1

Introduction

1.1 The Role of Rhizomes in Agriculture and Pharmacology

Plant rhizomes play an important role in agriculture and in food production. Some vegetables such as asparagus form rhizomes. This is also the case for some sugar cane varieties (Matsuoka and Garcia 2011). Rhizome tubers of potatoes, of yams (*Dioscorea* species) and of ginger (*Zingiber officinale* Roscoe) are consumed as food.

Several plant rhizomes produce natural substances which are used as drugs or drug precursors. Pharmacognosy books and books on medicinal plants are full of examples such as a textbook by Singh and Sharma (2020). In this book, compounds derived from rhizomes of *Asparagus*, *Colocasia*, *Curcuma*, *Dioscorea* and *Zingiber* species are described.

Many troublesome weeds spread via rhizomes such as purple nutsedge: *Cyperus rotundus* L., quackgrass: *Elymus repens* (L.) Gould, cogongrass: *Imperata cylindrica* (L.) P. Beauv, johnsongrass: *Sorghum halepense* (L.) Pers. or itch grass: *Rottboellia cochinchinensis* (Lour.) Clayton.

1.2 Characterization of Rhizomes in Literature

A rhizome is defined by Bell (2008) as 'A stem growing more or less horizontally below ground level. Rhizomes tend to be thick, fleshy or woody, and bear scale leaves or less often foliage leaves, or the scars when these leaves have been lost; they also bear adventitious roots most frequently at the nodes.' Troll (1935) stresses that rhizome internodes are stunted. Also, he highlights homorhizy as characteristic of rhizomes. He does, however, not mention the horizontal growth. This makes sense as the rhizomes of several plant species do not grow horizontally as we will show later.

The amount of comparative English synoptic literature on rhizomes is quite restricted.

Only few articles discuss general characteristics of rhizomes. One is Holm's article on the application of the term 'rhizome' (1929).

Burkill (1960) claims that the term rhizome was introduced to science by the British botanist Ker-Gawler without any reference. According to Burkill, a rhizome is characterized by its cauline nature, by horizontality and by thickness. The term thickness is, however, not specified. Ehrhart (1787) uses the term rhizoma for *Polypodium oreopteris* syn *Oreopteris limbosperma* (All.) Holub and makes clear that this fern rhizome is different from a root.

Unfortunately, most classical textbooks on plant anatomy just contain a few lines on rhizomes. Esau (1977) even does not mention them. Troll's German textbook on general botany (1973) is an exception insofar as it provides a few detailed and illustrated explanations. In volume 1 (1935) and volume 3 (1943) of his 'Comparative Anatomy of Higher Plants', Troll devotes several chapters to rhizome characteristics, especially to adventitious roots. Von Guttenberg (1968) created various histological illustrations on the formation of rhizome roots.

Rhizomes: Hidden Stems with Unknown Diversity, First Edition. Hansjörg Krähmer and Linnea Hesse.

In Arber's book on monocotyledons (1925), rhizomes are only referred to briefly. Her grass book (1934) contains a few details on bamboo and grass rhizomes. Other classical anatomy compilations of monocot plant orders or families contain short paragraphs on the anatomy of rhizomes only. Metcalfe (1971), for example, lists just a few general characteristics of the rhizomes of sedges. The general morphology of grass rhizomes is described by Metcalfe (1960) in two sentences only. His first statement 'Grass rhizomes, in species where these subterranean stems are well developed, are essentially similar in structure to the culms' can, however, no longer be supported. Kraehmer (2019) demonstrates that underground stems of some grasses may look quite different compared with above-ground culms. Tomlinson (1961, 1969, 1982) characterizes rhizomes of representatives in the Zingiberales order or in the former group Helobiae. Cutler (1969) reserves a few lines for representatives of the former Juncales order. Ayensu (1972) discusses the characterization of rhizomes in the order Dioscoreales on two pages.

Some of these authors admit that structures of monocot rhizomes deserve further investigations. When it comes to the description of the outer part of the stele and to the growth of the rhizome, Metcalfe (1971) concludes 'The reader's attention is drawn to this, more in the hope that the subject will receive further investigation on ontogenic lines than because the author feels certain about it'.

