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Presumable mesophyll optics of C_3 plants reconsidered

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Summary: The palisade and spongy chlorenchymata typical of C_3 plant leaves are hypothesized to interact differently with the light penetrating the leaf. The palisade chlorenchyma allegedly transmits the light into the deep mesophyll, whereas the spongy one scatters transmitted light and reflects it back to the palisade tissue. These tissues are concluded to function this way only under artificial experimental conditions which are radically different from the natural environments. Existence of the palisade and spongy chlorenchymata in a leaf is not caused by their alleged differences in optical traits. They jointly optimize the leaf photosynthesis, but in another way. The palisade chlorenchyma maximizes the number of intercellular airspace-exposed chloroplasts per unit of mesophyll volume and can thereby consume up to 95% of the light entering. It also maintains necessary cross-leaf diffusion of gaseous CO_2, but it is inefficient in lateral (paradermal) transmitting of CO_2 and solutes. The spongy chlorenchyma contains much less chloroplasts per unit of mesophyll volume. It is typically (much) inferior to the palisade counterpart in producing assimilates, but it is specialized in lateral transmitting of solutes and CO_2. Haberlandt's old assumptions about functional specificity of the spongy chlorenchyma in a leaf remain speculative. However, they seem to be more consonant to reality.

Keywords: anatomy, mesophyll, palisade chlorenchyma, spongy chlorenchyma, leaf, C_3 plants

Light energy is separately converted by every chloroplast into usable energy-rich chemical compounds. Therefore, leaf photosynthesis is highly dependent on light distribution across the mesophyll. The light penetrating the leaf is scattered and reflected by cell surfaces (Vogelmann 1993; Eschrich 1995; DeLucia et al. 1996; Smith et al. 1997; Gavrilenko & Zhigalova 2005; Terashima et al. 2011; Niklas & Spatz 2012) to result in inner local illuminations dependent on leaf anatomical structure (Vogelmann 1993; Smith et al. 1997). Hence, leaf anatomical structure must also have evolved to optimize light distribution across the mesophyll (Smith et al. 1997).

The leaf chlorenchyma of C_3 plants typically consists of palisade and spongy chlorenchymata (Napp-Zinn 1973, 1974; Esau 1977). The optimization of light distribution across the mesophyll is considered by some plant physiologists and plant anatomists the cause of palisade–spongy structure of the leaf.

Light transmission into the leaf interior is attributed to the palisade chlorenchyma (Meyer 1962; v. Guttenberg 1963; Vogelmann 1993; Vogelmann & Martin 1993; DeLucia et al. 1996; Smith et al. 1997). Its long cell vacuoles and intercellular airspaces which are perpendicular to the leaf surface are likened to optical fibers (Fig. 1). Thus transmitting light inwards, they enable illumination of deep parts of the mesophyll and align illumination profile of the latter one.

The spongy chlorenchyma is attributed to randomize transmitted light and to reflect it back mainly to the palisade chlorenchyma (Fig. 1) (Vogelmann 1993; DeLucia et al. 1996; Smith et al. 1997; Terashima et al. 2011). The concerned tissue thus contributes to the illumination alignment in the mesophyll. However, the main result is an elongation of the distances the

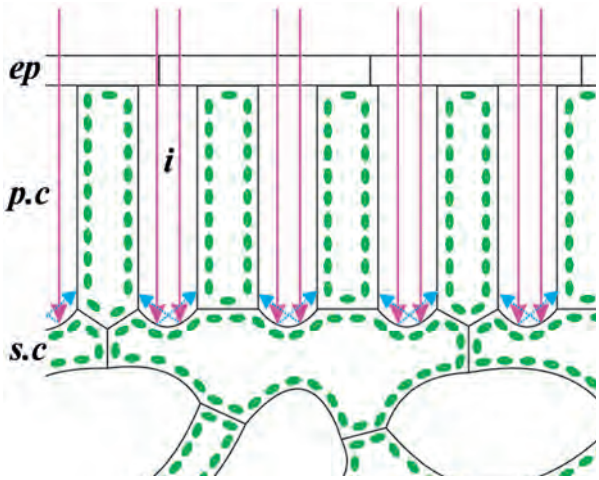

Figure 1. Theorized optical functioning of palisade and spongy chlorenchymata. *ep* – epidermis; *i* – intercellular air space; *p.c* – palisade chlorenchyma; *s.c* – spongy chlorenchyma; *magenta arrows* – incident light; *blue dotted arrows* – reflected light.

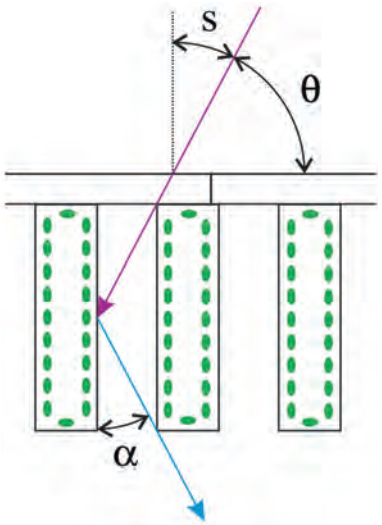

Figure 2. Optical angles in palisade chlorenchyma. α – light reflection angle; θ – light incidence angle; s – supplement.

photons have to pass in the mesophyll. The longer the distances are, the more probably the photons are absorbed by the chloroplasts. Besides, repeating reflection and scattering of the light could locally increase 1.2 to 3.4 times the light flux in the mesophyll over the incident sunlight (Vogelmann 1993). Such a flux increasing could enhance light absorption by the chlorophyll.

