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Survival strategies of plants during secondary growth: barrier properties of phellems and lenticels towards water, oxygen, and carbon dioxide

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Abstract

Ever since plants began to conquer the terrestrial environment, a simple but effective evolutionary strategy has been employed to cope with the combined necessities of preventing an excessive loss of water via the aerial surface while also supporting the vital exchange of CO₂ and O₂ for photosynthesis and respiration. Large areas of the primary above-ground surface of plants are covered by a hydrophobic, non-cellular cuticle which effectively minimizes evaporation and very strongly reduces exchange of CO₂ and O₂. Hence, gas exchange is controlled by regulating stomatal apertures. Upon wounding or entering into secondary growth, however, the epidermis, cuticle, and stomata are replaced by a phellem (cork), which is produced by a lateral cambium, the phellogen. Former stomata are replaced by lenticels, which are multicellular structures and functionally analogous to stomata. In the secondary plant body, phellems effectively prevent the loss of water from the cortex of the stem while lenticels support the exchange of vital gases such as CO₂, O₂, and water vapour. The permeance of these gases via the lenticels reaches a maximum during July and is minimal during autumn and winter. In contrast to stomatal control, gas exchange through phellems is regulated by long-term structural changes. The permeances of cuticles, phellems, and lenticels are compared and discussed.

Introduction

The first land plants evolved ~450 million years ago. The evolutionary move from an aquatic to a terrestrial existence demanded several structural innovations and adaptations, among them the establishment of supportive tissues (collenchyma and sclerenchyma), the evolution of organs for anchorage and absorption of water and minerals (roots), and the development of efficient fluid-conducting systems (xylem and phloem). Additionally, all above-ground parts of plants were and still are faced with competing demands. On the one hand, the water potential gradient between the plant body and the surrounding environment changes continuously and the atmosphere is mostly so far from water saturation that there is a danger of lethal dehydration. The demand for a protective barrier is obvious. On the other hand, plant surfaces have to enable the vital exchange of CO₂ and O₂ essential for photosynthesis and respiration. A perm-selective membrane discriminating actively and/or passively between water and CO₂/O₂ would cope with these demands. However, such a limiting barrier at the aerial surfaces of plants has never been realized during phylogenesis. Instead, another strategy evolved. This strategy was established with the first land plants and has varied only slightly during evolution up to the angiosperms (Edwards et al., 1996).

All primary aerial surfaces of vascular plants and some bryophytes are covered by a non-cellular and hydrophobic superficial film, the cuticle. Kidston and Lang (1920) described a conspicuous cuticle on aerial branches of Rhynia, believed to be one of the first plants that colonized land. The thalli of certain members of the Hepaticae (liverworts) are also covered by a cuticle (Schönherr and Ziegler, 1975). All Bryophyta (mosses) investigated were

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Abbreviations: EM, extractable material; EPM, extracted phellem membrane; PM, phellem membrane.

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found to have at least hydrophobic surfaces (although not necessarily cuticles) on gametophytes and sporophytes (Haas, 1999). All above-ground organs of ferns and seed plants are coated by a cuticle. Even the higher water plants that descended from land plants retained their cuticles as a reminder of their former environment (Arber, 1920). This extracellular layer covers leaves, primary stems, flowers, petioles, fruits, trichomes, and even glands, and it is an effective barrier against uncontrolled water loss and gas exchange (Schönherr, 1982; Lendzian and Kerstiens, 1991; Riederer and Schreiber, 2001). Roots do not develop a cuticle, and even aerial roots of the epiphytes lack this structure (Esau, 1977).

The functional solutions to the unhindered exchange of CO₂ and O₂ between the intercellular air space and the atmosphere were the establishment of the relatively poorly regulated air pores of the liverworts and the highly regulated stomatal apertures of all sporophytes. These pores are suitable gates for the diffusion of gases and vapours, but prevent liquid water from entering a plant’s intercellular space (Schönherr and Bukovac, 1972; Schönherr and Ziegler, 1975). Thus, adaptation to the atmospheric environment and to the varying water potential gradient between plant and atmosphere resulted in the concerted evolution of cuticles and stomata (Edwards et al., 1998). Both parts of the aerial plant surface contribute to a structurally and functionally integrated barrier system that optimizes respiratory and photosynthetic gas exchange under the constraint of maintaining a vital water balance.

This master plan works well during the ontogeny of many seed plants up to their final state, the primary plant body, which is typical for herbaceous plants, and in cases where the epidermis is able to stretch upon secondary growth (e.g. in the stem of the rose plant). However, when the cuticle—or usually the cuticle plus epidermis—becomes damaged or destroyed by wounding or secondary growth of the stem, the cuticle–epidermis–stomata complex is never regenerated but is replaced by completely new structures. A new, lateral meristem within the outer part of the cortex, the phellogen or cork cambium, generates the multicellular phellem (cork) centrifugally and the phellogen (cork parenchyma) centripetally. In a species-specific pattern, the phellem is interspersed with lenticels, aerenchymatous cork areas which are regarded as paths for the exchange of water vapour, oxygen, and carbon dioxide between inside and outside. The phellem–phellogen complex is called the periderm. It belongs to the secondary plant body and represents the new barrier between the secondary stem and the atmosphere. The periderm is believed to act in a way analogous to the cuticle–epidermis–stomata complex. In the final state, the phellem is made up of multiple layers of dead cells and waxes, and provides the barrier for water and gas transfer. In this context, it is worth pointing out the similarity between structures that have evolved in different organisms to protect them against water loss, all of which consist of a lipophilic matrix associated with waxes. This holds true for plant cuticles (cutin+waxes), phellem (dead cork cells+suberin+waxes), insect cuticles (chitin+waxes), and even for human skin (stratum corneum+keratin+waxes).

