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Determining the absorption coefficients of decay pigments in decomposing monocots

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ABSTRACT

Decomposition is an important biosphere process that recycles sequestered nutrients, plays a key role in carbon emissions, and accumulates compounds that exert negative feedbacks on primary production. In certain environments, litter comprises a considerable portion of the canopy, impeding the quantification of living biomass. Decomposition incurs physical changes and the genesis of decay pigments over time, causing the optical properties of litter to evolve in tandem. In order to simulate the spectral evolution of decaying leaves and relate the spectra to meaningful quantities of the biochemical compounds present, knowledge of the in-situ absorption properties of decay pigments is required. To determine the specific absorption coefficients of decay pigments in monocot leaf litter, we developed a spectral data set of multiple species at various decay stages concurrent with quantities of foliar compounds from fiber and humic acid analysis. Utilizing leaf humic acid content, the specific absorption coefficients for initial and advanced decay pigments were estimated using the PROSPECT model. For a 70-sample evaluation data set, simulated litter spectra closely matched the Reflectance, Transmittance, and Absorptance of measured leaves, with an average %RMSE (400–2500 nm range) of 4.95. Inversion of the expanded PROSPECT model had a moderate relationship between measured gravimetric humic acid content and the model inverted sum of initial and advanced decay pigments, as indicated by the $R^2 = 0.62$ and index of agreement = 0.72 goodness of fit statistics. Integrating the specific absorption coefficients of decay pigments into the PROSAIL model permitted the canopy reflectance of grassland scenes of intertwined photosynthetic leaves and litter to be simulated. Model inversion results aligned well with changes in canopy chlorophyll and biomass, cumulating in an $R^2 = 0.69$ between measured and predicted leaf area index. Sensitivity analysis further revealed that canopy level reflectance in the near infrared region for mixed green vegetation and litter scenes are driven mainly by advanced decay pigments. Hence, the inclusion of decay pigments' specific absorption coefficients are of high importance for accurate simulation of mixed vegetation scenes. Further, the derived specific absorption coefficients can be utilized to quantify humic acid content in monocotyledon leaves as a proxy for decay stage and the carbon quality of litter.

1. Introduction

Decomposition is a transformative process, by which dead plant matter undergoes a series of chemical and physical changes that lead to the formation of refractory soil organic matter (Daughtry et al., 2010). Decay end products form a large portion of the soil matrix that aids fertility and plant nutrition (Sanaullah et al., 2010). While it is tempting to believe that all plant matter is sequestered into the soil from whence it came, this conceptualization does not reflect the diversity of decomposition pathways. Litter compounds may be selectively decomposed by various fungi. Brown rots induced by *Laetiporus* spp. (sulfur shelf) selectively consume the hemicellulose and cellulose, leaving brown colored remains high in lignin. Conversely, white rots induced by *Lentinula edodes* (shitake) enzymatically break down lignin, leaving white cellulose remains. Disturbances, such as fire, remove carbon and nutrients altogether from soil (Fynn et al., 2003). In wetlands, oxygen availability determines decomposition gas by-products, with gas quantities inversely proportional to the degree of decomposition (Granéli, 1990; Miyajima et al., 1997).

In spite of its ecological importance, remote sensing of decomposition activities is atypical. While much research capital has been spent on quantifying foliar nitrogen and lignin content for the purpose of inferring litter decay rates (Daughtry et al., 2010; Martin and Aber, 1997), few studies have monitored the temporal evolution of litter (Nagler et al., 2000; Nagler et al., 2003). Decomposing litter obfuscates the detection and quantification of living biomass. Schile et al. (2013) reported extensive background effects from litter that interfered with efforts to measure the fraction of absorbed photosynthetically-active

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radiation. Many environments, such as grasslands, shrub lands, and aquatic environments, feature a considerable accumulation of litter, hampering the quantification of canopy chlorophyll (He and Mui, 2010). The fraction of non-photosynthetic vegetation was underestimated in four of twelve sites by Guerschman et al. (2009), due to substantial sub-pixel heterogeneity in litter spectra. Spectra of four crop and two tree litters varied considerably (Nagler et al., 2003), while Daughtry et al. (2010) observed the spectral evolution of litter during the decomposition cycle. As these studies indicate, decaying leaves cannot be stereotyped into a single spectra.

Spectral signatures of decaying leaves are controlled by initial foliar chemistry, physical changes during decomposition, and the genesis of decay pigments over time. After chlorophyll breakdown, foliar content of chemically-unidentified pigments of tan and brown coloration determine the initial spectral signature of litter. Monocots tend to be tan in color, in contrast to brown oak leaves which feature higher content of darker pigments such as lignin. Comparing the cellulose:lignin ratio of bushgrass (5.61) and birch litter (1.01), Frossard et al. (2013) showed that certain grass species are relatively low in lignin content. Regardless of initial signature, decomposition eventually yields spectra that begin to coincide with that of soil, featureless between 400 and 1100 nm (Nagler et al., 2003), with a gradual concave increase that sills well into the near infrared (NIR) region. As the leaf dries, the strong absorption features of water are reduced, and unique absorptance features due to dry matter compounds become apparent (Elvidge, 1990). Variations in the magnitude of reflectance are also documented, with the newly-formed litter of Ponderosa pine approximately three times more reflective than aged litter (Goward et al., 1994).

