42
	Perforations	**Predominantly simple, scalariform may occur as well in narrower vessels**
	Spiral thickenings	Observed occasionally
	Intervascular pits	**Alternate**
	Tyloses	Observed **occasionally**
	Deposits	-
	Other characteristics	-
Libriform fibres and fibre tracheids	Type	Libriform fibres
	Other characteristics	-
Rays	Size in height	Some of the rays exceed 1 mm in height
	Width	**1-3(4) cells wide**
	Pits to vessels	**Medium (7-10 µm) and round to oval, without border**
	Other characteristics	-
Axial parenchyma	Presence	Present
	Type	**Apotracheal - diffuse-in-aggregates, marginal**
Miscellaneous features		-
Crystals and other inorganic inclusions		**Prismatic, in ordinary cells of the rays**

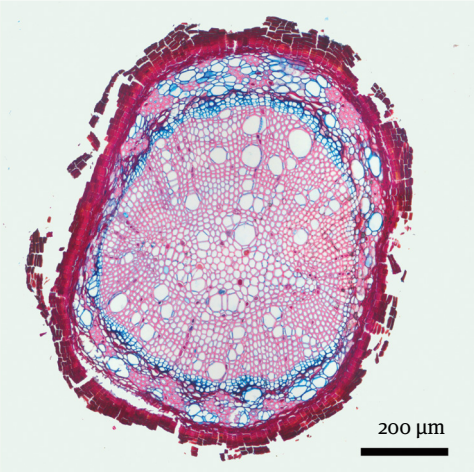
BARK	
Phloem	Uniform, thin, fibres may be present
Ray dilatations	**Occur in wider rays**
Fibres	Present, in pericycle (and occasionally in phloem), forming a **tangential band**
Sclereids	Present, large, in pericycle (and occasionally in phloem), **quantity +/- equal to fibres or predominate** (in samples thicker than 1 mm)
Crystals	Mainly solitary, a) **prismatic** - around and inside the sclereid/fibre tangential band, b) druses – occasionally in phloem rays and pericycle
Periderm	Phellem and phelloderm +/- distinct, **phellem cell lumina filled with contents**, outer cells of phellem become thinner and elongated and slough off in concave scales

PRIMARY TISSUES	
Shape	Star like, **Polyarch**
Miscellaneous features	Cells of two types, one type appears empty, other filled with stained content in the lumen.

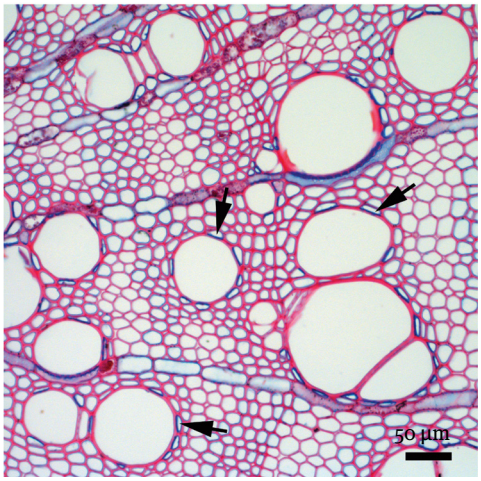
Acer pseudoplatanus L.



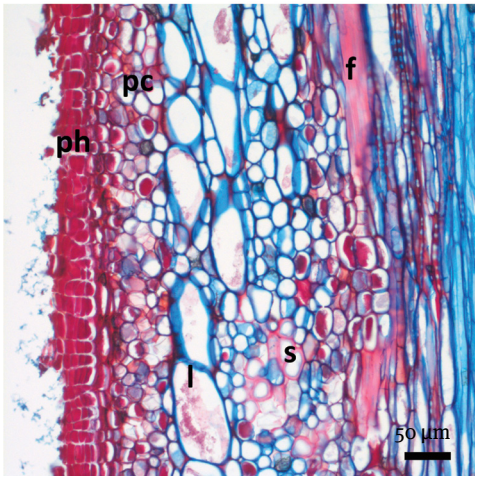
3 mm root, cross-section.



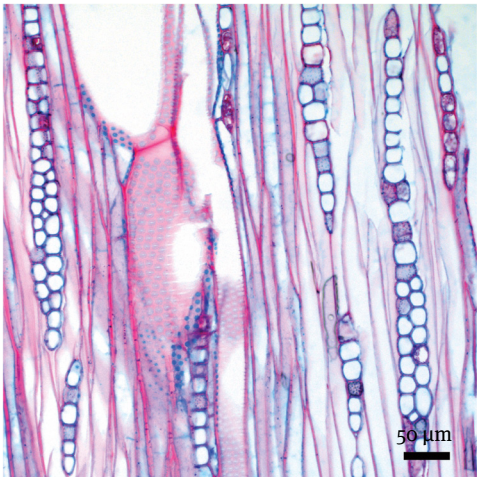
1 mm root, cross-section.



