Mini-review

UV-screening of grasses by plant silica layer?

Jörg Schaller[1,*], Carsten Brackhage[1], Ernst Bäucker[2] and E Gert Dudel[1]

[1]*Technische Universität Dresden, Institute of General Ecology and Environmental Protection,*

[2]*Technische Universität Dresden, Institute of Forest Utilization and Forest Technology, D-01062 Dresden, Germany*

**Corresponding author (Fax, +49351-46331399; Email, Joerg.Schaller@tu-dresden.de)*

UV-screening by terrestrial plants is a crucial trait since colonization of terrestrial environments has started. In general, it is enabled by phenolic substances. Especially for grasses it remains unclear why plants grown under the absence of UV-B-radiation exhibit nonetheless a high UV-B-screening potential. But this may be explained by the UV-screening effect of the silicon double layer. It was shown for seedlings of soybeans (*Glycine max* L.) and wheat (*Triticum aestivum* L.) that enhanced silicon supply reduces stress induced by UV-radiation. Even more important is a direct correlation between silicon content in the epidermis near area (intercellular spaces) and the absorption of UV-radiation in this area shown in other papers. The silicon double layer may act like a glass layer and decreases the transmission of UV-radiation at the epidermis near area. In summary, the absorbance/reflection of ultraviolet radiation is dependent on the characteristics of the epidermis near area of leaves, particularly the occurrence (qualitatively and quantitatively) of phenolic substances and/or a silicon double layer in this area. Consequently, UV-screening by plant silicon double layer should get more attention in future research with emphasis on effects of UV-radiation on plant physiology.

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1. Introduction

UV-screening by terrestrial plants is a crucial trait since colonization of terrestrial environments began. In general, it is enabled by phenolic substances. Phenolic secondary metabolites, especially flavonoids, have manifold functions in plant physiology. Besides defense against herbivores, absorption of UV-radiation and consequently protection of internal tissues are the most important properties of flavonoids (Winkel-Shirley 2002; Treutter 2005). Under the influence of UV-radiation, plants synthesize these phenolic compounds to protect themselves (Rozema *et al.* 1997; Cooper-Driver and Bhattacharya 1998). For grasses it is unclear why plants grown under absence of UV-B-radiation nonetheless show a high UV-B-screening potential (Schmitz-Hoerner and Weissenbock 2003). In some articles the accumulation of the element silicon in grasses is discussed to have a key role in UV-screening (Goto *et al.* 2003; Fang *et al.* 2006; Yao *et al.* 2011), and recently a reverse content of silicon and phenols was found (Schaller *et al.* 2012a), pointing to the same function phenols and silicon may have.

2. Silicon accumulation by grasses

Silicon (Si) is the second most abundant element on the ground level and is involved in physiological processes of many organisms. A large number of terrestrial (trees and grasses) and aquatic (emergent and submerged macrophytes) plants accumulate substantial amounts of silicon in their tissues (Struyf and Conley 2009; Schaller *et al.* 2012b). Currently, a lot of interesting research is published considering silicon to be involved in plant physiology (Schoelynck *et al.* 2010; Cooke and Leishman 2011a, b; Schaller *et al.* 2012b). Ecosystems dominated by Si-accumulating species cycle large amounts of silicon each year via plant root uptake and litter fall (Cornelis *et al.* 2010; Melzer *et al.* 2010). Silicon has positive effects on biomass production of grasses (Eneji *et al.* 2008), is beneficial for pathogen resistance (Fawe *et al.* 1998), and is altering the stoichiometry and carbon content of plants (Schaller *et al.* 2012a, b; Schoelynck *et al.* 2010). Furthermore, silicon is described to reduce the stress level of plants such as water stress (Eneji *et al.* 2008), heavy metal stress (Neumann and zur Nieden

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2001) and stress from nutrient imbalances (Cocker *et al.* 1998). The silica accumulation in plant tissues is important for herbivore defense by reducing leaf consumption (McNaughton and Tarrants 1983; Massey and Hartley 2009). Plant silica content is dependent on the amount of available silicon in soils and sediments (Liang *et al.* 2007; Schaller *et al.* 2012b) and may be related directly (specific transporter, longevity) (Hodson *et al.* 2005; Ma *et al.* 2006; Cooke and Leishman 2011b) and indirectly (transpiration rate) (Webb and Longstaffe 2000) to their phylogenetic traits. Silicon in the roots and shoots exists mainly as silicic acid [$Si(OH)_4$] an uncharged monomeric molecule (if pH is below 9), whereas in tissues with transpiration function (leaf blades and leaf sheath), silicic acid mainly polymerizes to different forms of silica gel [$nSiO_2$+nH_2O] (Q^3- and Q^4-groups), whereas [$(HO)Si\cdot(OSi^-)_3$] is shown as Q^3-group and [$Si\cdot(OSi^-)_4$] as Q^4-group with a higher condensation state (Ma and Yamaji 2006; Schaller *et al.* 2013). Silicon may be immobilized by biomineralization as plant opals (phytoliths) in the cell wall, cell lumen and in intercellular spaces (Epstein 1999) or in amorphous form as silicon double layer in the epidermis or epidermis near area (intra- and/or intercellular with connecting to either the cuticula and/or the mesophyll) (Hodson and Sangster 1988; Currie and Perry 2007). This silicon double layer is made of amorphous silica, a glass-like substance. Glass-like substances are known to reduce UV transmission (Tuchinda *et al.* 2006), which point to the potential of silicon for UV-screening in grasses.