The structural features of many periderms have been described in detail (Mader, 1954; Langenfeld-Heyser, 1997; Rosner and Kartusch, 2003), but few attempts have been made to quantify water and gas exchange of woody stems (Haberlandt, 1928; Geurten, 1950; Langenfeld-Heyser et al., 1996). From these scattered reports, it appears that it is mainly the lenticels that provide pathways for gas exchange. An important step towards understanding and unambiguous quantification of the transfer of molecules via phellem was the use of enzymatically isolated and well-defined phellem areas where lenticels were known to be either present or absent (Schönherr and Ziegler, 1980; Vogt et al., 1983; Groh et al., 2002; Schreiber et al., 2005). Such isolated phellem membranes (PMs) can be handled just like isolated cuticular membranes. They can be used in the same experimental devices for the determination of transport characteristics and manipulated in the same way as cuticles. The transport properties of phellem and lenticels can be characterized unequivocally for phellem from different plant species if the following variables are precisely controlled: type of diffusants, driving forces, temperature, water content, and presence or absence of lenticels. Thus, quantitative comparisons between periderms and cuticles are possible.

This communication summarizes recent data on the transport properties of phellem and lenticels from potato tubers and trunks of selected tree species. It is centred on the permeance to water vapour, CO₂, and O₂. New data describe the influence of varying lenticel structures on permeance. This set of data will be compared with others generated for plant cuticles to create an integrated approach to understanding how plants cope with the problems associated with vital gas exchange between the interior and exterior during primary and secondary growth.

**Mechanical and enzymatic isolation of phellem**

The bark of birch (Betula sp.) peels off in large sheets, which are made up of several layers produced by periodical growth. These can be easily separated mechanically, resulting in single layers of phellem. The individual phellem consists of 5–8 heavily suberized cell layers and highly variable numbers of cell layers that are only slightly, if at all, suberized (Schönherr and Ziegler, 1980). The thickness of such a single layer was determined to be ~150 μm, of which the heavily suberized part made up ~50 μm. The water permeability for such mechanically isolated sheets was determined in the same way as for leaf cuticular membranes. The disadvantage of this isolated membrane is its heterogeneity manifested in the differently suberized...
cell layers. However, water permeability was quantitatively characterized for the first time and it was assumed that transport data reflected the barrier properties of the heavily suberized cell layers (Schönherr and Ziegler, 1980). This was confirmed later on (Groh et al., 2002).

A further step towards working with isolated and well-defined phellem layers was the introduction of an enzyme-based isolation procedure previously applied to plant cuticles (Orgell, 1955; modified by Schönherr and Riederer, 1986). A fungal pectinase/cellulase system disintegrates plant tissues by destroying middle lamellae and primary cell walls, leaving all structures intact that are not accessible to the hydrolytic enzyme mixture. Application of this method resulted in intact phellem layers that were free from unwanted tissues and cells (Vogt et al., 1983; Groh et al., 2002). The isolated phellem consisted solely of heavily suberized cells, organized in typical radial rows, with the connecting middle lamellae completely intact. As with the isolated cuticles, investigation by transmission electron microscopy (TEM) and scanning electron microscopy (SEM) gave no indication of structural changes during the isolation procedure. In vitro systems, however, always provoke the question of how isolation procedures might affect vital characteristics. Technically, it is not possible to compare the integrity of the phellem barrier before and after isolation as with cuticles (Becker et al., 1986). However, when well-defined data from transpiration experiments, for example with twigs, were available and used to calculate permeance, this resulted in values comparable with those obtained with isolated phellem layers. To give one example, transpiration experiments were conducted by Haberlandt (1928) on 2-year-old twigs with sealed lenticels from Aesculus hippocastanum and Sambucus nigra. Loss of water (measured as loss of mass) at 18 °C and 55% humidity was given as gram per day and unit area. This information is sufficient to calculate the permeance (see below) and to compare data obtained with very different experimental approaches. Such an agreement between results indicates that the isolation procedure conserves basic functional characteristics.

The time required for isolation of phellem layers differs markedly. Peels from freshly harvested potato tubers (called mature throughout the text) needed to be incubated in the enzyme solution for up to 4 weeks before the phellem separated from phellogen and storage tissues. Upon storage of tubers in air, this incubation time became shorter the longer the tubers were stored. After a storage period of 9 months, isolation only took 1 week. Isolation of phellem from tree trunks is even more time-consuming (Groh et al., 2002). Sufficiently large areas of the outermost bark phellem, from which discs could be punched out for experimentation, could only be isolated after 2 months of incubation. Care was taken to select different areas so that lenticels were either present or absent in the individual discs. With this, the first application of the enzymatic isolation procedure to secondary tissue, an important tool is now available for analysis and characterization of the barrier properties of the secondary outermost tissue of plants, the phellem.

### Structural features of isolated phellem layers from potato tubers and tree trunks

All research groups using the enzymatic method for isolating phellem from different plants have found that the isolated PMs consisted of 5–8 layers of heavily suberized and dead phellem cells packed in radial rows (Schönherr and Ziegler, 1980; Vogt et al., 1983; Groh et al., 2002; Schreiber et al., 2005). The individual cells and cell layers were kept together by an intact middle lamella system. Intercellular spaces or disrupted cell walls that might indicate damage during isolation were absent. Further prolonged treatment with hydrolytic enzymes did not alter the structure or function. Therefore, it is clear that the conjunctions between cells, the middle lamellae, are not accessible to pectinases and cellulases. This information may be important as it indicates structural features different from those in middle lamellae keeping living cells together. As discussed for lignin and cellulose (Schmidt and Schönherr, 1982; Lendzian et al., 1986; Thomson et al., 1995), suberin and/or lignin seem to block the destruction by the hydrolytic enzymes. This not only indicates that suberin/lignin is part of the secondary cell wall but also that it must be interwoven with the middle lamella system.

Isolated peripheral PMs were obtained from a variety of plants. Important characteristic features are summarized in Table 1. Although the number of cork cell layers ranged from five to seven, phellem thickness varied much more widely between 50 μm (Betula pendula) and 328 μm (S. nigra). This variation was due to large differences in thickness of the individual cork cell layers between different species and varieties. The data are for potatoes that were just ready for harvest and for twigs and trunks of 30-year-old trees. Post-harvest storage of the potato tubers resulted in an increase in phellem thickness from 116 to 128 μm (cv. Combi N) and from 85 to 98 μm (cv. Erna) within 2 months. No further significant changes could be observed during longer storage periods. These changes occurred most clearly at high humidities and at temperatures of ~20 °C, indicating an impact of ongoing physiological processes. Tree phellem also undergo a significant change in thickness during ageing in vivo. Phellem from S. nigra had an average thickness of 92 μm in 5-year-old plants, 139 μm at 10 years and 328 μm at 30 years, i.e. the thickness increased by a factor of 3.6 over a period of 25 years. Similar changes have also been observed with the other tree phellem, but the thickness increased only by factors of between 1.4 and 1.6.