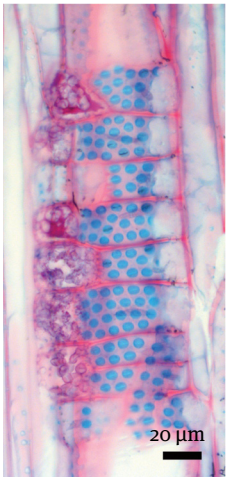
Axial parenchyma, cross-section: scanty paratracheal (arrows).



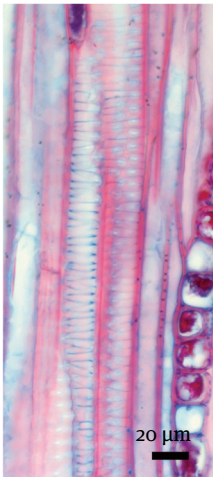
External tissues, longitudinal section (s: sclereids, f: fibers, c: pericycle, ph: phellem, l: laticifers).



Rays, tangential view.



Cross-field pits (pits to vessels), longitudinal section.



Spiral thickenings, longitudinal section.

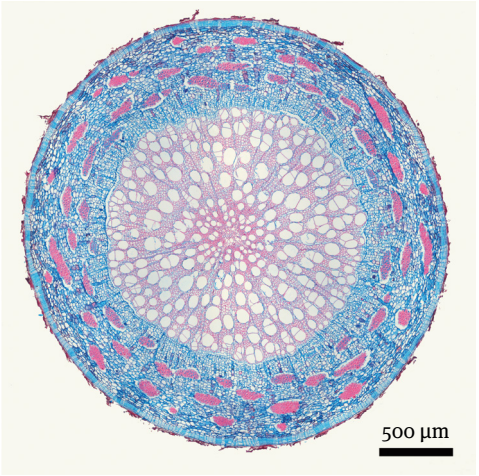
Characteristics of root tissues:

SECONDARY XYLEM		
Growth rings		Distinct, wedging growth rings present
Porosity pattern	Bordered pits	Diffuse porous
Vessels	Arrangement	Solitary, in small clusters and **radial multiples** (of up to 12, but mainly 2-4)
	Size	Growth ring (GR) number / No. of vessels measured / Mean tangential diameter ± stderr. (µm) GR1 315 28.7±0.93 GR2 681 32.7±0.76 GR3 917 45.1±0.74 GR4 952 46.5±0.75 GR5 662 46.1±0.98 GR6 472 49.6±1.40
	Perforations	**Simple**
	Spiral thickenings	**Present**
	Intervascular pits	**Alternate**
	Tyloses	Absent
	Deposits	Present occasionally
	Other characteristics	-
Libriform fibres and fibre tracheids	Type	Libriform fibres, thin and thick walled
	Other characteristics	-
Rays	Size in height	Mainly less than 1 mm
	Width	**1-3 cells wide**
	Pits to vessels	**Small (4-7 µm) and round**
	Other characteristics	-
Axial parenchyma	Presence	Present
	Type	**Scanty paratracheal, sometimes very inconspicious**
Miscellaneous features		-
Crystals and other inorganic inclusions		Absent

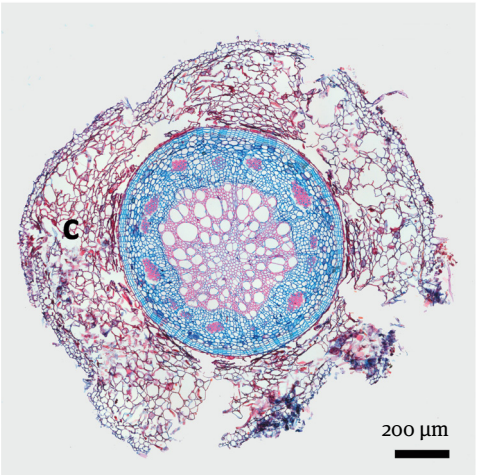
BARK	
Phloem	Very thin, fibres and sclereids might be present
Ray dilatations	Present
Fibres	Present, quantity varies, **in tangential groups** in phloem and pericycle, may form **+/- continuous tangential band**
Sclereids	Present, **thin walled**, accompanying fibres, quantity varies, may be completely absent
Crystals	**Prismatic**, in pericycle, may be accompanying groups of fibres and sclereids, rarely found in non-conducting phloem
Periderm	Phellem and phelloderm not distinctly different, **lumina filled with (polyphenolic) contents**, empty spaces between stacks of cells
Miscellaneous features	**Cells of laticifers** inside pericycle

PRIMARY TISSUES	
Shape	More or less flattened, **diarch**
Miscellaneous features	Some cells filled with contents, cells of larger size often present