Both theorizing and experimental testing were based on illumination of the leaf by stationary collimated light perpendicular to the leaf surface. Such an illumination is radically different from the natural one. The diffuse light takes nearly 50% of the direct sunlight (Larcher 1976) and can rise up to 100% when it is cloudy (Vogelmann & Martin 1993). When illuminated by diffuse light, the palisade and spongy chlorenchymata do not differ in their optical properties (Vogelmann & Martin l. c.). Additionally, direction of incident sunlight rotates about 15° per hour due to rotation of the earth. There are few species with leaves which track the sun (Vogelmann 1993), but this is not the case in the vast majority of C_3 plants. The leaves of the latter are thereat changeably exposed to the incident sunlight. The palisade chlorenchyma can hardly deflect the light which is parallel to its cells (Vogelmann & Martin 1993). Consequently, its ability to direct oblique incident light along its cells to the deep mesophyll decreases dramatically with the increase of the incidence angle θ (Smith et al. 1997; Terashima et al. 2011).

Thus, the palisade chlorenchyma of a C_3 plant leaf cannot permanently function the way the discussed theory proclaims. Therefore, the applicability of this theory needs to be revealed.

Limits of the applicability of the theory

Refractions and reflections of light in the mesophyll are too strong and various to allow the direction of light beams to be exactly calculated or measured (Eschrich 1995). Nevertheless, some rough plausible assessment of these processes seems feasible. Subsequent speculations are based on quite realistic assumptions.

I) Light absorption of mesophyll is ignored, because it decreases light penetration and inner illumination, but it affects neither light transmitting nor light reflection and scattering.

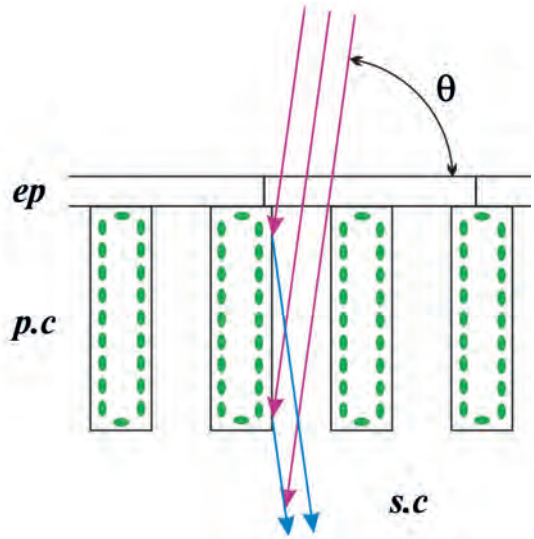

Figure 3. Light reflection by the palisade cell when θ is near to 90°. *ep* – epidermis; *p.c* – palisade chlorenchyma; *s.c* – spongy chlorenchyma; θ – light incidence angle; *magenta arrows* – incident light; *blue arrows* – reflected light.

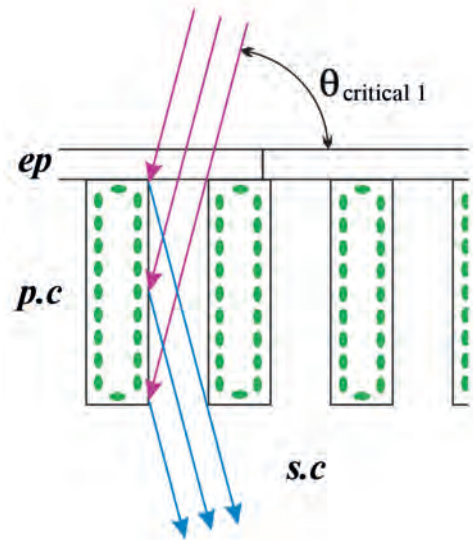

Figure 4. Light reflection by the palisade cell at $\theta_{critical\ 1}$. *ep* – epidermis; *p.c* – palisade chlorenchyma; *s.c* – spongy chlorenchyma; $\theta_{critical\ 1}$ – the first critical θ; *magenta arrows* – incident light; *blue arrows* – reflected light.

II) Light scattering by cell organelles is ignored, because it seems negligible in relation to light scattering and reflection by cell wall-intercellular airspace interfaces (Vogelmann 1993).

III) Scattered light illumination is ignored, because palisade and spongy chlorenchymata equally refract and reflect such a light (Vogelmann & Martin 1993).

IV) It follows from III) that optical properties of cell walls are identical in the palisade and spongy chlorenchymata; their different optical functionings could completely be attributed to different forms of constituting cells and different cell orientations relative to the incident light. The cells of palisade and spongy chlorenchymata equally reflect the incident light, if the incidence angles (θ) relative to their surfaces are the same.

If θ relative to the leaf surface is 90°, most light beams permeate the palisade chlorenchyma passing its chloroplasts. The spongy chlorenchyma could partly absorb this light and partly reflect it back to the palisade chlorenchyma with its much more numerous chloroplasts per unit of mesophyll volume in accordance with the theory under consideration. When the incident light is oblique, i.e. $\theta < 90°$, the palisade chlorenchyma should also reflect the light beams at the angle α which equals the supplement s of θ in accordance with the optical law of light reflection (Fig. 2). Thus, $\alpha = s = (90° - \theta)$. The result depends on θ and length to width ratio of the palisade cells. When θ is near 90°, the reflected light is completely directed into the spongy chlorenchyma (Fig. 3). Therefore, the palisade chlorenchyma operates as light guide, though it somewhat extends the distances the photons run through the mesophyll. The palisade chlorenchyma maintains operating this way up to $\theta_{critical\ 1} = [90° - s_{critical\ 1}] = [90° - \alpha_{critical\ 1}] = [90° - \mathrm{arctg}(W/L)]$, where W is width of light guide and L is its length (Fig. 4).