A second structural property of isolated phellem is the dry weight per unit area (DW; Table 1). This quantity is
Table 1. Characteristic features of phellem membranes (PMs) isolated from mature potato tubers and selected trees (30 years old)

<table>
<thead>
<tr>
<th>Plant material</th>
<th>Thickness (µm)</th>
<th>Dry weight of PM (mg cm⁻²)</th>
<th>Dry weight of EPM (µg cm⁻²)</th>
<th>Soluble lipids (µg cm⁻²)</th>
<th>Density of PM (g cm⁻³)</th>
<th>Lenticel area (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Solanum tuberosum</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>cv. Marittaᵃ</td>
<td>60</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>5</td>
</tr>
<tr>
<td>cv. Combi Nᵇ</td>
<td>116</td>
<td>3.1</td>
<td>2.8</td>
<td>28.5</td>
<td>0.21</td>
<td>4</td>
</tr>
<tr>
<td>cv. Ernaᶜ</td>
<td>85</td>
<td>2.1</td>
<td>1.8</td>
<td>18.3</td>
<td>0.26</td>
<td>4</td>
</tr>
<tr>
<td>cv. Désiréeᶜ</td>
<td>150</td>
<td>1–2</td>
<td>–</td>
<td>10–100</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Betula pendulaᵈ</td>
<td>45–50</td>
<td>2.5</td>
<td>1.25</td>
<td>1250</td>
<td>–</td>
<td>3.1</td>
</tr>
<tr>
<td>Betula potaniniᵈ</td>
<td>82</td>
<td>3.7</td>
<td>2.4</td>
<td>1300</td>
<td>0.45</td>
<td>10</td>
</tr>
<tr>
<td>Abies albaᵈ</td>
<td>175</td>
<td>13.1</td>
<td>10</td>
<td>3000</td>
<td>0.75</td>
<td>–</td>
</tr>
<tr>
<td>Aesculus pseudo-platanusᵈ</td>
<td>133</td>
<td>5.6</td>
<td>5.2</td>
<td>398</td>
<td>0.42</td>
<td>–</td>
</tr>
<tr>
<td>Aesculus hippocastanum⁵</td>
<td>185</td>
<td>13.3</td>
<td>12.9</td>
<td>399</td>
<td>0.72</td>
<td>–</td>
</tr>
<tr>
<td>Sambucus nigra⁵</td>
<td>328</td>
<td>36.4</td>
<td>31.9</td>
<td>4477</td>
<td>1.1</td>
<td>15</td>
</tr>
</tbody>
</table>

ᵃ Vogt et al. (1983);ᵇ Groh (2000);ᶜ Schreiber et al. (2005);ᵈ Schönherr and Ziegler (1980);⁵ Groh et al. (2002).

much easier to determine and it is a fairly good reference variable for linking structural and transport properties. Again, this quantity is not a constant but changes during development. Potato tuber phellem showed an increase in DW from 3.1 to 4.3 mg cm⁻² (cv. Combi N) and from 2.1 to 2.4 mg cm⁻² (cv. Erna) within 2 months of storage. An increase in DW has also been determined for the phellem of *A. hippocastanum* and *S. nigra*. While *Aesculus* hardly showed any change in DW between young and mature periderm, the development of the *Sambucus* phellem was accompanied by an increase in DW by a factor of 7. Again, *Sambucus* phellem diverged from other tree phellem. The increase in DW was accompanied not only by an increase in membrane thickness but also by a severe increase in density, which rose from 0.56 g cm⁻³ (5 years old) to 1.1 g cm⁻³ (30 years old). Such a significant change in density has not been observed with any of the other phellem presented here. In general, density is a fairly constant quantity. Although these examples point to the possibility that thickness and DW may not be correlated, a regression analysis of the thicknesses of all phellem investigated at different developmental stages against their DW showed that for thicknesses (d) between 50 and 328 µm, the relationship followed the linear equation

\[
DW (\text{mg cm}^{-2}) = 0.13(\text{mg cm}^{-2} \mu\text{m}^{-1})d(\mu\text{m}) - 7.48(\text{mg cm}^{-2})
\]

with a coefficient of determination \(r^2\) of 0.95 (calculated from the data in Table 1). The values of d were normally distributed. This equation allows a choice to be made between d and DW as the structural reference variable for analysing transport characteristics, which is especially useful when only one of the variables can be determined.

All isolated phellem investigated contained a certain amount of material extractable by organic solvents (Table 1). *Betula pendula* phellem contained up to 50% of its DW in the extractable fraction, whereas *Aesculus* contained only 3%. Even within species, but not significantly within varieties, variation seems to be pronounced. As with cuticular membranes, one may consider PMs to be made up of two components, the extractable material and the non-extractable matrix (polysaccharides and suberin). Only one report exists describing changes in the extractable fraction during development of phellem (Schreiber et al., 2005). Two apparently contradictory observations were made: on the one hand, the extractable fraction of potato tuber phellem (referenced to either thickness or area) decreased within the first 2 weeks of storage by 10–20% (cv. Erna) or 30–50% (cv. Combi N) and decreased in *Aesculus* with age by 60% (between 5 and 30 years); on the other hand, there are some preliminary indications that *Sambucus* increases the extractable fraction by a factor of 20 within a period of 25 years. While the following observations may muddy the waters even further, they need to be mentioned: phellem discs from freshly harvested potato tubers showed lateral shrinkage upon extraction with chloroform. The shrinkage amounted to up to 23% of their area for both varieties (Combi N and Erna). After 2 weeks of storage, during which the extractable fraction decreased, shrinkage also became less pronounced and amounted to only 17%. Shrinkage was also observed on phellem discs of trees upon removal of the extractable fraction, but this has not been quantified. The extractable material seems to play a role in maintaining the structural integrity of the phellem. As space fillers, they might support the three-dimensional network of the suberin. However, while this idea may be acceptable for those tree phellem showing a large extractable fraction, the fraction is very small in potato phellem, and still shrinkage is very high. This striking phenomenon cannot be explained at the moment and the relationship between extractable material and shrinkage remains unclear.