3. Silicon effects on UV-screening

A scan of the cross-section of a grass (*Phragmies australis*) leaf (figure 1) points to the possibility of silicon supplementing the UV screening effect of phenolics by revealing a silicon layer in the epidermis or epidermis near area of grass leaves. This silicon compounds known as silica in leaf blades of plants had a very low UV-absorption, indicating radiation resistance in leaves with high silica content (Fang *et al.* 2006). It was shown for seedlings of soybeans (*Glycine max* L.) and wheat (*Triticum aestivum* L.) that enhanced silicon supply reduces stress induced by UV-radiation (Shen *et al.* 2010; Yao *et al.* 2011). Even more important is a direct correlation between silicon content in the epidermis near area and the absorption of UV-radiation in this area shown by Goto *et al.* (2003). If silica is deposited in or near the epidermis of the leaves (Schaller *et al.* 2012b), lower intensity of UV-radiation can penetrate the sclerenchyma and even the mesophyll (Goto *et al.* 2003). Hence, the silicon double layer may act like a glass layer (figure 1) and decreases the transmission of UV-radiation at the epidermis near area (Gatto *et al.* 1998). This decrease of transmission within the silica layer (especially for shorter wavelengths) may be explained by the absorption bands from the interaction with electrons, impurity and the presence of OH-groups (Kitamura *et al.* 2007). The impurity of the silica layer by a broad range of other elements is mostly documented for germanium as an index for weathering processes (Derry *et al.* 2005). The UV-screening by the OH-groups within the silica layer, however, may occur from an uncompleted polymerization of silicic acid [$Si(OH)_4$] to silica gel [$SiO_2\cdot nH_2O$] (Ma and Yamaji 2006).

4. Conclusion

In summary, not only phenolic substances (especially flavonoids) but also the plant silicon double layer may be able to protect grass plants from UV-radiation. The absorbance/reflection of UV-radiation is dependent on the characteristics of the epidermis near area of leaves, particularly the occurrence (qualitatively and quantitatively) of phenolic substances and/or a silicon double layer in this area. It is not yet clear whether in plants the ability evolved to actively create a silicon double layer for UV-screening or whether this is a side effect of silicon accumulation. After all, the UV-

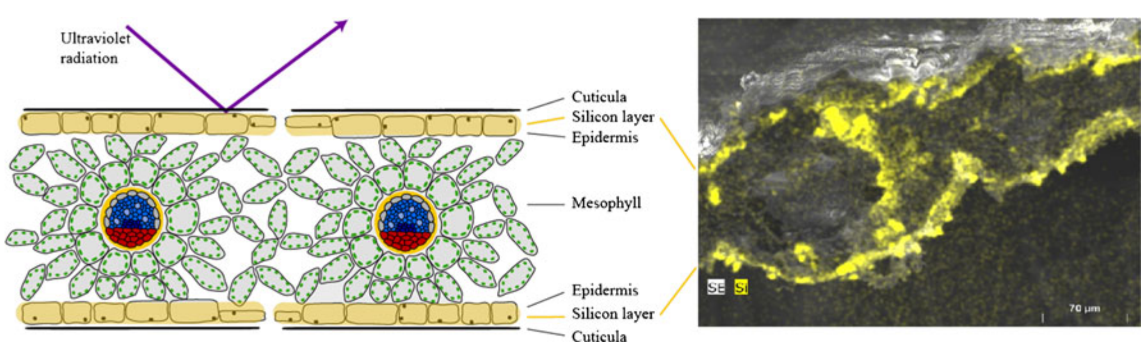

Figure 1. Scheme of leaf cross section (left) and (right) distribution of silicon (appearing in yellow) in the leaf cross-section of a dried leaf (from upper to lower cuticula) of *Phragmites australis* revealed by scanning electron microscope JEOL T 330A microscope was equipped with an element detector (EDR 288; Röntec, Berlin, Germany) and run at 15 kV, whereas the plant sample was critical-point-dried and subsequently coated with carbon (Zimmermann *et al.* 2000) (magnification 350×).

screening by the silicon layer should be an advantage with respect to the energy demand for producing phenolic substances, the alternative protection measure against UV-radiation. In addition, UV-screening by a plant silicon layer may be a crucial trait in the course of the expected earth magnetic field reversal. Consequently, UV-screening by plant silicon double layer should get more attention in future research with emphasis on effects of UV-radiation on plant physiology especially in grasses. Furthermore, the UV-screening effect of the silicon layer regarding the different qualities (wavelengths) of UV-radiation as well as the impact of the silicon layer on the level of repair enzymes for UV-damage has to be elucidated in future research.

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