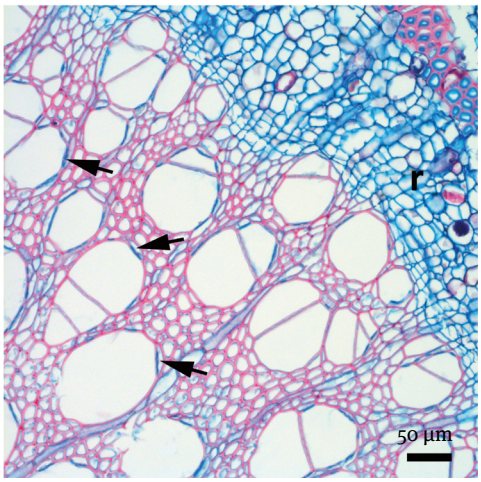
Populus nigra L.



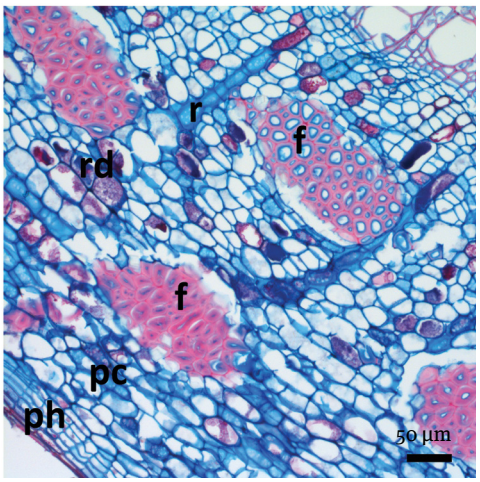
3 mm root, cross-section.



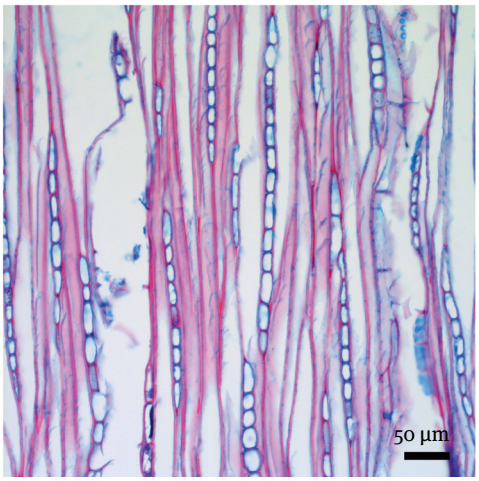
1 mm root, cross-section: cortex (c) still visible.



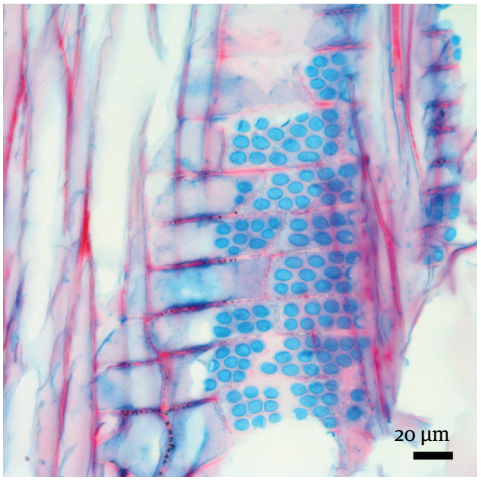
Axial parenchyma: scanty paratracheal (arrows), vessels in radial multiples and in small groups, r: ray.



External tissues, cross-section (f: fibres, pc: pericycle, ph: phellem, r: ray, rd: ray dilatation).



Rays, tangential view.



Cross-field pits (pits to vessels), longitudinal section.

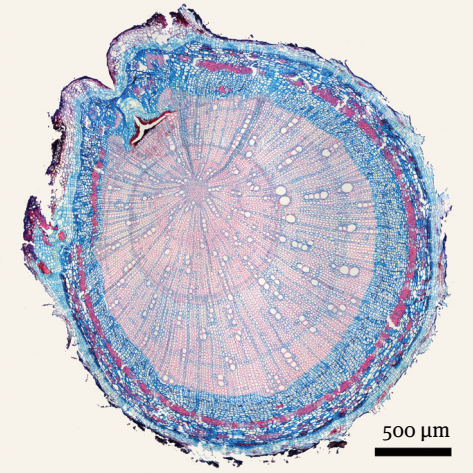
Characteristics of root tissues:

SECONDARY XYLEM		
Growth rings		Not visible or very inconspicuous
Porosity pattern	Bordered pits	Diffuse porous
Vessels	Arrangement	Solitary and in **radial multiples** (of mainly 2, but up to 4), some **small clusters** present
	Size	Distance from the centre of the root (mm) / No. of vessels measured / Mean tangential diameter ± stderr. (µm) 0.00-0.49 / 1084 / 34.3±0.60 0.50-0.99 / 1464 / 45.4±0.57 1.00-1.49 / 661 / 64.1±5.58 1.50-1.99 / 361 / 60.0±1.23
	Perforations	**Simple**
	Spiral thickenings	Absent
	Intervascular pits	**Alternate**
	Tyloses	Not observed
	Deposits	Not observed
	Other characteristics	-
Libriform fibres and fibre tracheids	Type	Libriform fibres
	Other characteristics	-
Rays	Size in height	Less than 1 mm
	Width	**Exclusively uniseriate**
	Pits to vessels	**Medium, round, without border**
	Other characteristics	-
Axial parenchyma	Presence	Present
	Type	**Paratracheal**
Miscellaneous features		-
Crystals and other inorganic inclusions		Absent

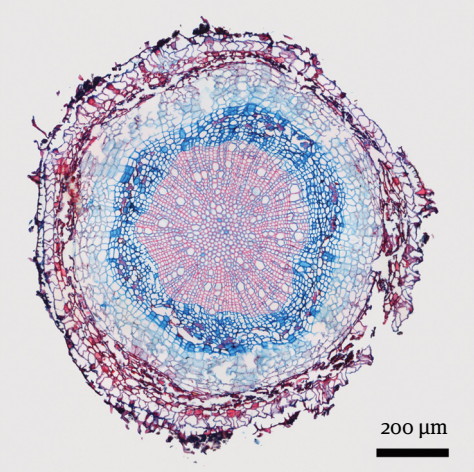
BARK	
Phloem	Sieve elements not collapsed, cells of axial parenchyma inflate with ageing
Ray dilatations	Occur in some rays
Pericycle	Cells more or less **isodiametric** to elongated, cell walls **do not undergo secondary changes**
Fibres	Present, **lumina decrease in diameter with distance from cambium due to thickening of cell walls**, fibres arranged in **tangential groups** inside phloem and pericycle
Sclereids	May be present in small quantities in pericycle
Crystals	Present, solitary, **prismatic**, around tangential groups of fibres, in **chamber cells**; small amount of **druses** in outer part of the pericycle
Periderm	Cell walls of periderm **thin**, lumina not filled with contents (it may be washed away during the sample preparation), **remnants of epidermis and cortex preserved for some time during secondary growth**

PRIMARY TISSUES	
Shape	Mainly **tetrarch (diamond shaped)**
Miscellaneous features	-

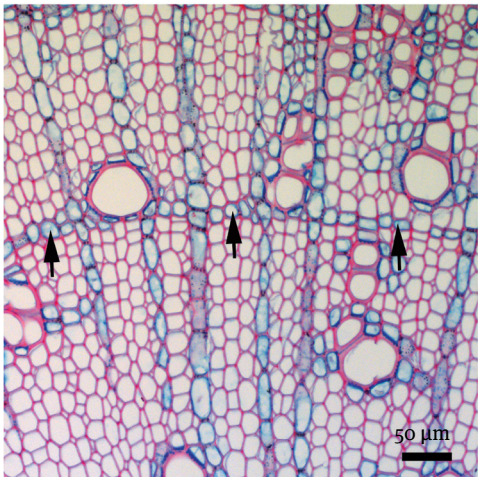
Fraxinus excelsior L.



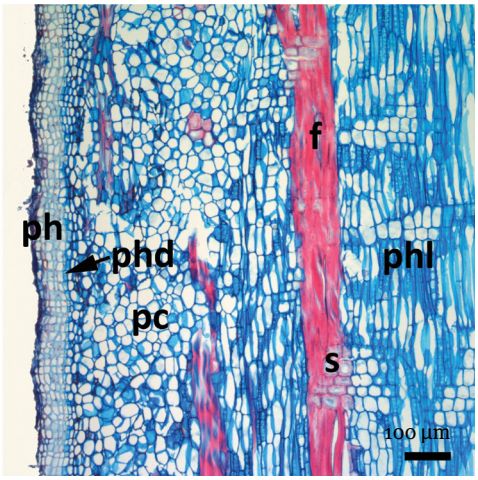
3 mm root, cross-section.



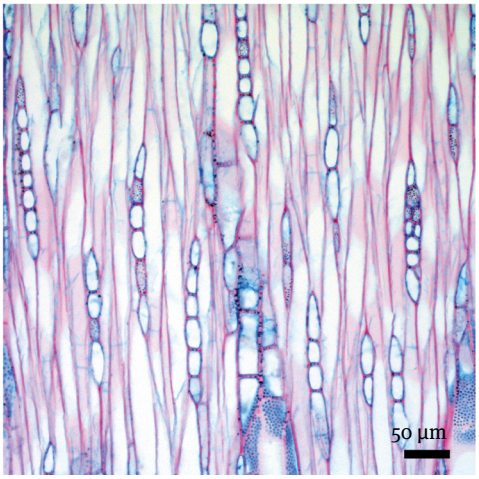
1 mm root, cross-section: remnants of epidermis and cortex visible.