A further characteristic feature of phellem is the presence of lenticels. These multicellular structures embedded in the corky tissue are characterized by loosely connected cells surrounded by an intercellular air space,
which enables the enhanced passage of gases across the phellem. Lenticels have been observed in almost all phellem (Langenfeld-Heyser, 1997). The portion of the phellem area they take up varies quite widely (Table 1). It must be pointed out that it is not the visible lenticel area on the surface of the phellem that is the effective cross-sectional area for diffusion but the minimum area of the intercellular space in a lenticel cross-section. Attempts have been made to determine this effective cross-sectional area. Light microscopy studies on thin sections revealed that in apple fruit skin, 0.16% of the lenticel area was made up of intercellular spaces (Park, 1991). However, this value seems to be a serious underestimation. A new approach in the author’s laboratory uses image analysis-based differentiation between cells and intercellular spaces in virtual cross-sections of individual lenticels. The intercellular spaces in a cross-section are marked and the areas calculated. Combining area and known depth of each measured spot results in the determination of air space volume (KJ Lendzian, unpublished data). The data obtained by this method allow the determination of the partial volume of the intercellular space within an individual lenticel. A 2-year-old S. nigra twig was found to have a lenticel area of 4%, ~6% of which was intercellular space. A twig from Corylus avellana of the same age showed 2% lenticel area, 6% of which was intercellular space. Thus, 1 m² of Sambucus phellem surface area comprised 400 cm² of lenticel area, of which 24 cm² was open to connect the atmosphere with the inner cortex via a continuous gas phase. The coefficient of variation for these determinations was always smaller than 20%.

**Water permeability of periderms**

Since the establishment of a method to isolate phellem enzymatically (Vogt et al., 1983; Groh et al., 2002), the focus has been on the quantification of their permeance to water. Permeances $P$ (m s⁻¹) were calculated using the same equation already introduced for the quantification of cuticular water permeability:

$$P = \frac{F}{A \times \Delta c}$$

with $F$ (g s⁻¹) representing the rate of water loss via the phellem area $A$ (m²), and $\Delta c$ (g m⁻³) being the driving force for the transfer of water from one side of the phellem to the other. Water loss was measured with a gravimetric method (Schönherr and Lendzian, 1981). Isolated phellem lacking lenticels were mounted on water-filled transpiration chambers made of brass or steel (volume 0.4–0.7 ml). The morphological inner side of the phellem was facing the liquid water. The area of exposed phellem on the chambers was 0.785 cm². Water could only leave the chambers via the PMs, and water loss was followed gravimetrically with a microbalance. As the transpiration rate was low, determinations of mass loss were made every other day. Chambers were kept in closed boxes containing dry silica gel in an upside-down position to ensure direct contact between phellem and water. Thus humidity above the morphological outer surface of the phellem was kept constant at 3% and the driving force was almost maximal. Under such experimental conditions, there are two possibilities for the definition of the driving force $\Delta c$. One is to use the liquid water concentration (density) inside the chambers, which amounts to 10⁶ g m⁻³. Then, permeances are related to liquid water as the driving force and are called water-based permeances (Becker et al., 1986). The second option is to use the concentration of water vapour in the gas phase in equilibrium with liquid water (23.05 g m⁻³ at 25 °C). Permeances calculated with this quantity as the driving force are called vapour based. Conversion of one permeance into the other is straightforward as all that is required is multiplication (or division) by the partition coefficient of water for the system liquid/vapour, which is 43.384 at 25 °C. A water-based permeance can be converted into a vapour-based one by multiplying it by the liquid/vapour partition coefficient (Becker et al., 1986; Lendzian and Kerstiens, 1991). All permeances given in this communication are vapour based.

Permeances for water determined with potato tuber and tree trunk phellem lacking lenticels range from 2.4×10⁻⁶ (Solanum tuberosum cv. Desireé following 2 weeks of storage after harvesting) to 17.7×10⁻⁶ m s⁻¹ in mature (just before harvesting) S. tuberosum cv. Combi N (Table 2). These values are of the same order of magnitude as those for many cuticles from leaves and fruits (Riederer and Schreiber, 2001). However, cuticles provide the same barrier with membrane thicknesses of only 1–10% of those of phellem. From the few observations collected to date, it seems that up to eight cell layers within the phellem are necessary to fulfill the demand of the plant for protection against water loss. However, upon wounding, a replacement phellem is formed over time, in which the number of layers is significantly higher than in the original one but the new barrier still remains less effective by more than two orders of magnitude (Schreiber et al., 2005). The plant compensates by adding more and more insufficient layers. Does that mean that the number of individual phellem layers is only one of several factors that determine the barrier properties for water? Thickness is certainly one important factor. The differences in permeances seen in the tree phellem (Table 2) are partly due to the different thicknesses (Table 1). Normalization of the different permeances from tree phellem to a unit-thickness basis (here 1 m), which gives a variable called the permeability coefficient (Becker et al., 1986), results in relatively small and statistically non-significant differences between Betula potaninii (0.6×10⁻⁸ m² s⁻¹), Aesculus (0.8×10⁻⁸ m² s⁻¹), Sambucus (1.1×10⁻⁸ m² s⁻¹), Abies (1.1×10⁻⁸ m² s⁻¹), Acer (1.2×10⁻⁸ m² s⁻¹), and B. pendula (1.6×10⁻⁸ m² s⁻¹).
Table 2. Vapour phase-based water permeances P (× 10\(^3\); m s\(^{-1}\)) of isolated phellem membranes before (PM) and after (EPM) extraction with chloroform