When $\theta < \theta_{critical\ 1}$, the reflected light inevitably hits neighboring palisade cells (Fig. 5). The smaller θ is, the more light reflected by the palisade chlorenchyma hits its cells. If θ is $\theta_{critical\ 2} = [90° - \mathrm{arctg}(2W/L)]$, the reflected light is completely directed to the palisade cells

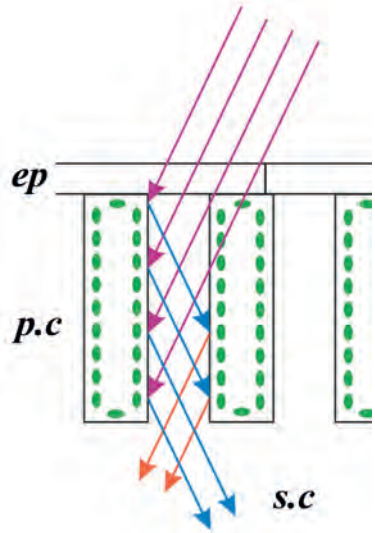

Figure 5. Light reflection by the palisade cell when $\theta < \theta_{critical\ 1}$. *ep* – epidermis; *p.c* – palisade chlorenchyma; *s.c* – spongy chlorenchyma; *magenta arrows* – incident light; *blue arrows* – reflected light; *orange arrows* – double-reflected light.

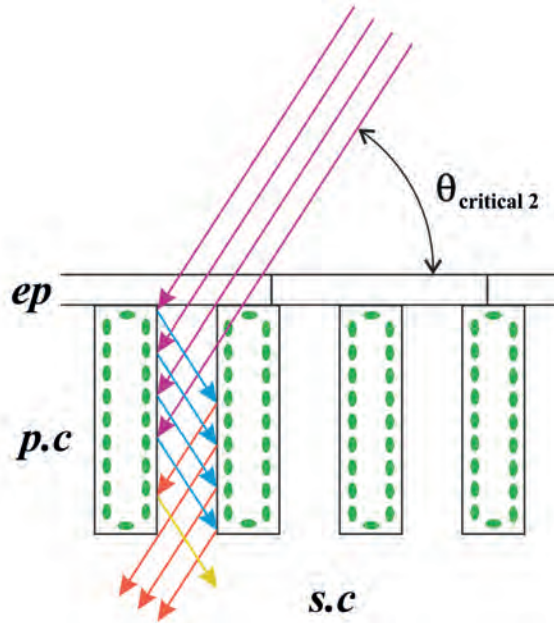

Figure 6. Light reflection by the palisade cell at $\theta_{critical\ 2}$. *ep* – epidermis; *p.c* – palisade chlorenchyma; *s.c* – spongy chlorenchyma; $\theta_{critical\ 2}$ – the second critical θ; *magenta arrows* – incident light; *blue arrows* – reflected light; *orange arrows* – double-reflected light; *smaragdine arrows* – trice reflected light.

(Fig. 6). In this case, the palisade chlorenchyma optically would operate the same way the spongy chlorenchyma is attributed to by the theory under discussion. When $\theta < \theta_{critical\ 2}$, the light is repeatedly reflected in the palisade chlorenchyma (Fig. 7). Then, the latter one would reflect the light toward palisade cells more efficiently than the spongy chlorenchyma when $90^{o} \geq \theta \geq \theta_{critical\ 1}$.

The operating angle of palisade cell reflection ε is $2s = 2\alpha$ (Fig. 8) due to the symmetry of optical guides. Therefore, optical functioning of the mesophyll tissues would completely fit the theory concerned, if only $\varepsilon = 2\alpha_{critical\ 1} = 2\text{arctg}(W/L)$. The palisade chlorenchyma would gradually take over the optical functioning of the spongy chlorenchyma up to $\varepsilon = 2\alpha_{critical\ 2} = 2\text{arctg}(2W/L)$. The palisade chlorenchyma would surpass its spongy counterpart as a light reflector, when $\varepsilon > 2\alpha_{critical\ 2}$.

The mentioned formulas show that the mode of functioning of these tissues depends on width to length ratios of the palisade cells. The ratios mostly range from 1 : 3 to 1 : 5 (Meyer 1962). If the ratio is 1 : 3 and the intercellular airspace widths equal the palisade cell widths, then critical ε is $2\text{arctg}(⅓) \approx 37°$ and $2\text{arctg}(⅔) \approx 68°$, respectively. The sunlight beams are rotated by these angles for about 2.5 h and 4.5 h, respectively. If the ratio is 1 : 5, the time slots under discussion are decreased up to 1.5 h and 2.9 h, respectively.

These rough estimates of the time slots are highly exaggerated, because

I) the intercellular airspaces are typically much narrower than the palisade cells;

II) the palisade cells are not parallelepipeds but rather cylinders; thereof, they would reflect more light to the neighboring cells (Fig. 9);

III) the collimated component of the sunlight often plummets to zero.

