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The optical, absorptive and chlorophyll fluorescence properties of young stems of five woody species

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ABSTRACT

To reveal the roles of stems in responding to the surrounding light environment, the optical properties of stem tissues of five woody species and their effect on bark, xylem and pith photosynthesis were investigated. Species-specific bark morphology and the distribution of pigments along the stem cross-section altered the radial conduction of light to a different degree, but in all investigated species light gradients within stems were markedly steep and visible light was largely depleted within the outer bark and cortex of the stems. Thereby, optical properties of the outer and inner bark resulted in an internal light environment, which is very different from outside according to intensity and spectral composition. Among species PAR-transmittance of outer bark or periderm varied in quantity between mean values of 8.5 and 42% and PAR-transmittance of total bark between 2.2 and 6.2%. The blue-band of the spectrum was totally absorbed by the outer and inner bark tissues. In the red-band total bark transmittance varied between 2 and 11%. Thus, blue light can only trigger photosynthetic electron transport in the cell layers of the cortex near the stem surface, whereas in the underlying cell layers of the xylem or pith the energy for photosynthesis can only be provided by longer wavelengths (green and particularly red light). In all species, the internal light gradient matched well with the chlorophyll fluorescence properties of the respective stem tissues. The maximum and effective quantum efficiencies of PSII clearly decreased from the cortex toward the innermost stem tissues (xylem, pith), which showed also a lower capability of photosynthetic electron transport of PSII. Our results indicate not only that light signals can enter the interior of stems and are modified in quantity and quality by its path through the stem. There is evidence to suggest that the light regime within stems has also profound effects on plastid differentiation and thus the photosynthetic properties of the respective stem tissues.

1. Introduction

Light drives photosynthesis and is the source of environmental signals that regulate plant growth and development. In this sense, plants strongly depend on their external light environment. Nevertheless, plants themselves modify the light environment by absorbing, reflecting or transmitting the incident light. The result is an internal light environment, which is very different from outside according to intensity, spectral composition and direction and which strongly depends on the optical properties of the involved plant tissues (Wallter-Shea and Norman, 1991). Optical properties of plant tissues have been investigated mostly in leaves, because of their importance in photosynthesis and/or photomorphogenesis (see Vogelmann, 1993; Vogelmann and Han, 2000). By contrast the light microenvironment within stems of woody plants has mostly been neglected, although the incident light is also modified on its path from outside to the stem interior. First the light has to pass the outer bark or periderm. Below the outer bark most stems of woody plants possess light absorbing, greenish inner bark or cortex parenchyma (Foote and Schaedle, 1976; Wittmann et al., 2001, 2006; Pfanz et al., 2002; Wittmann and Pfanz, 2008, 2014), but chloroplasts can also be found in internal tissues isolated from light scources like xylem, xylem rays and pith (Pfanz et al., 2002; Dima et al., 2006; Berveiller et al., 2007; Yiotis et al., 2009). In young stems these chlorophyll-containing tissues are able to use the transmitted light and the stem internal CO_2 for photosynthesis (e.g., Wittmann et al., 2001, 2006; Pfanz et al., 2002; Wittmann and Pfanz, 2007). Stem internal re-fixation of CO_2 in young twigs and branches may compensate for 60–90% of the potential respiratory carbon loss and thus contributes to maintain a positive carbon balance in woody plants (Foote and Schaedle, 1976; Wittmann et al., 2001, 2006; Aschan

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et al., 2001; Pfanz et al., 2002; Damesin, 2003; Berveiller et al., 2007; Wittmann and Pfanz 2007, 2008). The role of (inner) bark and woody tissues in refixation of respiratory CO_2 was also supported by measurements of fixation of isotopically labeled CO_2, which provided further evidence of an internal recycling mechanism for respired CO_2 in stem tissues (McGuire et al., 2009; Cernusak and Hutley, 2011; Bloemen et al., 2013). Furthermore, the oxygen evolved during bark and wood photosynthesis plays a decisive role in avoiding stem internal hypoxia or even anoxia (Wittmann and Pfanz, 2014).

Plant stems are thus not passive receivers of light energy. When light enters various tissue layers, its qualities are modified by the optical properties of each layer (Vogelmann, 1993). The light, which enters and moves through a plant organ, is thereby attenuated both by absorption and scattering, which creates a light gradient (Vogelmann et al., 1989). Yet, published data on the optical properties of stems tissues are restricted to measurements of overall PFD-transmittance of stem periderms, which varies (ca. 10–50%), depending on the tree species and stem age (Strain and Johnson, 1963; Kauppi, 1991; Pfanz et al., 2002; Wittmann and Pfanz, 2008). In addition, Sun et al. (2003) investigated the role of vascular tissues in axial light conduction of woody plants. They found that far-red light was conducted most efficiently by vascular tissue along the axial direction of both stems and roots, via their lumina (vessels) or cell walls (fibres and tracheids). Other components, such as sieve tubes and parenchymal cells, were not efficient axial light conductors.