<table>
<thead>
<tr>
<th>Plant material</th>
<th>PM</th>
<th>EPM</th>
<th>EPM/PM</th>
<th>EM (^a)</th>
<th>EM (^b)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Solanum tuberosum</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>cv. Maritta(^a) mature</td>
<td>30</td>
<td>90</td>
<td>3</td>
<td>60</td>
<td>45</td>
</tr>
<tr>
<td>cv. Maritta 2 weeks storage</td>
<td>2.7</td>
<td>90</td>
<td>33</td>
<td>87</td>
<td>2.78</td>
</tr>
<tr>
<td>cv. Combi N(^c) mature</td>
<td>177 (2.3)</td>
<td>319 (9.8)</td>
<td>1.8</td>
<td>142</td>
<td>398</td>
</tr>
<tr>
<td>cv. Combi N2 weeks storage</td>
<td>7.1 (0.8)</td>
<td>7.9 (0.6)</td>
<td>1.1</td>
<td>0.8</td>
<td>70</td>
</tr>
<tr>
<td>cv. Erna(^d) mature</td>
<td>24 (4.4)</td>
<td>31 (3.3)</td>
<td>1.3</td>
<td>7</td>
<td>106</td>
</tr>
<tr>
<td>cv. Erna 2 weeks storage</td>
<td>7.3 (1.4)</td>
<td>8.1 (0.8)</td>
<td>1.1</td>
<td>0.8</td>
<td>74</td>
</tr>
<tr>
<td>cv. Desirée(^e) mature</td>
<td>2.8</td>
<td>280</td>
<td>100</td>
<td>277</td>
<td>2.8</td>
</tr>
<tr>
<td>cv. Desirée 2 weeks storage</td>
<td>0.24</td>
<td>280</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Betula pendula(^f)</td>
<td>20</td>
<td>68</td>
<td>3.4</td>
<td>48</td>
<td>28</td>
</tr>
<tr>
<td>Betula potanini(^g)</td>
<td>7.7 (3.4)</td>
<td>10.9 (4.2)</td>
<td>1.4**</td>
<td>3.2</td>
<td>26.2</td>
</tr>
<tr>
<td>Abies alba(^h)</td>
<td>6.3 (5.8)</td>
<td>25.1 (7.8)</td>
<td>4***</td>
<td>18.8</td>
<td>8.4</td>
</tr>
<tr>
<td>Acer pseudo-platanus(^i)</td>
<td>9.2 (0.4)</td>
<td>25.5 (5.6)</td>
<td>2.8**</td>
<td>16.3</td>
<td>14.4</td>
</tr>
<tr>
<td>Aesculus hippocastanum(^j)</td>
<td>4.7 (4.8)</td>
<td>7.9 (3.3)</td>
<td>1.7***</td>
<td>3.2</td>
<td>11.6</td>
</tr>
<tr>
<td>Sambucus nigra(^k)</td>
<td>3.3 (6.1)</td>
<td>6.8 (5.1)</td>
<td>2***</td>
<td>3.5</td>
<td>6.4</td>
</tr>
<tr>
<td>Cuticular membranes(^l)</td>
<td>0.04–14</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^a\) PM calculated by treating EPM and extractable material as resistances in parallel: \(P_{EM}=1/P_{PM}+1/P_{EM}+1/P_{EM}; P=1/resistance.\)

\(^b\) EM calculated by treating EPM and extractable material as resistances in series: \(1/P_{EM}=1/P_{PM}+1/P_{EM}+1/P_{EM}; P=1/resistance.\)

\(^c\) Vogt et al. (1983); \(^d\) Groh (2000); \(^e\) Schreiber et al. (2005); \(^f\) Schönherr and Ziegler (1980); \(^g\) Groh et al. (2002); \(^h\) Riederer and Schreiber (2001).

It seems obvious to test for a correlation between thickness of phellem and their permeance to water. Whereas with plant cuticles, thickness and permeance show no correlation at all (Kamp, 1930; Becker et al., 1986; Lendzian and Kerstiens, 1991; Riederer and Schreiber, 2001), in isolated tree phellem thickness and permeance to water are fairly well correlated \([r^2=0.74]\). Water permeance decreased linearly with increasing thickness. In practice, thickness is not easily determined but it is closely and linearly correlated with dry weight per unit area, DW=0.13 (mg cm\(^{-2}\) μm\(^{-1}\)) d (μm)−7.48 (mg cm\(^{-2}\)) (r\(^2=0.95\)). Schönherr and Ziegler (1980) were the first to investigate the correlation between DW and P for B. pendula. However, DW was not well correlated with thickness because adhering unsuberized cell layers added variable amounts to DW. For the other five tree phellem in Table 2, water permeance P can be predicted from DW by the equation \(P (m s^{-1}) = -2 	imes 10^{-5} (m cm^2 s^{-1} \text{mg}^{-1}) \times DW (mg cm^{-2}) + 8 	imes 10^{-5} (m s^{-1}); \) \(r^2=0.74\). An even better prediction can be made by correlating P with the density of the phellem (g cm\(^{-3}\)): \(P (m s^{-1}) = -8 	imes 10^{-5} (m cm^2 s^{-1} \text{g}^{-1}) \times \text{density (g cm}^{-3}) + 10^{-4} (m s^{-1}); \) \(r^2=0.86\). The density seems to be a quite specific structural variable, but it is difficult to determine.

With respect to water permeance, the phellem of potato tubers show an extraordinary behaviour. As long as tubers stayed in the soil and reached maturity, their phellem had remarkably high permeance and the varieties showed large differences in P (Table 2). Upon harvest and subsequent storage, permeances decreased dramatically within a few days, by a factor of 25 (cv. Combi N), 3.3 (cv. Erna), or 11.7 (cv. Desirée). Constant values for P were usually reached after 2 weeks. Storage conditions such as relative humidity and temperature did not significantly affect the rapid enhancement of the barrier (Schreiber et al., 2005). However, two structural components changed during storage, DW and the amount of extractable material. DW for Combi N and Erna increased significantly by factors of 1.5 and 1.2, respectively (Groh, 2000), and that of Desirée by 2 (Schreiber et al., 2005). It is very unlikely that such small structural changes could be responsible for the remarkable reduction of water permeance during storage. The role of the soluble material will be discussed next.
part of the barrier against diffusion of water (Schönherr, 1982). The cutin network is of relatively minor importance and has to be seen predominantly as a matrix for the embedded lipids. No experimental evidence points to a direct correlation between the amount of soluble lipids or their composition on the one hand, and cuticular permeance to water on the other (Schreiber and Riederer, 1996; Jetter et al., 2000).

