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Optical trait indicators for remote sensing of plant species composition: Predictive power and seasonal variability

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ABSTRACT

Most plant species feature similar biochemical compositions and thus similar spectral signals. Still, empirical evidence suggests that the spectral discrimination of species and plant assemblages is possible. Success depends on the presence or absence of faint but detectable differences in biochemical (e.g., pigments, leaf water and dry matter content) and structural properties (e.g., leaf area, angle, and leaf structure), i.e., optical traits. A systematic analysis of the contributions and spatio-temporal variability of optical traits for the remote sensing of organismic vegetation patterns has not yet been conducted. We thus use time series of optical trait values retrieved from the reflectance signal using physical models (optical trait indicators, OTIs) to answer the following questions: How are optical traits related among patterns of floristic composition and reflectance? How variable are these relations in space and time? Are OTIs suitable predictors of plant species composition?

We conducted a case study of three temperate open study sites with semi-natural vegetation. The canopy reflectance of permanent vegetation plots was measured on multiple dates over the vegetation period using a field spectrometer. We recorded the cover fractions of all plant species found in the vegetation plots and extracted gradients of species composition from these data. The physical PROSAIL leaf and canopy optical properties model was inverted with random forest regression models to retrieve time series of OTIs for each plot from the reflectance spectra. We analyzed these data sets using correlation analyses. This approach allowed us to assess the distribution of optical traits across gradients of species composition. The predictive performance of OTIs was tested in relation to canopy reflectance using random forest models.

OTIs showed pronounced relationships with floristic patterns in all three study sites. These relationships were subject to considerable temporal variability. Such variability was driven by short-term vegetation dynamics introduced by local resource stress. In 72% of all cases OTIs out-performed the original canopy reflectance spectra as indicators of plant species composition. OTIs are also easier to interpret in an ecological sense than spectral bands or features. We thus conclude that optical traits retrieved from reflectance data have a high indicative value for ecological research and applications.

1. Introduction

Remote sensing of vegetation has a long history. Fundamental factors and processes that determine the reflectance characteristics of vegetation canopies have largely been identified. According to established theories, these factors include the biochemical compositions and structures of vegetation (Asner, 1998; Kokaly et al., 2009; Ollinger, 2011). The concentrations of leaf biochemical components such as pigments, water, and dry matter determine the spectral regions and rates through which light is absorbed or reflected. Leaf and canopy architectures (e.g., leaf structure, leaf orientation, and vegetation density) are responsible for the scattering of incoming, transmitted, and reflected light. In this study, we refer to these optically effective plant properties, as they are expressed in and can be retrieved from canopy reflectance, as ‘optical traits’. Many plant species feature similar optical traits (Sorby, 1873) and thus similar spectral signatures (Price, 1994). Optical traits as they are defined above are further intermingled (i.e., spec-

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trally mixed) with spectral responses of litter or fractions of bare soil and effects of sensor and illumination geometries (Asner, 1998), producing complex relationships between vegetation properties and reflectance.

As most green plants present similar reflectance characteristics, distinct patterns in species composition do not necessarily correspond to unique reflectance patterns (Castro-Esau et al., 2006). It is thus difficult to explain why compositional patterns in vegetation can be detected in spectral data. Such detection tasks are frequently attempted using optical remote sensing data for purposes of nature conservation or ecological applications (Vanden Borre et al., 2011; Schmidtlein et al., 2014), but are sometimes impaired by weak relations between patterns of plant species composition and reflectance (e.g., Feilhauer et al., 2010; Feilhauer and Schmidtlein, 2011; Thomas et al., 2003). Several studies have aimed to find an explanation for observed relationships between plant species composition and spectral data. It is frequently argued that success may depend on the presence or absence of faint but detectable spectral differences and thus on differences in optical traits between individual species and assemblages (e.g., Asner and Martin, 2009, 2011) or on accompanying stand properties such as litter or soil cover fractions (Verrelst et al., 2009; Feilhauer and Schmidtlein, 2011). However, these faint spectral differences between species or plant assemblages can become blurred by the plasticity of species' spectral signatures. This intra-species spectral variability may arise from spatio-temporal heterogeneities in terms of plant ages, phenological stages, vigor, and abiotic factors (e.g., Carter, 1993; Castro-Esau et al., 2006; Roberts et al., 1998). Furthermore, relations between compositional vegetation patterns and reflectance may be dependent on the spatial scale of observations made (e.g., Marignani et al., 2007; Underwood et al., 2007).