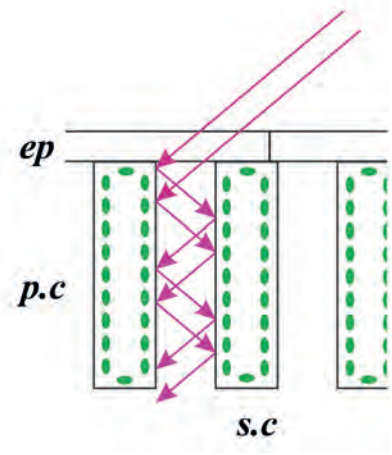

Figure 7. Multiple light reflection by the palisade cell at $\theta < \theta_{critical\,2}$. *ep* – epidermis; *p.c* – palisade chlorenchyma; *s.c* – spongy chlorenchyma.

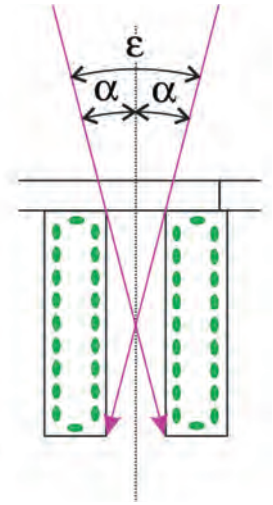

Figure 8. Operating angle of palisade chlorenchyma. α – light reflection angle; ε – operating angle.

All of these arguments are applicable only to leaves that are regularly perpendicular to the incident collimated sunlight. This would only be possible, if all the leaves of a plant were turned permanently southwards and were directed at the latitude angle to the horizon. This is obviously not the case in nature. The vast majority of the leaves of C_3 plants are naturally never perpendicular to the incident sunlight, only if turned occasionally by a gust for a moment. The palisade chlorenchyma and spongy one could generally operate optically the way this theory attributes to them for a few minutes to seconds per a day or less, if any. So short and irregular functioning is unlikely to have caused the palisade chlorenchyma and its spongy counterpart to have evolved in leaves of C_3 plants.

Light distribution in the mesophyll essentially influences leaf photosynthesis. Optimizing of the light distribution was undoubtedly one of the main directions of mesophyll evolution (Smith et al. 1997). However, this optimization is unlikely to have been achieved by the emergence of the palisade and spongy chlorenchymata in the leaf.

Presumable specificity of the palisade chlorenchyma functioning

The palisade chlorenchyma is not typically a light guide, but it develops correlatively with luminous intensity (Meyer 1962; Napp-Zinn 1984; Smith et al. 1997; etc.). Such a correlative development of the palisade chlorenchyma is by no means caused by its specific optical properties.

More intense light is more penetrating to enable development of more bulky chlorenchyma. The mesophyll is generally thicker in the heliophytes and in the sun leaves than in the sciophytes and in shadow leaves (Eschrich 1995; Napp-Zinn 1984; Oguchi et al. 2005), so more chloroplasts can absorb energy of extra light. The chloroplasts have to be near intercellular airspace-exposed cell walls to photosynthesize efficiently (Evans & Loreto 2000; Evans et al. 2009; Terashima et al. 2011). Therefore, intense absorption of the extra light needs to maximize chloroplast number per unit of mesophyll volume and to maximize specific surface of the exposed cell walls. Specific surface of exposed cell walls of a spongy chlorenchyma cell can be the same or even larger than that of a palisade cell (Vogelmann & Martin 1993). Notwithstanding, the total

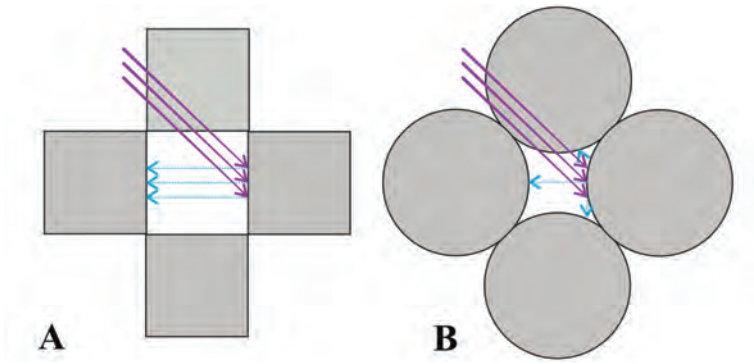

Figure 9. Distances the light beams run if reflected by parallelepiped (A) and by cylinder (B), base projections.

specific surface of exposed cell walls is typically much larger in the palisade chlorenchyma than in the spongy one due to a more tightly packing of cells of the former (Turrell 1936, cited by Hanba et al. 1999). Tighter cell packing causes the palisade chlorenchyma to have more numerous chloroplasts per unit of tissue volume than the spongy chlorenchyma (Meyer 1962). Tissue of parallel cylindrical cells potentially exceeds every tissue of cells of any other shape both in specific surface of the exposed cell walls and in number of near-walled chloroplasts per unit of tissue volume (Evans & Loreto 2000).

Cylindrical cells can equally absorb the incident light regardless of its direction (Niklas & Spatz 2012). Therefore, efficient light absorption would not affect orientation of the cylindrical cells in the palisade chlorenchyma. Their characteristic arrangement is obviously due to other cause(s). Intensive photosynthesis needs intensive diffusion of gaseous CO_2 through the intercellular airspaces to every assimilating cell (Eschrich 1995; Evans & Loreto 2000). As the leaf absorbs CO_2 by its stomata directly from the ambient air, there is mostly cross-leaf diffusion of CO_2 in its mesophyll (Parkhurst 1994; Morison et al. 2005). CO_2 diffuses along the palisade cells through more or less straight intercellular airspaces in typical palisade chlorenchyma. If the palisade cells are oblique or parallel to the leaf surface, the cross-leaf diffusion of CO_2 would be through tortuous intercellular airspaces which gird the cells.