How important are the soluble lipids in isolated phellem from potato tubers and trees? As with cuticles, one may consider phellem to be made up of two components: the soluble material and the insoluble polymer matrix (poly-

saccharides, suberin, and lignin). Upon removal of the soluble fraction, water permeances of phellem increased significantly but mostly only by factors between 1.1 and 4 (with the exception of two potato varieties), which are comparable with those observed with fruit cuticles from tomato, green pepper, and aubergine (Schönherr, 1982). Transport properties of the extracted lipids from phellem cannot be characterized separately. Instead they must be deduced from comparisons of the intact PM with the EPM. For a rough estimate of the extent to which the soluble material in the phellem participates in the overall barrier, $P_{PM}$, $P_{EPM}$, and $P_{EM}$ were considered as parts of an electrical circuit and treated as resistances acting either in parallel or in series (Schönherr, 1976). However, the calculated values for $P_{EM}$ (Table 2) do not really contribute much to clarifying the role of the soluble material. The parallel resistance model only gives meaningful results for the phellem of Abies, Acer, and B. pendula. Here $P_{EM}$ values were very similar to those of the EPM, indicating that both components contributed almost equally to the overall permeances. This kind of calculation makes little sense when differences between $P_{EPM}$ and $P_{PM}$ are very small (Aesculus, B. potaninii, Sambucus, and S. tuberosum cv. Combi N and cv. Erna) or very high (cv. Maritta and cv. Desirée). Treating phellem resistances in series gives a clearer picture of the role of the extractable material in the phellem from cv. Maritta and cv. Desirée, as well as from Abies. The calculated resistances of the soluble lipids were identical or similar (Abies) to the resistances of the native phellem. $P_{PM}$ is completely or almost completely determined by $P_{EM}$, the contribution of the EPM to the overall resistance being negligible or of minor importance. Vogt et al. (1983) previously suggested treating the various component resistances of phellem in series and developed a structural and functional model for the potato tuber phellem. They distinguished two parallel pathways for water flow. Middle lamellae and primary cell wall represent pathway 1, with a very small diameter for volume flow but with a high specific permeance for water. The su-

berized secondary cell walls encrusted with soluble lipids make up pathway 2, a lipophilic phase but with a very large diameter for water flow. The removal of the soluble material increased permeances by factors of between 33 and 100 (Table 2). It is unclear why this model does not fit the other potato phellem listed in the table. Lateral heterogeneity may be responsible, and phellem may be as laterally heterogeneous as cuticles.

The structure of the potato phellem is very similar to that of tree phellem (Esau, 1977; Schönherr and Ziegler, 1980; Vogt et al., 1983; Schreiber et al., 2005) and there are no reasons not to expect the presence of two pathways here as well. In such a model, it is very unlikely that the chloroform-soluble lipids are located within the hydrophi-

lic phases of the middle lamellae and primary cell wall. Phellem lipids have a preference for the lipophilic components of the suberin polymer (Matzke and Riederer, 1991). When treating the lipids and the EPM as two resistances in series, it becomes obvious that the lipids, although present in large amounts, were approximately as effective as resistances as was the rest of the phellem. Only in Abies are there indications that the lipids contribute the major part of the total resistance. Further observations add to the confusing picture. The chloroform-extracted phellem from tubers and tree trunks still show very different permeances for water, and variability among species is as high as in unextracted PM. Cross-sections show that PMs have a heterogeneous structure. There is a tendency for the cell lumina along the radial cell rows to become smaller towards the periphery. That may explain the significant asymmetry (influx versus efflux) in water transport for the phellem from Acer (Groh et al., 2002). It is crucial to obtain more information about the physico-chemical make-up and the exact chemical composition (suberin polymer and extract-
able fractions) of these periderms.

An important attempt has been made recently to study the relationship between composition and/or amount of aliphatic suberin, soluble material, and the functional suberized cell walls, and their contributions to the resistance to water transport in potato phellem (Schreiber et al., 2005). These phellem serve as a good model system as all classes of substance found were also present in other suberized tissues. Compilation of data from different plants and different suberized tissues demonstrates the large variation in the absolute amounts of aliphatic suberin, and especially in chemical composition. Such large variability was also observed when development of native and wound suberin in phellem was analysed in parallel experiments (Schreiber et al., 2005). Storage-dependent changes in water permeance could not be correlated with the formation of the suberin polymer or synthesis of associated soluble lipids. During the first days of storage, water permeance decreased and suberin and wax production increased. After that period, permeance remained constant while the content of suberin and waxes continued to rise. Phellem from different varieties of potato differed greatly in the way in which their chloroform-extracted matrix changed during storage. EPM of the varieties Maritta and Desirée did not show any change in water permeance even though the
suberin content increased (Vogt et al., 1983; Schreiber et al., 2005). The other varieties mentioned in Table 2 behaved completely differently: DW increased while the amount of soluble material decreased. Both strategies led to a significant reduction of water loss during storage. Clear correlations between content and/or composition of suberin, soluble material, and water permeance are missing, and ‘obviously, the occurrence of suberin and wax in cell walls does not allow us to conclude that these cell walls must necessarily form pronounced barriers to water transport’ (Schreiber et al., 2005).

**Oxygen and carbon dioxide permeances of periderms**

Information on the mass transfer of the physiologically important gases oxygen and carbon dioxide via primary and secondary plant–air interfaces is scant (Lendzian, 1982; Lendzian et al., 1986; Lendzian and Kerstiens, 1988, 1991; Groh et al., 2002). The main pathways for these gases are the regulated stomata of primary interfaces. To enforce the use of the regulated diffusion pathways, it is clear that selection was directed towards an effective reduction of cuticular fluxes, especially for water. To date, it is not clear whether the simultaneous reduction of oxygen and carbon dioxide permeances is a consequence of lowering water permeances or if special structural features are responsible for the reduced gas permeances. Many other data on permeances of cuticles for different molecules point to a membrane whose barrier properties have evolved in response to a whole spectrum of different requirements (Kerstiens, 2006; Schönherr, 2006; Schreiber, 2006).

Plant cuticles are permeable to oxygen and carbon dioxide (Lendzian and Kerstiens, 1991). Permeances for CO₂ and O₂ are significantly lower than those reported for water. The central 50% of all water permeance data collected from cuticles fall within the range from 2.2 × 10⁻⁶ to 1.8 × 10⁻⁵ ms⁻¹ (Riederer and Schreiber, 2001). The few permeances determined for CO₂ and O₂ were smaller by one and three orders of magnitude, respectively; therefore, cuticles are even better barriers for these two gases.