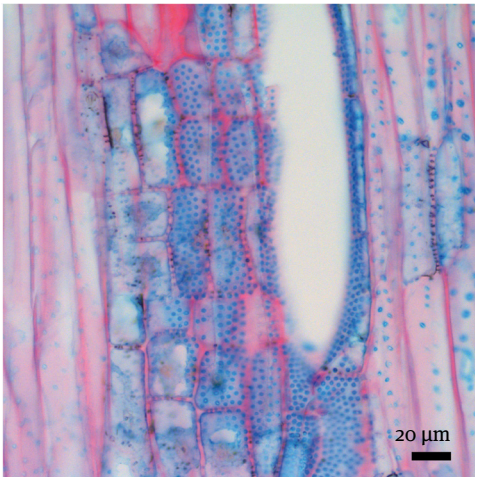
Axial parenchyma, cross-section: marginal (arrows); thickened cell walls of vessels.



External tissues, longitudinal section (phl: phloem, s: sclereids, f: fibres, pc: pericycle, phd: phelloderm, ph: phellem).



Rays, tangential view.



Cross-field pits (pits to vessels), libriform fibres, longitudinal section.

Characteristics of root tissues:

SECONDARY XYLEM		
Growth rings		Distinct, wedging growth rings present
Porosity pattern	Bordered pits	No typical ring porosity, larger size of early-wood vessels in external growth rings
Vessels	Arrangement	Solitary, in pairs, groups and **radial multiples** (of 3, 4 and more)
	Size	Growth ring (GR) number / No. of vessels measured / Mean tangential diameter ± stderr. (µm) GR1 332 18.3±0.32 GR2 615 27.7±0.51 GR3 479 32.3±0.83 GR4 308 41.0±1.16 GR5 132 34.5±1.09
	Perforations	**Simple**
	Spiral thickenings	Absent
	Intervascular pits	**Minute** (< 3 µm), alternate
	Tyloses	-
	Deposits	-
	Other characteristics	**Thick cell wall**
Libriform fibres and fibre tracheids	Type	Libriform fibres
	Other characteristics	-
Rays	Size in height	Less than 1 mm
	Width	**1-4 cells wide**
	Pits to vessels	**Minute**, similar to inter-vessel pits in size and shape throughout the ray cell
	Other characteristics	-
Axial parenchyma	Presence	Present
	Type	**Marginal Paratracheal**
Miscellaneous features		-
Crystals and other inorganic inclusions		Absent

BARK	
Phloem	Wide, uniform (fibres and sclereids may be present)
Ray dilatations	**Present in wider rays**
Fibres	Present in **tangential bands inside pericycle (and phloem)**, quantity varies
Sclereids	Present, accompanying fibres, quantity varies, may be completely absent
Crystals	**Navicular**, inside phloem parenchyma, phloem rays and pericycle, quantity varies (in thinner roots may be absent)
Periderm	**Periderm** thick/multilayered, **thin walled**, distinct phellem and phelloderm, remnants of epidermis and cortex preserved and visible in the bark over many years, phellem tears in triangular form due to root thickening

PRIMARY TISSUES	
Shape	Circular to star like, **polyarch**, sometimes inconspicuous
Miscellaneous features	Some parenchyma cells with thick cell walls and blue-stained content in the lumen

2.4 Anatomical identification of roots thinner than 1 mm

In samples of roots collected with a corer and from ingrowth mesh bags, the majority of roots are fine roots. Identification of the distal fine roots when they are disconnected from the thicker parts can be a very difficult task. When samples of roots are taken, tree species that grow in the vicinity should be noted, as this may eliminate unnecessary work with identification (Agerer 1987-2008). If morphological identification does not provide reliable results, anatomical investigation can help. However, the most distal roots lack the secondary xylem, which is the best part for identification purposes, whereas primary tissues lack specific structures that would enable easy identification. Therefore, for identification it is recommended to take the highest available root order. With great certainty it is possible to distinguish between conifers and broadleaved trees.

Primary resin ducts are common in many conifers (Fig. 2.4.1), even in some species that normally do not form secondary resin canals. Resin ducts are initiated already in embryos still within the seed. Initial cells appear near the root apex in the region of procambial differentiation, with the number of canals corresponding to the number of xylem poles in the root. The canals develop adjacent to the protoxylem strands (Larson 1994).

Resin ducts were present in all investigated conifers, from which *A. alba* (Fig. 2.4.1a), which normally does not form resin ducts in secondary xylem, was easily recognized by the presence of a central resin duct. A central resin duct was also observed by Brundrett et al. (1990) in *Abies balsamifera*. The primary xylem in *A. alba* can be 2-4 arch (Kutschera & Lichtenegger 2002). In all remaining investigated species two resin ducts corresponding to diarch primary xylem were observed. Although thicker roots in *P. sylvestris* can be di-, three- or tetra-arch, it is believed that root architecture affects the disposition of primary xylem within the root, with diarch roots positioned apically relative to triarch or tetrarch roots (Hishi & Takeda 2005).