Existing equipment enables rough measuring of gas distribution in the mesophyll, but it is unable to trace gas diffusion through specific intercellular airspace (Griffith & Helliker 2013). However, the tortuous girding intercellular airspaces would evidently be $\pi/2$ or more times longer than the straight cross-leaf ones (Morison & Lawson 2007). The longer the ducts are, the more resistant they are, the lower is the diffusion rate of a gas therein (Parkhurst 1994; Niklas & Spatz 2012). Moreover, the longitudinal intercellular spaces seem to highly outnumber their transverse counterpart per unit of palisade chlorenchyma volume. As a result, the palisade chlorenchyma would be more gas-permeable along its cells than in the transverse direction. The lateral diffusion rate is thought to be sufficient to support photosynthesis in the palisade chlorenchyma of loosely packed cells (Terashima et al. 2011), but it is unlikely so, when the cells are tightly packed. The assumption that the palisade chlorenchyma would typically be more gas-permeable along its cells than across them could indirectly be confirmed by the data below.

There are only a few species whose palisade cells are highly oblique or even parallel to the leaf surface (Meyer 1962; Guttenberg 1963). All of them have a rather thin chlorenchyma of such

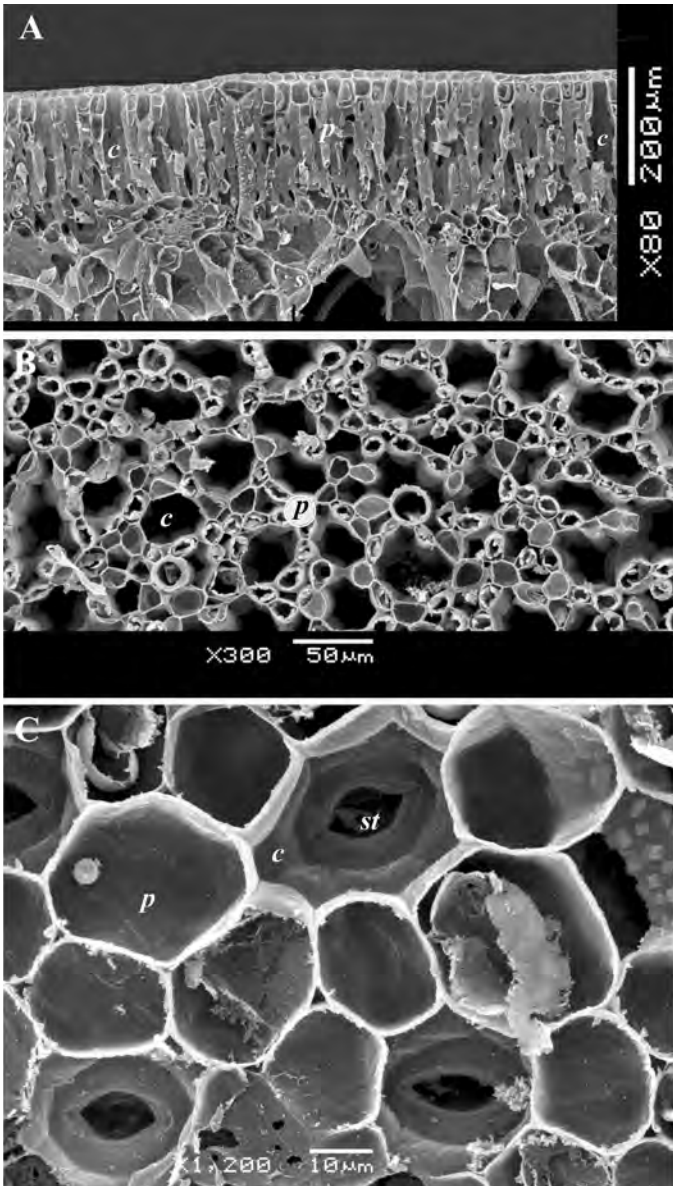

Figure 10. Anatomy of lamina of the floating leaf of *Nymphaea candida* J. Presl & C. Presl, SEM. A – transverse section; B – palisade chlorenchyma, paradermal section; C – palisade chlorenchyma, paradermal section, detail. *c* – substomatal chamber; *p* – palisade chlorenchyma; *s* – spongy chlorenchyma; *st* – stoma.

cells (Napp-Zinn 1984), perhaps, to shorten the transverse (= cross-leaf!) intercellular airspaces and to reduce thus diffusion resistance therein. There are also extra transverse intercellular air spaces girding the palisade cells (Meyer 1962). These intercellular spaces seem to increase transverse (= cross-leaf!) gas permeability of this chlorenchyma.

Floating leaves of *Nymphaea* spp. have a very thick multilayered adaxial palisade chlorenchyma of long tightly packed cells (Fig. 10A). These leaves are invariably epistomatous, so the substomatal chambers are in the palisade chlorenchyma. Some lateral diffusion of gases would be necessary in this chlorenchyma because of dispersed stomata (Guttenberg 1963; Parkhurst 1994). Such a diffusion is hardly possible due to dense arrangement of the palisade cells. Then, the substomatal

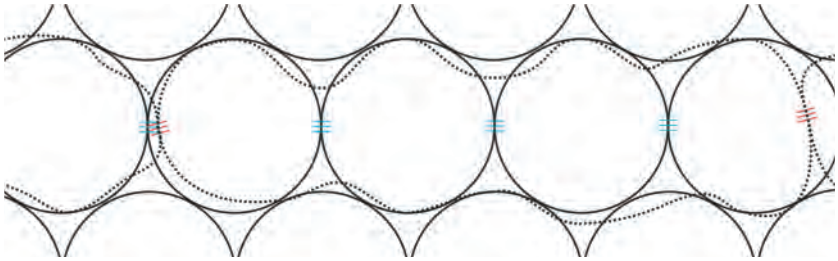

Figure 11. Different numbers of the cell-to-cell interfaces per unit of lateral distance in the palisade and spongy chlorenchymata, projections of the paradermal sections. *solid line* – palisade chlorenchyma; *dotted line* – spongy chlorenchyma.

chambers extend over the full thickness of the palisade chlorenchyma the latter being 1–2-layered septa between these chambers (Fig. 10B, C), thus making the lateral diffusion of CO_2 unnecessary for supplying every palisade cell.