When the epidermis–cuticle–stomata complex is replaced by the phellem–lenticel complex during secondary growth of the stem, the same strategy that has proved successful for the cuticle takes over again. Phellem permeances for these gases are very much smaller compared with those for water (Groh et al., 2002). Phellems are sealed off so perfectly that fluxes of both gases could not (Abies, Acer, and Sambucus) or could only just (Aesculus) be detected in these experiments. Extraction of the soluble lipids did not change this situation. Thus, vapour-based permeances of PM and EPM must be smaller than 10⁻⁹ ms⁻¹. Differences between the two gases could not be investigated due to these experimental limitations, with one exception. The isolated, native phellem of *B. potaninii* became measurably permeable to oxygen upon the removal of the soluble fraction. An increase in permeance of at least one order of magnitude must have occurred. Thus, the lipids of the *Betula* phellem constituted the main resistance to oxygen transport, assuming that the ‘series resistance’ model can be applied (see above). The last observation may give a hint as to how oxygen could pass through the cork tissue. The solubility of oxygen in water is very low, but is higher in most organic solvents. It can be assumed that O₂ does not diffuse along the hydrophilic middle lamellae. Since permeance increased upon removal of the lipids, the less hydrophilic area of the phellem may serve as the preferred pathway. Similar conclusions have been drawn previously for the transfer of oxygen across plant cuticles (Lendzian, 1982). Experimental evidence indicated that oxygen does not diffuse along the same pathway that water molecules take. Data to elucidate the transfer of CO₂ are lacking.

**The permeances of lenticels**

The permeability of cuticles and phellems for water, oxygen, and carbon dioxide is low or below the detection limits. The primary and secondary interfaces are ideal barriers for minimizing water and gas exchange and directing the main fluxes of these molecules to the stomata or lenticels. There is no doubt that stomata fulfill this task using a highly regulated mechanism which ensures survival even under highly adverse environmental conditions. Their morphology and anatomy make lenticels also suitable for gas exchange. The presence of lenticels in phellems provided a pronounced permeability to water, oxygen, and carbon dioxide (Table 3). The first quantitative data were published by Schönherr and Ziegler (1980) for *B. pendula* phellem. They compared permeances for water of phellem areas with or without lenticels. By calculating the differences between the two kinds of specimens and introducing the lenticel area, they concluded that lenticel areas were 32 or six (calculated for two different phellems) times more permeable than the surrounding phellem. In another experiment, reliable data for permeances of lenticels to water, oxygen, and carbon dioxide could only be obtained with *B. potaninii* and *Sambucus*. In contrast to others, these two phellems have well-defined lenticel areas and could be mounted on the measuring devices (Groh et al., 2002). Again, lenticels were much more permeable than phellem lacking these structures (Table 3). Water vapour permeance was higher by a factor of 39 (*B. potaninii*) or 12 (*Sambucus*), and oxygen permeance by a factor of at least 1000 (*B. potaninii*) or 50 (*Sambucus*). The permeances of the individual lenticels were unchanged after treatment with chloroform. Lipids seem not to be involved in controlling the diffusion process for water vapour and gases within the intercellular spaces.
of the lenticels. However, it has been reported that wax may cover the entire inner surface of lenticels (Park, 1991) and even the lenticel–atmosphere interface, probably to prevent liquid water from entering the lenticel. It is an important feature of lenticels to remain accessible to gas molecules even during rain.

The question needs to be asked, how reliable are the data for individual lenticels? Different methods for determining their permeances have been introduced. Masking the surroundings of a lenticel with an impermeable brass diaphragm or sealing the phellem area with nail varnish led to identical results (Groh et al., 2002). Additionally, when the permeances of phellem areas with or without lenticels were determined and these pathways were treated as occurring in parallel, calculation of permeances for individual lenticels also resulted in similar values (Table 3), except for oxygen.

As mentioned above, permeance $P$ is calculated from the flux rate (amount per unit time), the area through which transfer occurs, and the driving force. Lenticel permeances in Table 3 were calculated with the areas visible under a stereo microscope, which can be easily measured. However, only a small part of the lenticel surface corresponds to the intercellular air space. Using the whole lenticel area for calculation of permeance leads to a severe underestimation of the permeance of this air space. If it is taken into account that the air space in a lenticel cross-section is ~5%, the permeances of the lenticels must be corrected upwards by a factor of 20. Formally this estimation is ‘more correct’ than the values given in Table 3, but the question arises of whether these permeances reflect the situation in situ. Such high permeances are almost identical to those calculated for open surfaces when unhindered diffusion occurs. However, when individual gas molecules diffuse in small pores, they experience more collisions with the walls than with other gas molecules. This type of diffusion is called Knudsen diffusion (Cussler, 1986). It applies when the average distance between molecular collisions (the mean free path length) is greater than the pore diameter. However, at room temperature and normal pressure, the gaseous components of air have a free path length of ~60–70 nm, whereas diameters of individual intercellular spaces in lenticels of Betula were found to be ~500–1000 nm. Thus, collisions of water and other gas molecules with cell walls will not significantly reduce their diffusion rate, and it appears that the intercellular space of lenticels allows unhindered diffusion of gas molecules and the calculated permeances are appropriate. Still, one has to consider that at least water vapour may interact with the cell walls of the filling tissue of the lenticels, thus having an influence on transfer processes. Sorption and swelling may be such interactions (Groh et al., 2002).

### The regulation of lenticel permeance

Compared with stomata, lenticels seem to be under no regulatory control. However, several reports point to some properties of lenticels changing with the seasons (Klebahn, 1884; Kohlert, 1925; Liu et al., 1992; Speck, 1995; Langenfeld-Heyer et al., 1996). The statements are contradictory and have little in the way of a quantitative basis. A new attempt has been made to characterize the permeances of lenticels to water and oxygen at different times of the year. This experiment was carried out with mechanically or enzymatically, isolated lenticels (Groh et al., 2002). Lenticels of B. potaninii were chosen because plant material was available in sufficient amounts and it was easy to determine lenticel areas and prepare cross-sections for checking of anatomical integrity. Samples were taken from February to October and during two consecutive years to check the reproducibility of data (Fig. 1). In 2003, membranes were reused after the measurement of water permeance to determine oxygen permeance in a different device (Lendzian, 1982). Oxygen permeances were determined with hydrated (in equilibrium with 100% humidity) and unhydrated (in equilibrium with dry air) lenticels (Fig. 2).