On the other side, it must be stressed here that several anatomical rhizome descriptions of selected species or groups were published within the last decades. This is the case for several agricultural weeds such as for *Cyperus* species, *Elymus repens* (L.) Gould syn *Agropyron repens* (L.) P. Beauv., *Imperata cylindrica* (L.) Raeusch., *Rottboellia cochinchinensis* (Lour.) Clayton, *Sorghum halepense* (L), for invasive weeds such as *Arundo donax* L., for aquatic monocots or for bamboo. Literature on these groups was summarized by Kraehmer and Baur (2013) and Kraehmer (2016, 2019). A more systematic and comparative approach to the anatomy of rhizomes was provided for a few groups such as, for example, for the family Iridaceae (Rudall 1984) or for Marantaceae (Tomlinson 1961).

A recently published book designed for archaeologists in the first instance provides an interesting compilation of a few facts and principal considerations on rhizomes (Hather 2017). It contains some findings we will elaborate on here more in detail. Also, we will try to cover many aspects not specified in this book with a 'detailed description of the morphological and anatomical characters used in the identification of charred vegetative parenchymous organs'.

A number of terms for stem modifications are used in literature without precise definitions.

A clear distinction between rhizomes, runners and stolons is for example not easy. Troll (1935) defines a runner as a lateral shoot of basal leaves that develops in a peculiar form insofar as it grows along the soil surface and that it has prolonged internodes. In his chapter on potato runners, he distinguishes, however, between below-ground and above-ground runners. He uses the term stolon in this context also. Bell and Tomlinson (1980) discuss the term rhizome in a general way including organs such as stolons, offsets, or suckers which may intergrade with tubers and corms. We will try to find criteria which allow a distinction between several existing rhizome modifications.

Unfortunately, we can only use selected species here for general conclusions. We will try to describe rhizomes of lycophytes, ferns and monocot, eudicot, ANA grade and magnoliid species separately. We will then concentrate on differences between these groups.

We will begin with lycophyte and fern rhizomes as these plant groups are assumed to be related with the evolutionary early tracheophytes. We will continue with monocot rhizomes as these often differ considerably from above-ground stems. The anatomical differences between dicot rhizomes and above-ground stems are less pronounced in many cases as we will see. Among the gymnosperms, rhizomes are only those found in the Gnetaceae family (McLean 1950).

1.3 Rhizome Anatomy

Rhizomes of many eudicots can be divided into an outer cortex and an inner central bundle cylinder. Falkenberg (1876) discusses the question if this distinction is also possible for monocot stems as bundles in monocots may be distributed all over the stem section. This question can, however, be answered easily for most rhizomes as Von Guttenberg (1943) explained and as we will see later in our book.

The innermost cortex cells of rhizomes often differentiate into a sheath that can appear in different modifications. This sheath, for example, can be differentiated as a starch sheath or as an endodermis with Casparian strips. It is often part of a boundary that is differentiated in a characteristic way. Lateral roots may arise from this boundary. In consequence, some authors use the same boundary terminology for roots and rhizomes. Following Esau (1977), we believe that the undifferentiated use of the two terms endodermis and pericycle is not always justified, neither for above-ground stems nor for rhizomes.

Many authors have applied these terms for stems in the past. Troll (1943) uses the terms endodermis and pericycle when describing below-ground and above-ground stem boundaries.

Von Guttenberg (1943) applies the term endodermis in his German overview of plant sheaths to all kinds of sheaths in roots, stems and leaves. He even provides a list of plant orders with an endodermis in shoots ('Sproßendodermen'). With others, he uses it as a functional term. In some cases, he calls non-suberized sheaths starch sheaths. He clearly distinguishes, however, an endodermis from the exodermis of roots which he defines as a hypodermal layer following the rhizodermis in his book on primary roots of angiosperms (Von Guttenberg 1968). He admits on the other side that some scientists actually named the exodermis 'outer endodermis' in the 19th century.

A few molecular biologists see similarities between the root endodermis and the exodermis (Geldner 2013). Based on the existence of Casparian strips, these similarities could justify the classification of the exodermis as a layer with the function of an endodermis.

