ISPRS Journal of Photogrammetry and Remote Sensing 125 (2017) 132–145

Contents lists available at ScienceDirect

ISPRS Journal of Photogrammetry and Remote Sensing

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

Identifying leaf traits that signal stress in TIR spectra

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ARTICLE INFO

Article history:
Received 27 July 2016
Received in revised form 19 January 2017
Accepted 21 January 2017
Available online 31 January 2017

Keywords:
Spectral emissivity
Water stress
Temperature stress
Leaf traits
Leaf water content
Rhododendron cf. catawbiense

ABSTRACT

Plants under constant water and temperature stress experience a chain of reactions that in the long term alter their leaf traits (morphology, anatomy and chemistry). The use of these traits as proxies for assessing plant stress was so far mainly based on conventional laboratory methods, which are expensive and time-consuming. Remote sensing methods based on spectral changes can detect changes in pigments and productivity using the visible and near infrared. However, the use of infrared spectra, where changes in the spectra are associated with physical changes of the leaf, is still incipient.

In this study plants of *Rhododendron* cf. *catawbiense,* were exposed to low temperatures and low soil water content during a six months experiment. The spectral response in the infrared region 1.4–16 μm, microstructural variables, leaf water content, leaf area and leaf molecules such as lignin and cellulose concentrations were measured in individual leaves after the period of stress. This study revealed that under cold conditions plants have most changes in leaf water content, lignin and cellulose concentrations and leaf area, while under drought conditions the most striking change is water loss. These leaf trait modifications are also correlated with changes in thermal infrared spectra, showing their potential as proxies for detecting plant stress in this species. A multinomial model allows the estimation of the stress treatments imposed on these plants from their infrared spectra. This model reveals a group of 15 bands in the SWIR and MWIR between 2.23 and 7.77 μm, which show relatively large changes, and had an overall accuracy of 87%.

Finally, individual partial least squares regression models show that lignin, cellulose, leaf water content and leaf area are the leaf traits reacting significantly to long-term stress and that are also generating measurable changes in the infrared spectra. Although these models are based on laboratory data, the congruence of the identified bands with the fundamental molecular vibrations used in remote sensing, shows the potential of these findings in the assessment of plant stress.

1. Introduction

Plants growing under suboptimal conditions generate various responses in leaves, of which some are relatively fast and others slower. The fast responses are chains of chemical reactions to cope with a temporary stressor. While under permanent stressors, plants display slower, semi-permanent changes, from the relocation of molecules (including water) to avoid desiccation and damage of internal cellular structures, up to more physical changes like more compact leaves to reduce water loss (Chaves and Oliveira, 2004; Prasad, 2001; Wahid et al., 2007).

Under stress cell size and cell wall thickness tend to increase (e.g. Huner et al., 1981; Stefanowska et al., 1999), production of cuticle lipids and waxes increases resulting in thicker cuticles and reduced evapotranspiration (Cameron et al., 2006; Fitter and Hay, 2002; Kosma et al., 2009; Riederer and Schreiber, 2001; Stefanowska et al., 1999; Wang et al., 2011) and mesophyll and palisade layers grow thicker causing leaf thickness to increase (Bracale and Coragio, 2003; Fitter and Hay, 2002; Huner et al., 1981; Nautiyal et al., 1994). Readjustments in the outer layers lead to smaller stomatal sizes and higher stomatal densities to cope with long-term suboptimal temperatures or dryer environments (Nautiyal et al., 1994). These strong responses of leaves to external conditions make these leaf traits appropriate proxies for a wide variety of stressors.

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http://dx.doi.org/10.1016/j.isprsjprs.2017.01.014

Techniques to assess plant stress range from manual diagnosing of individual plants to remote sensing of large areas. Remote sensing and spectral evaluation are among the most accurate and cost efficient techniques to assess the status of natural ecosystems and economic crops (Nautiyal et al., 1994). In plant assessment, remote sensing is mainly used to evaluate changes in photosynthetic activity of plants and changes in pigments through variations in the visible (VIS, 0.4–0.7 μm) and near infrared (NIR, 0.7–1.4 μm) (Behmann et al., 2014; Dobrowski et al., 2005; Lichtenthaler, 1996; Peñuelas and Filella, 1998; Stagakis et al., 2012; Zarco-Tejada et al., 2009). The shortwave infrared (SWIR, 1.4–3 μm) is widely used in the evaluation of changes in leaf water content (LWC), especially related to stress caused by drought (Ceccato et al., 2002; de Jong et al., 2012; Eitel et al., 2006; Feng et al., 2013; Fensholt and Sandholt, 2003). The thermal infrared (TIR 3–16 μm) has been used to evaluate the health status of plants (e.g. Calderón et al., 2013; French et al., 2000), canopy temperature (e.g. Grant et al., 2007; Leinonen and Jones, 2004) and LWC changes (e.g. Jones et al., 2004; Ullah et al., 2014).