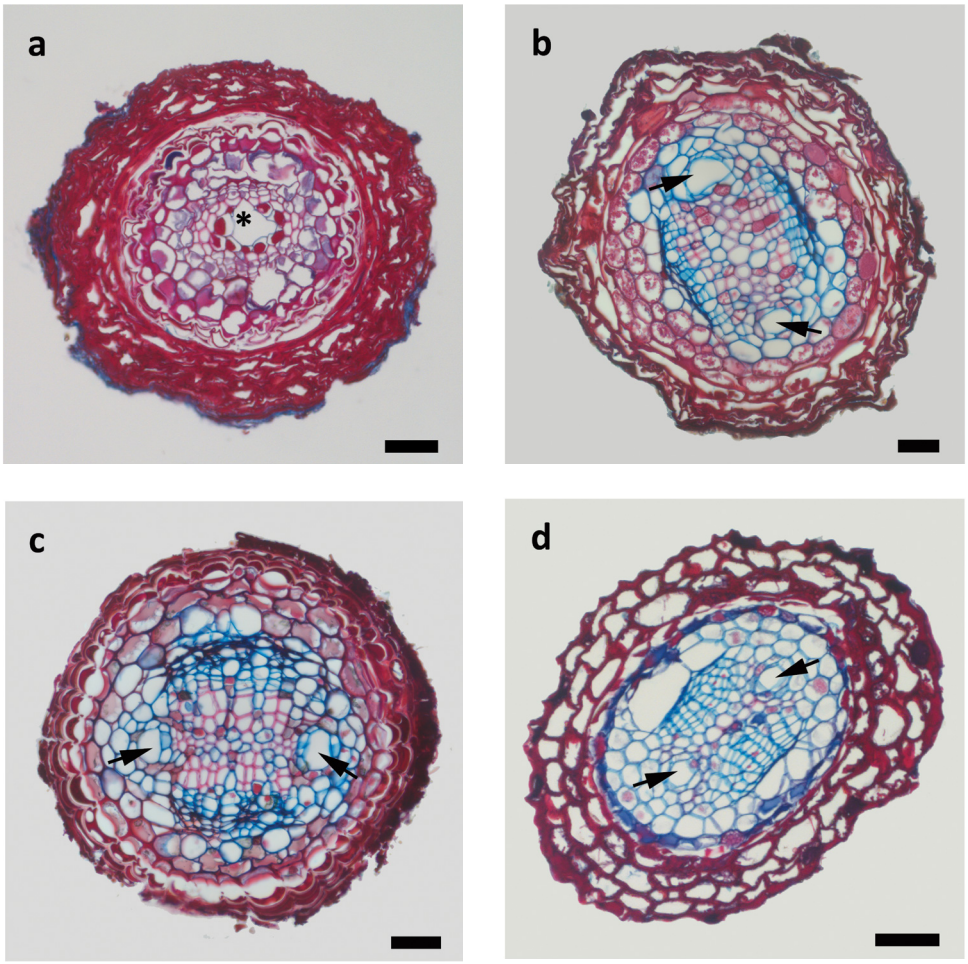


Fig. 2.4.1: Cross-sections of conifer fibrous roots thinner than 1 mm: a) A. alba, central resin duct marked with an asterisk, b) P. abies, c) L. decidua, d) P. sylvestris; bar = 50 µm, except in d), where it is 100 µm. Arrows show primary resin ducts.