Leersten (1997) highlights the occurrence of an endodermis in stems and leaves and provides an update on 20th-century literature. He stresses that from his point of view, the term endodermis can just be defined based on its function as a border.

On the other side, position and ontogeny often lead to the use of different expressions for structures which are similar to an endodermis: the exodermis as a hypodermal sheath, the mestome sheath as a special layer in leaves, the starch sheath as a border between cortex and vascular cylinders in many stems.

The identification of an endodermis is rather easy in roots. Initially, it contains lignin and at later developmental stages suberin which can easily be stained. For stems, it is, however, more complicated. A recent overview of the endodermis in angiosperm shoots (Seago 2020) claims the occurrence of sheaths with Casparian strips in 95 plant species. Its depictions often show, however, cells in a secondary or tertiary stage but not true Casparian strips as defined, for example, by Evert (2006) or Esau (1977). Also, this paper does not reflect on the ontogeny of sheaths and the position of an endodermis in stems when compared with that in roots.

Some authors attribute the monocot endodermis meristematic properties leading to secondary growth as, for example, in *Cyperus* rhizomes (De Menezes et al. 2005). Kroemer (1903) and Bond (1930) report on dividing endodermis cells in dicot roots. Also, endodermis and endodermis-like structures of angiosperms are often associated with meristematic cell layers. Esau (1977), however, stresses that the endodermis is usually uniseriate with the exception of a few dicot species with secretory canals. She defines a structure that is usually associated with the endodermis of roots and shows a meristematic character: the pericycle. She defines the pericycle as the limiting layer of the stele. Within the root, it arises from the same part of the apical meristem as vascular tissues. Some authors call this layer pericambium as, for example, Von Guttenberg (1968).

The pericycle of eudicot and monocot roots can easily be defined. It surrounds the coherent elements in the case of actinostelic centres and forms the outer layer of the stele. It is located between endodermis and stele.

The definition of a pericycle in above-ground eudicot stems becomes, however, much more complicated when considering various stem specificities. Vascular bundles often do not form a coherent vascular bundle cylinder. Endodermises, endodermoids and starch sheaths can often not be identified in stems at all.

Foster and Gifford (1974) make clear that 'the pericycle is not present in all vascular plants' and that the 'so-called pericycle in the stems of many angiosperms is actually the outermost portion of the primary phloem'. Metcalfe and Chalk (1965) use the terms pericycle and pericyclic regularly for stems despite declaring in their introduction: 'In the stems of many plants, the "pericycle" is not clearly defined, nor, in fact, is there any general agreement concerning the precise meaning of this term. There is, nevertheless, a portion of the stem between the inner boundary of the primary cortex and the outer part of the primary phloem in which mechanical elements usually arise'. Stover (1934) uses the term pericycle for peripheral sclerenchyma layers in grass stems. His understanding of a pericycle has nothing in common with the definition of a layer of meristematic cells.

As already stated above, monocot rhizomes and above-ground monocot stems do not form coherent xylem or phloem layers at all. It is impossible therefore to find coherent 'primary phloem or xylem' in monocots.

On the other side, separation layers between a cortex and a central bundle cylinder are quite common in monocot rhizomes. Their origin can, however, not be associated with an endodermis or a pericycle in a root as we believe.

The term pericycle is also used in descriptions of the rhizome of ferns. The position and function of fern pericycles are, however, quite different from that of pericycles in eudicot and monocot roots. Ogura (1972) defines the fern pericycle as 'a zone between the phloem and the endodermis, consisting of one or more parenchyma layers which are more or less larger than the cells of the phloem or endodermis'.

We will discuss the term pericycle in Chapter 11 and at the end of our book again (Chapter 22).

The boundary layer between the rhizome cortex and the central vascular bundle cylinder is sometimes accompanied by a primary thickening meristem (PTM, Rudall 1991). Roots often arise from this boundary.

Weber (1936) distinguishes between different types of species with stem-borne roots:

- dicot representatives with roots arising from the hypocotyl,
- plants with roots at nodes,
- those with roots at internodes,
- species with roots at buds.