This last range, which can be divided into the mid-wave infrared (MWIR 3–6 μm) and long-wave infrared (LWIR, 6–16 μm), has been claimed to have less influence of water, especially after 5 μm (e.g. Ribeiro da Luz, 2006), and therefore the spectra could contain more information about physical leaf traits (e.g. Buitrago et al., 2016; Elvidge, 1988; Ribeiro da Luz, 2006; Ribeiro da Luz and Crowley, 2007).

Previous studies have shown that molecules of the outer surface of the leaf such as lignin, cellulose, hemicellulose, cutin and cuticular waxes, configure the main features of the leaf spectra at the NIR and the TIR (e.g. Elvidge, 1988, 1990; Ribeiro da Luz, 2006). Spectra of pure lignin and cellulose, show clear features from the SWIR to the LWIR which are explained mainly by the molecular vibrations of their molecular O-H, C-H and CH_2 bonds (e.g. Elvidge, 1988). Cellulose has indexes based on bands such as 2.0, 2.1 and 2.2 μm (e.g. Cole et al., 2014), while water has been associated strongly with bands in the NIR to the SWIR, especially between 2.5 and 6.0 μm (e.g. Fabre et al., 2011; Ullah et al., 2014). It is expected that changes in these leaf traits, but also other physical leaf traits which change as a stress response of plants, could be tracked in this section of the infrared spectra.

A previous study showed that different water and temperature regimes in plants change the spectral behaviour in the TIR (Buitrago et al., 2016). However, the physical adaptations in the leaves that cause these changes in the TIR spectra have not been investigated.

In the present study, we quantify the effect of prolonged temperature and water stress on some leaf traits, and how modifications of these leaf traits generate changes in the leaf spectra.

Additionally, we use the relation between stress treatments, leaf traits and spectra inversely to estimate stress in plants from spectra. Fig. 1 serves as a guide to explain the methods and results. Firstly, we explore the effect of stress on leaf traits and spectra (Fig. 1a). Buitrago et al. (2016) showed that TIR spectra change when plants grow under stress conditions (Fig. 1 arrow 1). In this study, we test if stress generates measurable changes in leaf traits (arrow 2) and if leaf traits can be linked to specific features in TIR spectra (arrow 3). This last step allows us to identify leaf traits that can be used for the estimation of plant stress (Fig. 1b) which are the basis to identify the real causes for spectral changes generated by stress.

We fit inverted models from the empirical relations to make estimations whether a plant has been subjected to stress conditions based on spectral measurements (Fig. 1b). We fit models to estimate changes in leaf traits from the spectral variations (arrow 4) and to estimate stress from variations in leaf traits (arrow 5). Finally, we identify how spectral changes are proxies to detect stressed plants (arrow 6) using TIR spectra.

2. Materials and methods

2.1. Species

Rhododendron cf. catawbiense was selected for this study because it is an evergreen species widely distributed in alpine ecosystems, from lowlands up to the tree lines. Due to its wide distribution across mountains, this genus has a wide variety of mechanisms to cope with suboptimal conditions. Among these mechanisms are changes in the structure of the plant, wilting of the leaves and microstructural and biochemical changes in the leaves (Wang et al., 2008). Its high tolerance to extreme conditions combined with high plasticity makes it a suitable species to track leaf changes under long-term suboptimal conditions.

2.2. Experiment

During the growing season of 2013, 60 plants between 45 and 60 cm of height were randomly assigned to one of four treatments. Rhododendrons grow a cohort of rosettes with new leaves each season and only these new leaves were measured in this study. For each plant, five mature leaves from the last cohort were marked and tracked during the experiment. In total for each treatment, 75 leaves were measured at the end of the experiment. Individual leaves of plants in each treatment were labelled and tracked throughout the study.

The experiment consisted of stressing the plants during six months on two aspects: cold temperature and reduction in soil water in a full factorial design. The temperature aspect was implemented with two treatment groups (see Table 1 and Fig. 2): ambient (i.e. the control) and cold temperature. In the ambient treatment the first three months (in summer) the plants were growing outside (mean temperature: 18.1 °C) and consecutively (in autumn) they were growing three months in a warmed greenhouse (mean temperature: 20.0 °C). In the cold treatment the plants were growing three months (in summer) under low temperatures inside a cooled greenhouse (mean temperature: 11.2 °C), and consecutively (in autumn) they were growing three months outdoors (mean temperature: 8.7 °C).

The water aspect was implemented with two treatment groups as well: dry- and well-watered (referred to hereafter as the "wet treatment"). For the wet treatment, plants were watered up to field capacity, which was determined gravimetrically. For the dry treatment, plants were watered up to 20% of their field capacity, and the pots were covered with plastic to avoid additional rainfall. The combination of both treatments resulted in four possible

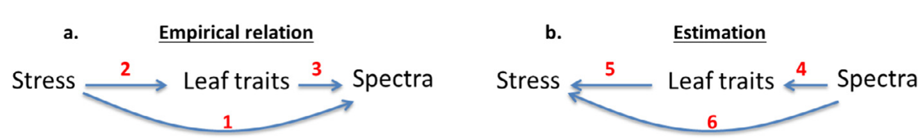

Fig. 1. Diagram of the relations between stress treatment, spectra and leaf traits. Blue arrows indicate "has an effect on" in (a) and "is used to estimate" in (b). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)