Knowledge about the light environment that exists within stems is requisite for understanding light absorption by photoreceptors that control growth and development, and for understanding light absorption by chlorophyll for photosynthesis. In the present work the optical and absorptive properties of different stem tissues are studied in five tree species. The aims were: (1) to quantify the light microenvironment within young stems of different woody species according to light intensity and spectral composition, (2) to determine possible gradients of visible light along the radial direction of stems due to maybe tissue anatomy or pigmentation, and (3) to find out how the quantity and quality of light penetrating to the various tissue layers relate to its chlorophyll fluorescence properties. Therefore, measurements of tissue specific PFD-transmittance and absorption as well as chlorophyll-fluorescence imaging of stem cross sections of different woody species were performed.

2. Material and methods

2.1. Site description and plant materials

The experiment was conducted in 2010 on five tree species (*Abies nordmanniana* Stev. Spach, *Fagus sylvatica* L., *Fraxinus excelsior* L., *Prunus avium* L., *Quercus robur* L.) grown outside in the botanical garden of the University Duisburg-Essen (Germany). Three-year-old seedlings of each species were lifted in April 2008 at a German nursery. After lifting a morphological uniform set of 15 trees per species was selected and transplanted in 30-l plastic containers. Since then, plants were grown under sufficient nutrition (Einheitserde Typ T, Balster, Germany) and water supply provided by periodic fertilisation with Osmocote (Bayer, Germany) and daily irrigation. In June 2010 ten trees per species were sampled. Samples were taken from healthy, south facing stems of the current growth season (0-year-old) at a plant height of about 1–1.5 m. Therefore stems were cut before noon, watered, shaded and directly transported to the laboratory. Mean plant heights and stem diameters are given in Table 1. During the measurement period (June 2010) mean diurnal temperature was 17.6 °C, the sum of precipitation was 19.8 mm and the sum of sunshine duration was 260.6 h.

2.2. Chlorophyll fluorescence measurements across stem cross sections

Images and profiles of fluorescence parameters (Fv/Fm, ΔF/Fm′) across stem cross sections of all investigated species were made with the MICRO-version of the IMAGING-PAM (WALZ, Effeltrich, Germany). Therefore, current year stems of ten different trees of each species were harvested. From each stem a 0.4 cm thick piece (Microtom Leica RM2025, Germany) was taken, placed on the center of a 26 × 76 mm microscope slide and covered with a moistened filter paper. Each sample was fixed on the microscope slide with a small weight that is delivered together with the MICRO-head. When using the MICRO-head, the CCD camera is pointing upwards and the LED-light is applied from below, in contrast to the situation with the standard head.

Images of Fv/Fm were determined after dark-adaptation of the stem for at least 5 min. This comparably short adaption time was sufficient, because samples were kept in darkness since they were harvested and sample preparation in the lab was done at an illumination of below 5 μmol photons $m^{-2}\,s^{-1}$. Consequently, the real dark adaption time was much longer than 5 min (around 30–60 min). Afterwards the effective quantum yield (ΔF/Fm′) of PSII

Table 1
Plant height, stem diameter, chlorophyll content (chl (a + b)) and chl a/b ratio of inner bark (= cortex) and xylem of current-year stems of different tree species. Mean ± s.d. of 10 independent measurements ($n = 10$). Asterisks indicate significant differences between pigment values and ratios of cortex and xylem as examined by Student's *t*-tests (*$P < 0.05$: **$P < 0.01$; ***$P < 0.001$).

Parameter		Species				
		Abies	*Fagus*	*Fraxinus*	*Prunus*	*Quercus*
Plant	Plant height (m)	1.15 ± 0.25	1.48 ± 0.07	2.01 ± 0.11	1.93 ± 0.19	1.65 ± 0.0.08
Stem	Diameter (mm)	5.33 ± 0.41	2.96 ± 0.37	4.44 ± 0.49	3.44 ± 0.46	3.95 ± 0.40
Cortex	chl (a + b) ($mg\,m^{-2}$)	117.01 ± 7.86	249.78 ± 73.24	162.81 ± 22.49	136.53 ± 29.10	330.87 ± 43.82
Xylem[a]	chl (a + b) ($mg\,m^{-2}$)	12.16 ± 3.94***	44.81 ± 10.02***	72.23 ± 17.71***	134.56 ± 16.30	170.08 ± 42.50***
Cortex	chl (a + b) ($mg\,g^{-1}$ FW[b])	0.17 ± 0.02	0.80 ± 0.26	0.38 ± 0.05	0.32 ± 0.03	0.71 ± 0.07
Xylem[a]	chl (a + b) ($mg\,g^{-1}$ FW[b])	0.02 ± 0.01***	0.15 ± 0.02***	0.10 ± 0.01***	0.12 ± 0.02***	0.21 ± 0.06***
Cortex	chl a/b	2.37 ± 0.19	2.37 ± 0.19	1.89 ± 0.42	1.74 ± 0.10	1.19 ± 0.07
Xylem[a]	chl a/b	1.28 ± 0.45***	1.96 ± 0.38**	1.26 ± 0.13**	1.36 ± 0.10***	0.83 ± 0.07***

[a] Pith cells included.
[b] Fresh weight.