A comparison of the permeances to water vapour, oxygen, and carbon dioxide of lenticels and lenticel-free phellem areas supports the idea that most of the gas and

### Table 3. Vapour phase-based water, oxygen, and carbon dioxide permeances $P$ ($\times 10^2$; m s$^{-1}$) of phellem areas lacking lenticels and of individual lenticels

Sample sizes varied between 15 and 20.

<table>
<thead>
<tr>
<th>Plant material</th>
<th>Permeance $H_2O$</th>
<th>Permeance $O_2$</th>
<th>Permeance $CO_2$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Phellem</td>
<td>Lenticle</td>
<td>Phellem</td>
</tr>
<tr>
<td>Aesculus hippocastanum PM*</td>
<td>0.47±0.48</td>
<td>–</td>
<td>0.07±0.05</td>
</tr>
<tr>
<td>Betula potaninii PM*</td>
<td>0.77±0.34</td>
<td>30.2±1.6</td>
<td>12.02±4.1</td>
</tr>
<tr>
<td>Betula potaninii EPM*</td>
<td>1.10±0.42</td>
<td>30.8±1.2</td>
<td>0.1±0.06</td>
</tr>
<tr>
<td>Sambucus nigra PM*</td>
<td>0.33±0.61</td>
<td>3.86±3.11</td>
<td>n.d.</td>
</tr>
<tr>
<td>Betula pendula PM1b</td>
<td>6×</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Betula pendula PM2b</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

*a* Groh et al. (2002); *b* Schönherr and Ziegler (1980).

*c* n.d.=not detected.
vapour exchange occurs via the lenticels. While these pores seemed to be more or less invariable with respect to their structure, it has now been demonstrated that at least the permeability of the lenticels from *Betula potaninii* changed significantly during the year (Figs 1, 2). The passage of gases was minimal but not negligible in autumn and winter. In spring, permeance increased to a maximum, which lasted from June to August. Hydrated and unhydrated lenticel areas differed in oxygen permeance during the growing season. No differences were detectable during the rest of the year. Due to experimental difficulties, the dependence of water permeance on the hydration status was not investigated, but it can be expected that water permeability was also affected by it. In this context, it has to be pointed out that the intercellular spaces of the lenticels are gas filled; water is unable to penetrate this volume in liquid form under natural conditions (Schönherr and Ziegler, 1980). Even with isolated membranes, liquid water does not diffuse into the capillary intercellular system of the lenticels.

At least two processes determine the permeance of *Betula* lenticels for water and oxygen. On the one hand, it is a seasonal change that enables gas exchange to be significantly higher during the summer season than in autumn, winter, and spring. On the other hand, changes in permeance are modulated by the status of hydration during summer. It is expected that the hydrated situation is the most common one. Upon dehydration, the flux of oxygen was reduced. A complete removal of sorbed water within the filling tissue (which makes up most of the lenticel) reduced permeance by half. Preliminary morphological observations point to a shrinkage of the filling tissue and a reduction of the free air space. This modulative regulation targets the area within the lenticel. It is obvious that such a mechanism is also of ecological significance. Without it, lenticels would allow increased water loss following a decrease of the water potential in the atmosphere adjacent to the stem. A reduction of this loss by shrinkage of the filling tissue would at least help to reduce transpiration of the bark and maintain the plant’s water status during a dry period.

A possible explanation for the seasonal changes, especially the remarkable increase in permeance from June to August, is based on observations of the seasonal activity of the phellogen (responsible for the production of phellem, closing layer, and lenticels) and structural changes of the closing layer (one to three cell layers between phellogen and filling tissue of the lenticel; Langenfeld-Heyser, 1997; Rosner and Kartusch, 2003). During dormancy from September to the end of April, the phellogen is inactive. Phellogen and the adjacent closing layers form a compact tissue, lacking intercellular spaces, and separate the intercellular spaces of the cortex from the lenticels. Gas exchange via this compact tissue is reduced during the dormant period. At the end of April, phellogen activity picks up and new filling cells are produced centrifugally, putting tension on the existing closing layers. With the formation of filling cells, the closing layers become separated and middle lamellae are partly destroyed. This process takes place during the growing season, leaving the tissue outside the phellogen with a continuum of intercellular spaces. The permeance of the pathway from cortex to the atmosphere increases by a factor of six (water vapour) or eight (oxygen). Before the phellogen re-enters its

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**Fig. 1.** Vapour phase-based water permeances (*P*) of individual lenticels isolated from *Betula potaninii*. Lenticels embedded in a phellem sheet were sampled in 2003 and 2004 from branches of the same age. Date of sampling are indicated on the x-axis. Values of *P* are given as percentages of the mean values measured in February (mean *P* in 2003, 5×10⁻⁴ m s⁻¹; mean *P* in 2004, 2×10⁻⁴ m s⁻¹). Sample sizes varied between 10 and 15; error bars represent 95% confidence intervals.

**Fig. 2.** Vapour phase-based oxygen permeances (*P*) of single lenticels isolated from *Betula potaninii*. Samples were taken in 2003. The same samples were used for the determination of water and oxygen permeances. Oxygen permeance was first determined with hydrated lenticels, followed by the determination with unhydrated (dry) lenticels. Values of *P* are given as percentages of the mean values determined in February (mean *P* hydrated, 1.5×10⁻⁴ m s⁻¹; mean *P* unhydrated, 1.1×10⁻⁴ m s⁻¹). Sample sizes varied between 10 and 15; error bars represent 95% confidence intervals.
dormancy in September, it produces compact closing layers, which again results in a decrease of permeance. Therefore, in a concerted action of changes in structure and water content, the phellem–lenticel complex manages to regulate transpiration and vital gas exchange in line with variable requirements.

Conclusion

A comparison of the function of primary and secondary plant–air interfaces points to many similarities. This may not be unexpected because selection during evolution was directed towards the protection of the aerial parts of plants from uncontrolled water loss and allowing effective regulation of gas exchange. Both cuticle and periderm serve these demands. It is obvious that there are several parallels between phellem and lenticels on the one hand and cuticle and stomata on the other. Protection afforded by phellem and cuticles is very effective, and their resistances lie within the same orders of magnitude, but they are established by different strategies. Future work has to clarify the respective roles of suberin and soluble materials in phellem for protection, and further research is necessary to verify the regulatory mechanisms which govern lenticel functions.

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