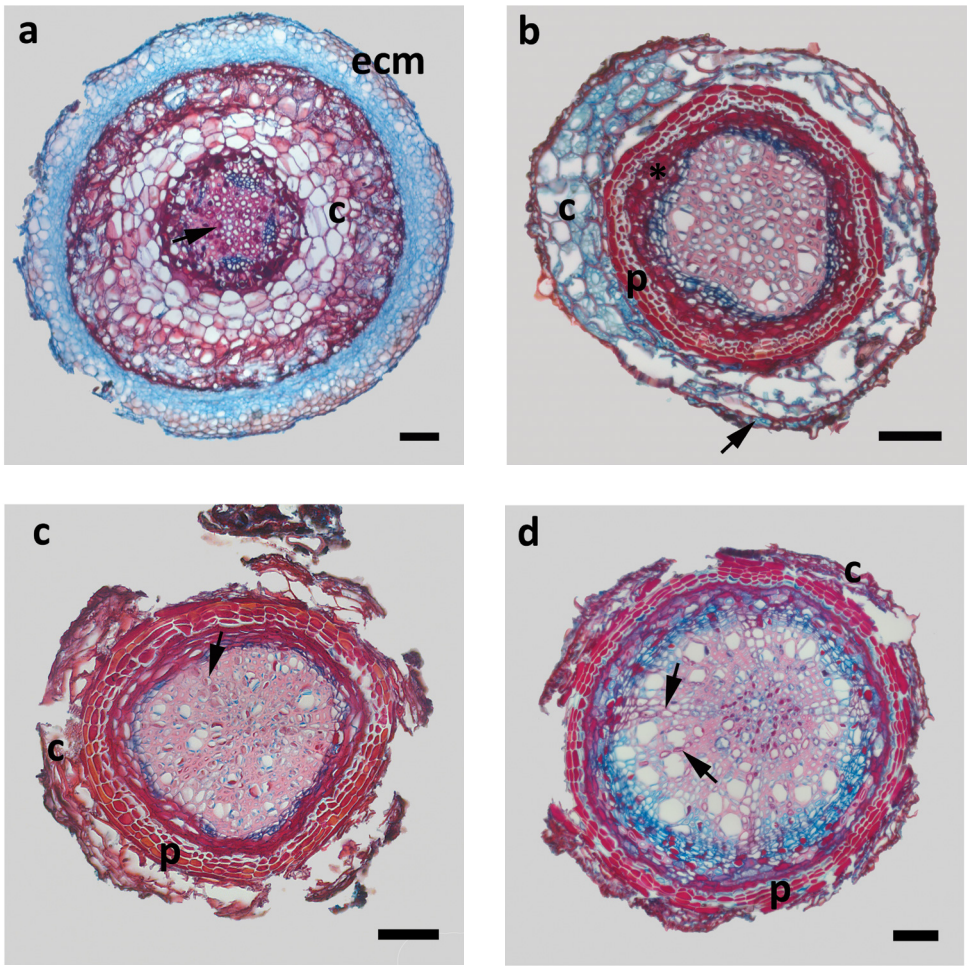


Fig. 2.4.2: Fibrous roots of F. sylvatica in different ontogenetic stages. a) Root tip with pentarch primary xylem (arrow). Endodermis (not clearly visible) separates vascular cylinder from the cortex (c). Epidermis is not evident. Root tip is surrounded by the ectomycorrhizal fungal mantle (ecm). Hyphae of fungus grow between outer cells of cortex. b) Secondary growth has produced first vessels and periderm (p), while the remaining cells of the pericycle (*) form a structure similar to cortex. Cortex (c) is still present as well as ectomycorrhizal hyphae. Here epidermis is evident (arrow). c) Rays begin to form (arrow), periderm is clearly visible and remnants of cortex (c) are still evident. d) With further growth rays become more evident (arrows), up to three cells wide, vessels are clearly visible, while remnants of cortex still cover the periderm (p) to some extent. Note that root diameter does not correspond to ontogenetic stages. Bar = 50 µm.

The chances of being able to identify the root increases with increasing level of ontogenetic development of the root. In Fig. 2.4.2 different ontogenetic stages in roots of *F. sylvatica* can be observed. The shape of primary xylem is sometimes barely evident or not evident at all. Arrangement of primary xylem in roots in general rarely corresponds with the ideal disposition shown in textbooks (Schweingruber 2007), while in the apical roots the situation is even more complicated, as the apical roots have a lesser amount of primary xylem/protoxylem than roots that are positioned more basally (Hishi & Takeda 2005), and pioneer roots have more protoxylem groups than do fibrous roots (Zadworny & Eissenstat 2011). With the beginning of secondary growth (Fig 2.4.2 b-d), the more characteristic anatomical structures are formed.

It is not necessarily the case that each primary root undergoes secondary growth. Many roots die before they advance to secondary growth and the longevity of the root is believed to be related to the amount of primary xylem (protoxylem) (Hishi & Takeda 2005). It must be emphasized that the thickness of the root itself does not necessarily mean that the root is in a later ontogenetic stage than thinner roots that occur in the same root system. Pioneer roots of the first root order and same age as fibrous roots have larger diameters than

fibrous roots (Zadworny & Eissenstatt 2011), but their beginning of primordial tracheary element formation starts later (Bagniewska-Zadworna et al. 2012). However, the functional xylem vessel elements were developed at the same time in fibrous and pioneer roots of the same age, but the secondary vascular development proceeded much more rapidly in pioneer roots (Bagniewska-Zadworna et al. 2012).

From the anatomical viewpoint, at certain points the distal roots of *A. pseudoplatanus* and *C. betulus* might appear very similar to each other (Fig. 2.4.3 b-e and c-f).

However, *A. pseudolatanus* is a tree species with arbuscular mycorrhiza, while *C. betulus* is ectomycorrhizal. In cross -sections of the most distal roots we should be able to find evidence of different symbiotic relationships in those two species – an ectomycorrhizal fungal mantle similar to one shown for *F. sylvatica* in Fig. 2.4.2a for *C. betulus*, with fungal hyphae growing between the cells of cortex and root hairs not preserved and arbuscular mycorrhizal structures – vesicles and arbuscules inside the cells of cortex in *A. pseudoplatanus* (as in Fig. 2.3.3 d) with root hairs preserved.