The CO_2 diffusion transversely to the palisade cells can be highly reduced up to completely excluded without affecting photosynthesis, if only this diffusion is lateral. As the cross-leaf diffusion of CO_2 can be neither excluded nor reduced, it needs efficient cross-leaf ducts to maintain intensive photosynthesis of the palisade chlorenchyma. Such ducts are nearly straight intercellular airspaces along the long palisade cells. The latter are thereof caused to be perpendicular to the leaf surface.

Presumable specificity of the spongy chlorenchyma functioning

The palisade chlorenchyma has much more chloroplasts per unit of tissue volume than its spongy counterpart. That is why the palisade chlorenchyma produces the major amount of assimilates the leaf produces (Mokronosov 1983; Evans & Loreto 2000). It sometimes absorbs up to 95% of the light entered the mesophyll (Vogelmann 1993) and thus maintains nearly total photosynthesis of the leaf. Nevertheless, the palisade chlorenchyma always seems to be accompanied by the spongy chlorenchyma. There are C_3 species without palisade chlorenchyma in their leaves (Meyer 1962; Napp-Zinn 1974; Vogelmann & Martin 1993), but species without spongy chlorenchyma in their flattened leaves seem to have never been described. Thus, the spongy chlorenchyma has some essential function(s).

As CO_2 enters the leaf through dispersed stomata, then the principal cross-leaf diffusion of this gas is accompanied by its lateral diffusive distribution (Parkhurst 1977; Syvertsen et al. 1995; Evans & Loreto 2000; Pieruschka et al. 2006; Morison & Lawson 2007).

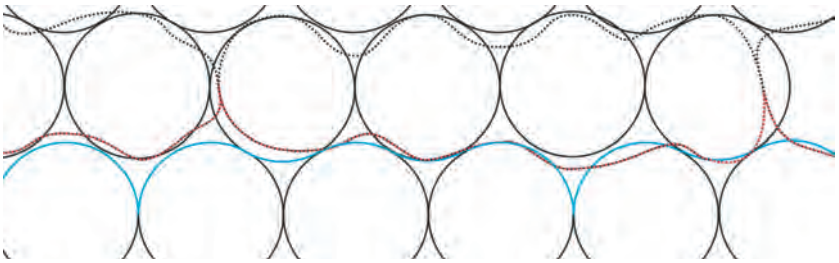

Figure 12. Different distances of lateral apoplastic transport of water through palisade and spongy chlorenchymata, projections of the paradermal sections. *solid line* – palisade chlorenchyma; *dotted line* – spongy chlorenchyma; *colour lines* – water flows.

The latter is occasionally even as intensive as the cross-leaf diffusion (Pieruschka et al. 2005; Evans et al. 2009). Though the diffusive paths of CO_2 in the mesophyll still remain untraceable (Griffith & Helliker 2013), the lateral component of its distribution is mainly attributed to the spongy chlorenchyma (Parkhurst 1994; Pieruschka et al. 2005) because of its higher porosity (Parkhurst 1994; Pieruschka et al. 2005; Evans & Loreto 2000; Morison & Lawson 2007) and isotropic resistance (Morison & Lawson 2007). However, lateral diffusion of CO_2 through loose palisade chlorenchyma is believed to be sufficient (Meyer 1962; Morison et al. 2005; Morison & Lawson 2007; Terashima et al. 2011). Specialization of the spongy chlorenchyma in lateral distribution of CO_2 seems not to be universal. Such a distribution "is not a primary selection factor" of this tissue (Morison et al. 2007: 689).

Not only CO_2 but also other substances involved in photosynthesis are transferred laterally through the mesophyll. Relative location of most palisade cells and vascular bundles in a leaf causes the assimilate solutes to be transferred laterally from these cells to the phloem. The opposite lateral transfer of water from the xylem is thought to be negligible (Schobert et al. 2000), because nearly the whole water is consumed by transpiration which is attributed either to bundles (Schobert et al. 2000) or to substomatal chambers (Parkhurst 1994). Both assumptions seem untenable as they ignore that the diffusion does not transfer solute assimilates, but the mass-flow (Eschrich 1995; Schobert et al. 2000). The latter is maintained by the water inflow. Besides, some water is used by chlorenchyma cells for producing carbohydrates (Gavrilenko & Zhigalova 2005). Therefore, 2 obligate opposing nearly equal lateral flows of solutes take place in the mesophyll.

Localization of these flows have not been exactly determined instrumentally (Schobert et al. 2000), but it is almost certain that they occupy different compartments of the phragmoblastem sensu Hagemann (1982), viz. apoplast and symplast (or endoplast according to Gamalei 2004). The localization probably differs in various species (Gamalei 2004), but assimilate solutes are more likely to be transferred symplastically (Eschrich 1995; Schobert et al. 2000). This conclusion is indirectly evidenced by the mass development of the secondary plasmodesmata just at the time the leaf starts exporting assimilates (Schobert et al. 2000).