The importance of optical traits for remote sensing is recognized, and this has led to the development of adapted concepts of vegetation patterns (Asner and Martin, 2009; Huesca et al., 2015; Ustin and Gamon, 2010. It has further led to a discussion on which of the recently proposed essential biodiversity variables (Pereira et al., 2013) can be addressed with remote sensing (Skidmore et al., 2015). Still, an in depth quantitative analysis on contributions of optical traits for the successful application of remote sensing to map floristic patterns is currently missing. Furthermore, an assessment of the variability of these inter-relations for different vegetation types and dates is lacking. Such knowledge is essential for a comprehensive understanding of mechanisms that underlie the remote sensing of vegetation and may provide explanations for occasional failures of statistical approaches. Additionally, in monitoring approaches based on remote sensing, an assessment of the robustness of methodologies is desirable, as reliance on canopy optical traits with variable relations to species composition in space and time affects the capacity to quantify actual changes in monitored vegetation patterns.

Physical canopy reflectance models such as PROSAIL can predict the vegetation reflectance spectrum by incorporating only a few parameters (Jacquemoud et al., 2009). PROSAIL consists of the leaf-optical-properties model PROSPECT 5 (Jacquemoud and Baret, 1990) and the 4SAIL canopy reflectance model (Verhoef, 1984). PROSPECT simulates the absorption, reflectance, and scattering of light within a plant leaf; 4SAIL models the scattering of light within a vegetation canopy. Merged to PROSAIL, these models can estimate in forward mode a resulting canopy reflectance signal from 400 nm to 2500 nm based on six parameters describing leaf properties (chlorophyll, carotenoid, brown pigment, and leaf water content, leaf mass per area (LMA), as well as the mesophyll structure), three parameters describing canopy characteristics (leaf area, leaf angle distribution, and the soil background), and four parameters used to quantify illumination and observation geometries. Some of these parameters correspond directly to ecological traits that can be measured in the field. These traits include the concentrations of chlorophylls and carotenoids, LMA, leaf water content, as well as leaf area index (LAI) and average leaf angle, which describe the leaf area and orientation. Various studies show that the PROSAIL model can be inverted for grassland ecosystems to retrieve optical traits from spectral data (e.g., Atzberger et al., 2013; Darvishzadeh et al., 2008, 2011; Si et al., 2012; Vohland and Jarmer, 2008), although such inversions can create ill-posed problems because multiple trait combinations can result in very similar spectral responses (Baret and Buis, 2008). Because the upscaling of in-situ leaf measures to the canopy level is costly and affected by various uncertainties (Roelofsen et al., 2013), the validation of retrieved optical trait values is challenging. Other optical traits incorporated into the PROSAIL model such as brown pigment content and mesophyll structure are artificially designed parameters that have been introduced as pragmatic solutions to otherwise complex problems (Jacquemoud and Baret, 1990). The related parameter values cannot be measured directly in the field, although they can explain features of spectral responses of vegetation.

Table 1
PROSAIL parameters and corresponding optical traits (in italics). Range denotes the ranges of trait/parameter values used in this study.

PROSAIL parameter	*Optical trait*/explanation	Unit	Range
Cab	*Chlorophyll a + b concentration*	$\mu g\,cm^{-2}$	5–80
Car	*Carotenoid concentration*	$\mu g\,cm^{-2}$	2–24
Cbrown	*Brown pigment concentration*	–	0–1
Cm	*Leaf mass per area*	$g\,cm^{-2}$	0.002–0.018
Cw	*Leaf water content/Equivalent water thickness*	cm	0.005–0.020
N	*Mesophyll structure*	–	1.1–2.3
LAI	*Leaf area index*	–	1–7
lidfa	*Average leaf angle*	°	30–75
psoil	Soil brightness	–	0–1
tto	Observer zenith angle	°	0
tts	Solar zenith angle	°	30
psi	Relative azimuth angle	°	180

In the present study, we treat the PROSAIL parameters as retrieved from canopy reflectance data as optical trait indicators (OTIs) and use these indicators for further analyses. OTIs feature a similar informational content but a lower degree of dimensionality than the original spectral data. We consider OTIs featuring thematically optimized informational content, which include a large percentage of vegetation-related information that can be gleaned from spectral reflectance data. OTIs as defined in this study are thus, for example, in the tradition of the Tasseled Cap transformation, which aims to optimize spectral information of Landsat data for agricultural applications (Kaunth and Thomas, 1976). By consequence, observed relations to OTIs can be easily interpreted in ecological terms, and the predictive power of OTIs is assumed to be high. Some OTIs correspond to essential biodiversity variables such as LAI and specific leaf area. We consider OTIs as latent variables that cannot be fully validated in the field. This limitation is widely accepted in the context of remotely-sensed vegetation indices (for example, the normalized difference vegetation index NDVI, Tucker, 1979), simple ratios or difference ratios of reflectance values measured in different wavelength regions, which correlate with a broad range of vegetation properties. In comparison to these commonly used indices, the generation of OTIs is less user-friendly and requires more computational efforts (Verrelst et al., 2015). However, the proposed OTI set allows one to exploit information of the full spectrum rather than that of a few spectral bands, and it is less dependent on individual sensor characteristics (Atzberger et al., 2011, 2015; Verrelst et al., 2015). To differentiate between the actual traits and indicators, we refer to the individual OTIs with the respective name of the PROSAIL parameter listed in Table 1.