Remote Sensing of Environment 174 (2016) 181–196

Contents lists available at ScienceDirect

Remote Sensing of Environment

journal homepage: www.elsevier.com/locate/rse

Analysis of the effect of chloroplast arrangement on optical properties of green tobacco leaves

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ARTICLE INFO

Article history:
Received 15 July 2015
Received in revised form 5 November 2015
Accepted 9 December 2015
Available online xxxx

Keywords:
Diffuse reflectance
Diffuse transmittance
Absorptance
Leaf absorbance
Infiltration
Chlorophyll fluorescence
Collimated light
Diffuse light
Nonlinearity

ABSTRACT

There are many studies showing the active optical reaction of a green leaf to the changing surroundings based on chloroplast movement and their rearrangement in plant cells. These studies concentrated mostly on the effect of one feature (leaf type, leaf side or light type) on the leaf optical spectra. We have measured the diffuse reflectance and transmittance spectra of tobacco green leaves in combination of 4 variants: in normal and water infiltrated leaves, in collimated or diffuse incident light, on both the adaxial and abaxial leaf sides, and for the face or side chloroplast arrangement. A Simple Explicitly Non-Linear Empirical model for Leaf Optical Properties (SENLELOP model) is used to theoretically describe, simulate and fit the deviations from the Lambert–Beer's law causing nonlinearity in the measured spectral changes. It is shown that the incident diffuse light is captured by the leaf more effectively than the collimated light. The light incident from the adaxial leaf side is more effectively absorbed than the same light incident from the abaxial leaf side. The air in intercellular spaces of natural leaf increases about twice the beam path and strongly deepens the non-linearity of the absorption process when compared with water infiltrated leaf. The chloroplast arrangement in the palisade cells is reflected in most of the studied differences. The leaf absorbance changed in our case of tobacco leaves up to 30% when the chloroplasts moved from the face to the side position. This change depends strongly on the wavelength and quite slightly on the character of incident light. Further analysis predicts that in practice the effect of chloroplast rearrangement on the reflectance spectra is in dependence on the wavelength of the light about 2–5% in our case of fully developed green leaves but can be higher in some cases. Thus it can affect values of some of the indices used in the remote sensing.

1. Introduction

A green leaf of higher plants can, to some extent, react and adapt to the changing light conditions. This reaction is aimed to optimize the absorption of light quanta both to maximize the energy utilization in photosynthesis and to avoid harmful over-excitation. The process of this adaptation is rather complex occurring in different time-scales and may cover a change in the leaf position, leaf structure (e.g., swelling), chloroplast movement, pigment composition, the state transitions or energy quenching. We concentrate in this paper on the effect of chloroplast arrangement on the optical properties of leaves.

The ability of leaves to adapt its inner chloroplast arrangement to the light conditions also influences the resulting optical properties of leaves, i.e., the leaf spectra of reflectance, transmittance, absorptance and fluorescence. The leaf reflectance is usually the basis of the image detection of a canopy by the spectral or multispectral cameras, both in laboratory and in remote sensing studies. This implies that the detected spectral image can be also influenced by the chloroplast arrangement in leaf cells without changes in leaf structure or chlorophyll content. It can be expected that even the light environment within the canopy (light spectrum, geometry, intensity) can be influenced by the chloroplast arrangement in the individual leaves and leaf layers. This indicates that the knowledge of this phenomenon, including its theoretical description, should be taken into account in the remote sensing studies.

Our work aims to attract the attention of researchers to the changes in optical spectra of leaves due to changes in chloroplast arrangement in leaf cells. We suggest a simple method of mathematical description and evaluation of these changes. Our work is based on previous original experience showing the effect of chloroplast movement in the signal of chlorophyll fluorescence or in the readings of a chlorophyll meter (Brugnoli & Björkman, 1992; Nauš, Prokopová, Řebíček, & Špundová, 2010). Our study is restricted to the situation on a level of one leaf. The upscale transfer to the level of whole plant or canopy is a matter of further research.

1.1. Optical parameters

By optical parameters we mean here the spectra of leaf reflectance, transmittance, absorptance and fluorescence. From this point of view,

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http://dx.doi.org/10.1016/j.rse.2015.12.011

the most important physical quantity is the leaf absorptance (Gates, Keegan, Schleter, & Weidner, 1965) showing that part of the incident light which is really absorbed in the leaf tissue (e.g., Davis, Caylor, Whippo, & Hangarter, 2011). To get a reliable information about the leaf absorptance, the method of integration sphere should be used and both reflectance and transmittance spectra should be measured from both sides of the leaves (see, e.g., Davis et al., 2011; DeLucia, Shenoi, Naidu, & Day, 1991; Hlavinka, Nauš, & Špundová, 2013).

The ability to measure the optical parameters from a distance, remote sensing, has received extensive study. Much of this research has focused on indices such as NDVI (Gamon, Peñuelas, & Field, 1992; Rouse, Haas, Schell, & Deering, 1974; Tucker, 1978), calculated from reflectance measurements. Transmittance measurement has been also included (Bergsträsser et al., 2015; Daughtry & Walthall, 1998; Mariotti, Ercoli, & Masoni, 1996) but it is not so common.

1.2. Natural versus infiltrated leaf

Leaves contain in their structure intercellular spaces filled with the air. These spaces cause most of the complexity of the measured spectra as the difference in refractive index of cell walls and cytoplasm on one side and the air on the other side causes light refraction and reflection. Including also light diffraction, scattering (Rayleigh and Mie scattering), and interference (Steinhardt & Fukshansky, 1987), the complex phenomenon describes light propagation and is sometimes generally referred to as scattering.