The desmotubuli are 10 to 20 times narrower than the adjoining endoplasmic reticulum (Chentsov 2004). So, they are 10^4 to 20^4 times more resistant in accordance with Poiseuille's law (Pfitzner 1976). That is why the cell-to-cell interface has high flow resistance. The more numerous per unit of distance the cell-to-cell interfaces are, the more flow resistant is the tissue the flow has to pass through. The palisade chlorenchyma has typically much more cell-to-cell interfaces per unit of lateral distance than the spongy one (Fig. 11). It is accordingly much more resistant to the assimilate solutes (Schobert et al. 2000). Then, the lateral transport of assimilate solutes across the palisade chlorenchyma is inefficient. The lateral transfer of the assimilate solutes was absolutely correctly attributed to the characteristic functioning of spongy chlorenchyma (Haberlandt 1918; Lundegårdh 1960; Meyer 1962; Guttenberg 1963; Mokronosov 1983; Eschrich 1995). This functioning is especially characteristic of paraveinal chlorenchyma of Fabaceae (Eschrich 1995; Schobert et al. 2000).

The lateral transport of the water seems to be apoplastic. Palisade and spongy chlorenchymata are evidently identical in their cell wall structure. Therefore, water conductivity of these tissues only depends on the distance the water runs. Apoplastic water distances are longer in the palisade chlorenchyma (Fig. 12), so lateral transport of water across this tissue is less efficient.

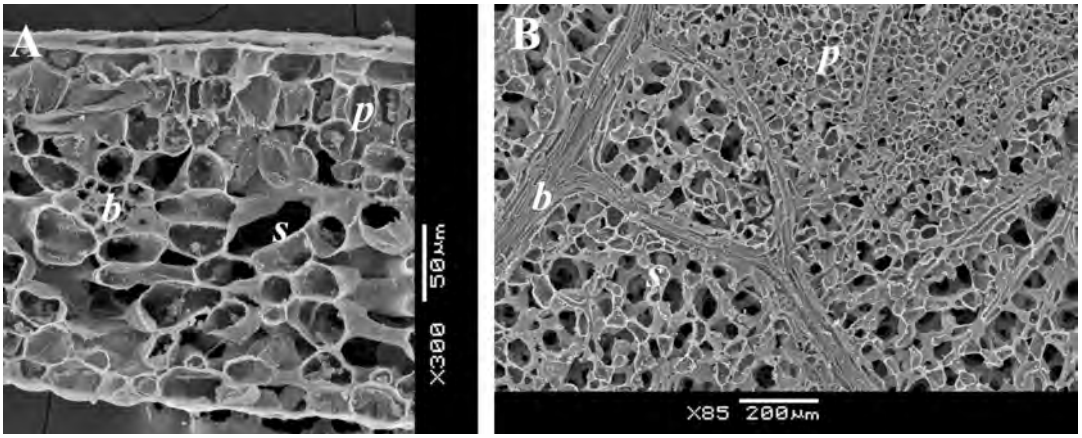

Figure 13. Anatomy of the leaf lamina of *Codiaeum variegatum* (L.) Rumph. ex A. Juss., SEM. A – transverse section; B – oblique paradermal section. *b* – vascular bundle; *p* – palisade chlorenchyma; *s* – spongy chlorenchyma.

Indeed, the lateral diffusion of gaseous CO_2 is not a primary selection factor for spongy chlorenchyma, but a lateral transport of solutes. The cells of spongy chlorenchyma constitute a transport network which connects every palisade cell with a vascular bundle (Fig. 13). Specialization of the spongy chlorenchyma in short-distant transferring of solutes is indirectly confirmed by the absence of this tissue when the solutes (and also CO_2) have to be transferred along the palisade cells (Fig. 14).

Conclusion

There is little doubt that the leaf structure has been evolving toward optimizing photosynthesis (Smith et al. 1997). This optimization has almost certainly resulted in palisade–spongy structure of the mesophyll in most C_3 plants. The palisade and spongy chlorenchymata clearly differ in their optical properties under stationary collimated light. Such a condition would be an exception in nature, if any. It could certainly not be a cause of palisade–spongy structure of the mesophyll of C_3 plants.

The photosynthesis rate of a leaf is proportional to the number of chloroplasts therein which are close to exposed cell walls. The palisade chlorenchyma enables to maximize the number of such chloroplasts per unit of mesophyll volume. Maximizing of specific number of chloroplasts is the primary advantage of the palisade chlorenchyma not its optical properties.

Optimizing of gaseous CO_2 and solutes transfer through the mesophyll is necessary for optimizing photosynthesis of a leaf. The paths of the CO_2 and solutes cross therein. CO_2 mostly diffuses cross-leaf, whereas the solutes flow laterally. The palisade chlorenchyma efficiently conducts gaseous and liquid substances along its cells, i.e. cross-leaf, but it is inefficient for lateral transport of substances. That is why the palisade chlorenchyma is accompanied by the spongy one. The latter contributes (much) less to the photosynthesis of a leaf, but it laterally transfers mostly solutes (Haberlandt 1918; Lundegårdh 1960; Meyer 1962; Guttenberg 1963; Mokronosov 1983; Eschrich 1995) and also gaseous CO_2 (Parkhurst 1994; Pieruschka et al. 2005 etc.).