In Fig. 2.4.4 there are some further examples of variability of roots in primary growth and early stages of secondary growth.

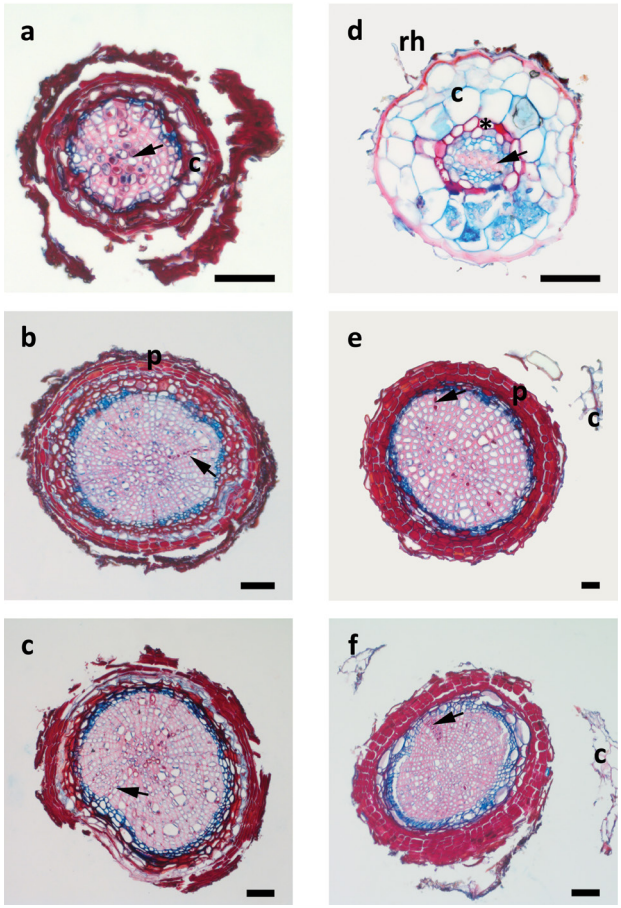


Fig. 2.4.3: Distal fibrous roots of C. betulus (a-c) and A. pseudoplatanus (d-f), abbreviations: p: periderm, c: cortex, rh: root hair. a) Transition from primary to secondary growth in C. betulus. Arrow: primary xylem, shape not clear. b), e) First year of secondary growth. Arrow: beginning of ray formation. c), f) Second year of secondary growth, rays begin to grow in width (arrow). d) Primary root of A. pseudoplatanus, here with distinctive diarch primary xylem (arrow), which usually gives roots of A. pseudoplatanus a slightly laterally compressed shape in later ontogenetic stages. Bluish structures inside some cells of the cortex are arbuscules of an arbuscular mycorrhizal fungus. Asterisk shows endodermis. Bar = 50 µm.

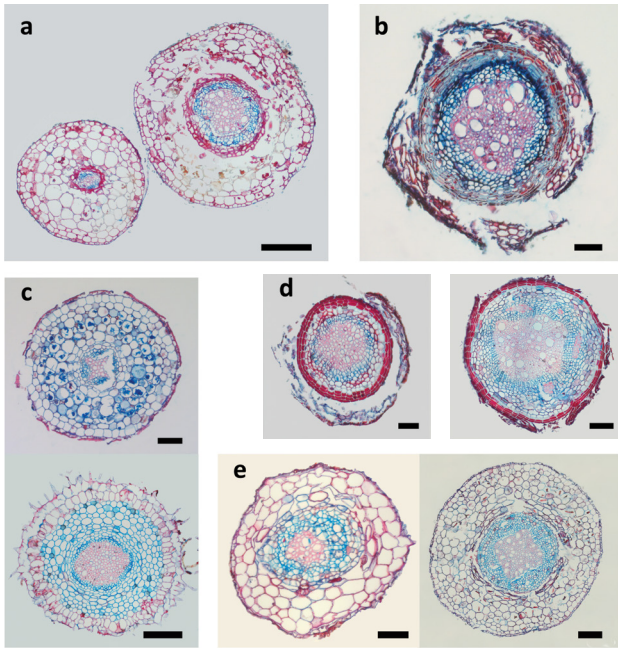


Fig. 2.4.4: Distal roots of a) P. avium (bar = 100 µm), b) Q. petraea (bar = 50 µm), c) F. excelsior (upper bar = 50 µm, lower bar = 100 µm), d) C. sativa (bar to the left = 50 µm, bar to the right = 100 µm) and e) P. nigra (bar to the left = 50 µm, bar to the right = 100 µm).

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