In order to simplify the optical properties and to obtain some extreme parameters and spectra, the leaves may be vacuum infiltrated with water or suitable solution or oil. The obtained spectra may be a basis for a discussion on the role of the intercellular spaces in the optical processes (DeLucia, Nelson, Vogelmann, & Smith, 1996).

1.3. Adaxial versus abaxial leaf side

In many bifacial leaves the leaf structure visualized by microscopic cross section differs in the parts adjacent to the adaxial (upper) and abaxial (lower) leaf sides (see, e.g., Smith, Vogelmann, DeLucia, Bell, & Shepherd, 1997). The mesophyll cells at the adaxial leaf side are of palisade character whereas those at the abaxial leaf side are of spongy structure, see Fig. 1. These differences are reflected in different spectra of diffuse reflectance (see, e.g., DeLucia et al., 1991; Hlavinka et al., 2013). The reflectance of a leaf can be divided into the external one, *Re*, and internal one, *Ri* (Hlavinka et al., 2013; McClendon & Fukshansky, 1990a,b). The adaxial and abaxial leaf sides differ both in the *Re* and in *Ri*. These differences may be attributed to the structural differences of palisade and spongy parenchyma. It should be noted

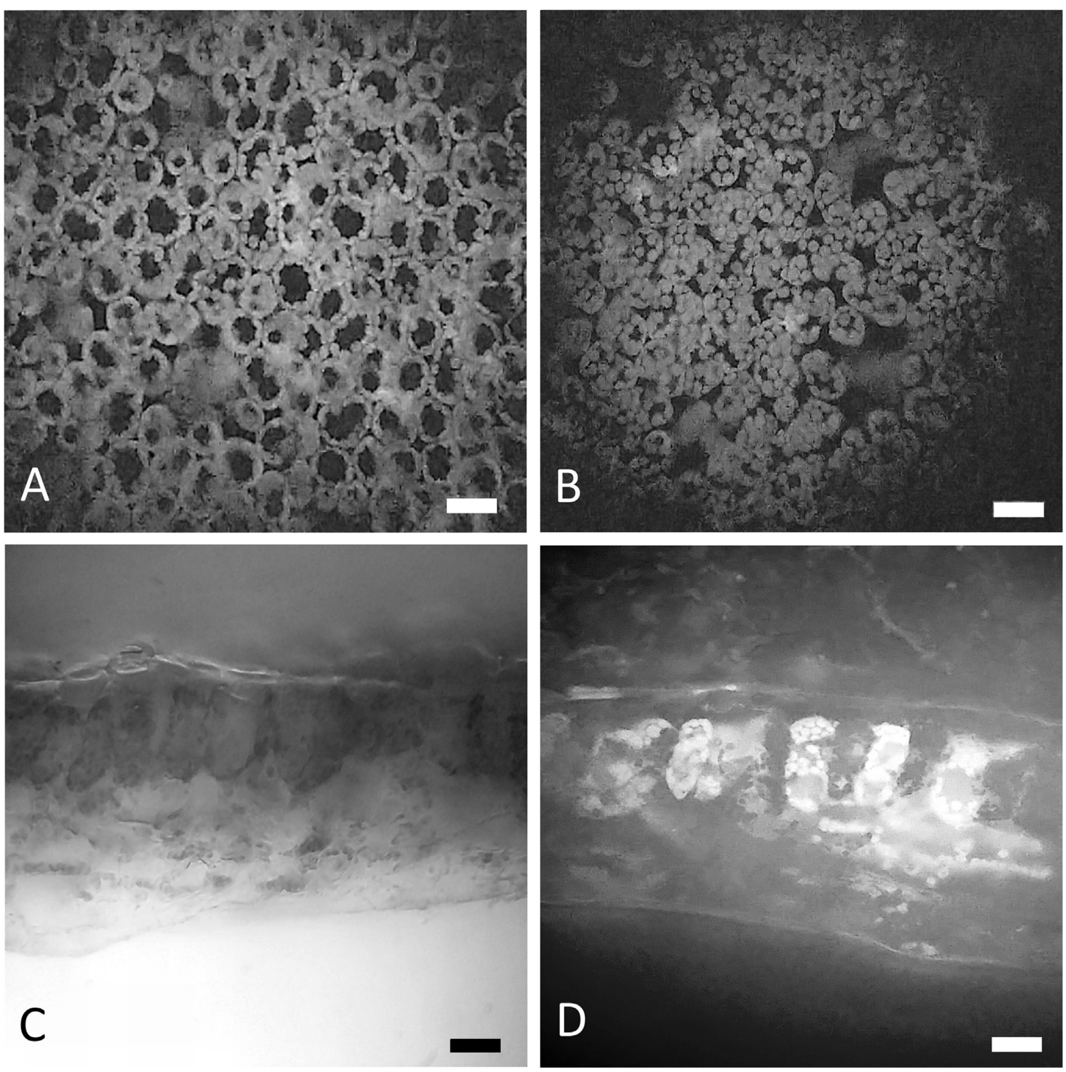

Fig. 1. Images of tobacco leaf parts from optical microscope using transmission (C) or fluorescence (A, B, D) modes. A and B show side (A) and face (B) chloroplast positions as seen from adaxial leaf side. C and D show leaf cross section with different architectures in the adaxial (top) and abaxial (bottom) leaf sides. The lighter “dots” in A, B, and D show fluorescing chloroplasts. The bar indicates 20 μm.