Rhizome boundaries often differ considerably from root boundaries. Mangin (1882) proposes the term 'couche dictyogyogène' or dictyogenous layer for the rhizome cortex border with the intention to characterize its special anatomy. The Greek word δίκτυον means 'net'. The term can therefore be translated as a 'net-forming layer'. The resulting layers of vascular bundles and fibres are the result of anomalous thickening and of root extensions. We will show examples later. Other than Von Guttenberg (1968), we do not regard the dictyogenous layer as equivalent to the pericycle.

Boundaries are often not found at early rhizome stages and not in all monocot rhizomes. The anatomy of borders can vary considerably during plant development. In many cases, an endodermis, endodermoid or starch sheath is only formed at advanced developmental stages.

The secondary formation of roots requires meristematic cells such as the cells of the pericycle in the root. Within *Arabidopsis* roots, the role of pericycle cells was investigated on a gene expression level. The pericycle is regarded today as a site where plant stem cells are able to generate new tissues (Perez-Garcia and Moreno-Risueno 2018).

When using terms for stem sheaths separating cortex and central vascular cylinders, we often tend to follow Tomlinson (1969), Metcalfe (1971), Rudall (1984), Kraehmer and Baur (2013) and Kraehmer (2019) who prefer the term endodermoid instead of endodermis when analysing organs other than roots. We use this term especially for rhizomes in which we cannot find characteristic Casparian strips with our methods employed when they just look like starch sheaths or when the border between cortex and cylinder is not closed. Some authors called border layers between cortex and cylinder phloeoterma (Von Guttenberg 1968).

It should be noticed here that earlier Marantaceae rhizome descriptions of Tomlinson (1961) contain the term endodermis whereas later ones (1969) use the term endodermoid presumably due to changing insights.

The inner bundle sheath of many grass leaves has characters of an endodermis (Brown 1958). Schwendener (1890) had called these sheaths mestome sheaths. Again, this term has to do with its special location within a leaf. Also, its surrounding is quite different from that of an endodermis in roots.

Unfortunately, the term endodermoid is not accepted by several scientists. Van Fleet (1961), for example, was a strong opponent of it. We will try here to justify our view on terminologies used for boundaries between cortex and central cylinder of monocot rhizomes based on our own findings.

Also, we will demonstrate that the structure of underground monocot rhizomes is usually quite different from that of regular aerial stem parts.

Some above- or near-ground stems may adopt or keep features of underground rhizomes (Bell and Tomlinson 1980) such as the formation of stem-borne roots. This fact makes it difficult to distinguish in a clear way between rhizomes and regular, above-ground stems.

A very exact definition is apparently not always possible. It appears that scientists from the 18th and 19th centuries were already aware of this. The word rhizome contains the Greek origin ῥίζα (rhiza), meaning root, and tells us presumably just that a rhizome looks similar to a root.

1.4 Genomics of Rhizomes

Within the last decade, molecular geneticists have started to analyse molecular mechanisms

and signalling processes leading to stolon and rhizome initiation and development (Guo et al. 2019). Gene mapping data and transcriptome sequencing results were published for several rhizome-producing species such as *Phyllostachys praecox* (Wang et al. 2010), *Oryza* species (Hu et al. 2011), *Phragmites australis* (He et al. 2012), *Miscanthus* species (Kim et al. 2014), *Sorghum* species (Zhang et al. 2014) and for *Nelumbo nucifera* (Yang et al. 2015).

We will reserve a chapter for the discussion of these new insights into molecular regulatory mechanisms in rhizomes.

Rhizome-producing species may form large colonies or groups of genetically identical individuals. Examples are bamboo forests (Fig. 1.1) or clones of perennial weeds in arable fields such as of perennial *Cyperus* species or of *Sorghum halepense*. Advantages and disadvantages of such 'uniform' units will be discussed later.

Figure 1.1 Little bamboo forest of *Phyllostachys flexuosa* clones in the Botanical Garden of Frankfurt am Main (Germany).

Many open questions and a missing up-to-date overview on rhizomes make it worthwhile from our point of view to summarize all these aspects and to provide a compilation that shows what rhizomes of different plant groups have in common and which features are species- or group-specific.

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