The palisade–spongy structure of the mesophyll in most C_3 plants is an adaptive compromise. The palisade chlorenchyma is specialized in maximum light absorption, whereas the spongy

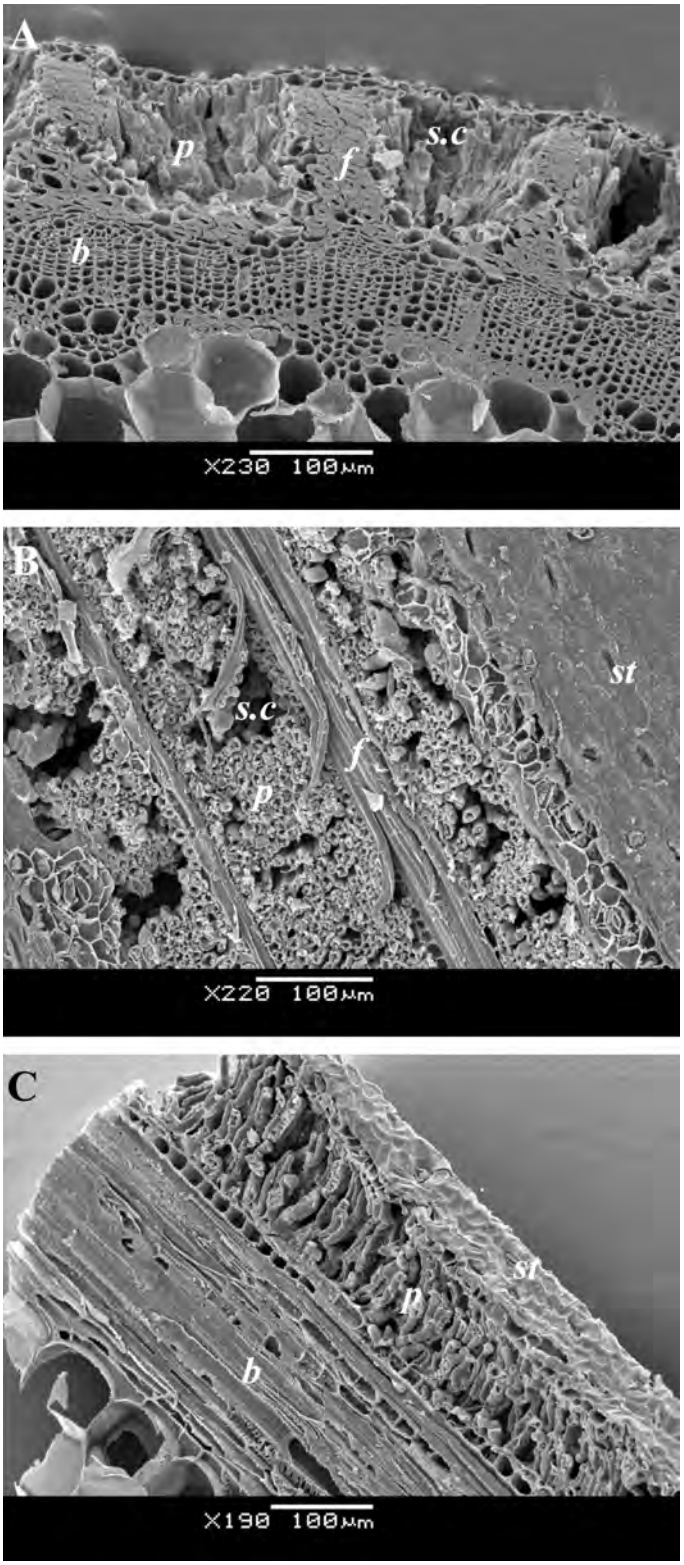

Figure 14. Anatomy of the cortex of annual stem of *Spartium junceum* L., SEM. A – transverse section; B – tangential section; C – radial section. *b* – vascular bundle; *f* – protophloem fibers; *p* – palisade chlorenchyma; *st* – stoma; *s.c* – substomatal chamber.

chlorenchyma is specialized in efficient short-distant lateral transport mostly of solutes and also gases.

The higher the illumination is, the more light enters the mesophyll, and the more light energy is accessible for chloroplasts therein. The sun leaves and those of heliophytes are accordingly thicker with more specific volume of the palisade chlorenchyma of more tightly packed, longer cells to increase the number of chloroplasts for consuming extra light energy. The huge palisade chlorenchyma nearly completely consumes the accessible light energy entering the mesophyll. The spongy chlorenchyma actually functions in this case as conductive tissue for short-distant lateral transport of CO_2 and solutes. On the contrary, illumination of the shadow leaves and those of sciophytes is too low to bring sufficient energy to be consumed by numerous chloroplasts. These leaves are accordingly thinner with smaller specific volume of looser palisade chlorenchyma of shorter cells to reduce superfluous chloroplasts which would not get light energy in any case. The palisade chlorenchyma is absolutely absent in extreme cases.

Instrumental researches under strictly controlled conditions are highly attractive in virtue of accuracy and reproducibility of their results. They often facilitate measurements and calculation of correlation values, the latter usually beeing considered a criterion of advanced science (Kedrov 1983). However, instrumental researches in biology only show that living beings exhibit certain properties, if they were put under experimental artificial conditions. These properties could promote recognizing some intimate characteristics of living things, but it would be naïve to think that the living beings have evolved to fit artificial experimental conditions. Griffith & Helliker (2013) headlined the section of their article eulogizing experimental researches 'What the eye does not see?' The eye certainly does not see much of what the devices detect. The experimental researches are inevitable and they will surely progress further on. However, anticipating new discoveries, any person should better remember the question 'What does an experiment hide and misrepresent?' If so, the person would be able to segregate facts from artifacts shown by the experiment.

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