Given the spectral evolution of litter, remote sensing techniques relying upon a finite number of end members may be ill-suited for scenes featuring a high degree of spatial heterogeneity in decomposition. In contrast, techniques such as radiative transfer modelling are quite flexible, as they simulate leaf spectra from the concentration of multiple biological compounds. Provided the specific absorption coefficients of the compounds that genesis during decomposition are known, radiative transfer models can generate the full range of decaying leaf spectra at any stage of the decomposition process, and yield meaningful quantities of the decay compound(s) present.

To date, a number of leaf-level radiative transfer models have been developed, ranging in theoretical underpinnings and complexity. One of the most developed models in terms of leaf biochemical components is PROSPECT (Feret et al., 2017; Feret et al., 2008; Jacquemoud et al., 2009), which has been continually expanded to erudite the pigments controlling the reflectance of green and senescent leaves in the 400-2500 nm range. In the latest version, the specific absorbance coefficients of chlorophyll $a + b$, carotenoids, anthocyanins, water, dry matter (comprised of cellulose, lignin, sugars, etc.), and brown pigments (unidentified, likely products of oxidation of polyphenolic compounds) have been documented. Utilizing these coefficients has permitted the precise simulation of leaf spectra, and inversion of measured reflectance and transmittance to estimate the content of said pigments. Recently, PROSPECT was expanded into the FluorMOD leaf model to simulate chlorophyll fluorescence, which relates to plant vitality and biomass production (Zarco-Tejada et al., 2006). By coupling PROSPECT to a canopy-level model, the spectra of forests (Kötz et al., 2004) and crops (Casa and Jones, 2004) have been successfully simulated. More remarkably, inversion of radiative transfer models has shown good agreement between model outputs and their measured quantities. Verrelst et al. (2014) utilized a look-up table inversion of simulated Sentinel 2 and 3 imagery to quantify crop canopy biophysical parameters in Barrax, Spain. Coupling PROSPECT to the SAILH (Verhoef, 1984) and FLIGHT (North, 1996) canopy-level radiative transfer models permitted Zarco-Tejada et al. (2013) to determine the chlorophyll and carotenoid content of vineland imagery acquired from a unmanned aerial vehicle with multispectral and hyperspectral sensors. Furthermore, a coupled PROSPECT-DART (Gastellu-Etchegorry et al., 1996) radiative transfer modelling approach utilizing continuum removal, allowed Malenovský et al. (2013) to retrieve leaf-level chlorophyll $a + b$ in Norway Spruce stands.

The PROSPECT model has achieved great success in deriving the specific absorbance coefficients of the pigments in living leaves. However, radiative transfer modelling has rarely been applied to simulate decaying leaf spectra, nor have the biochemical constituents concomitant with decomposition been identified. To erudite the decay pigment(s), this research investigates the relationship between decay-induced spectral changes to foliar water content, fiber composition, and humic acid content for a data set of monocots (grasses) at initial to advanced decay stages. The specific absorption coefficients for the identified decay pigment(s) are derived using a modification of the PROSPECT radiative transfer model approach. The derived decay pigment(s) specific absorption coefficients are evaluated on their efficacy at simulating litter spectra at the leaf and canopy levels. Specifically, at the leaf level, the expanded model is evaluated for its ability to correctly quantify the content of decay pigments. At the canopy level, its efficacy in estimating leaf area index in mixed grassland ecosystems is assessed. Sensitivity analysis by wavelength is performed at the leaf level to assess the relative contribution of the two introduced decay pigments, while a canopy level sensitivity analysis is undertaken for mixed grassland scenes where decayed leaves are prominent. A canopy-level radiative transfer model, infused with the pigments responsible for green leaf and litter spectra, would permit the spectra of mixed scenes to be simulated, thus providing landscape-level temporal monitoring of decomposing monocotyledon leaves during early spring and fall senescence. In addition, this model could aid the quantification of the biophysical and biochemical attributes of the living vegetation in mixed vegetation scenes.

2. Methods and approaches

Monocots are utilized as a model organism, since the coloration of this group tends not to deviate from tan coloration, suggesting a low diversity of senescent pigments. Other leaves, such as oak, feature a high content of other compounds, such as tannins, which are spectrally similar to decay pigments and thus would require additional chemical procedures to quantify. Selection of which compounds to examine as the source of decay-induced spectral change is challenging. There are thousands of compounds found in leaves, from those involved in the photosynthetic apparatus, structural compounds providing mechanical strength, and a host of other pigments that provide UV protection, defense against predators, and other survival functions (Matile, 2000). In order to limit the analysis of foliar chemistry to a reasonable number of compounds, this study focuses on two types of analysis aimed at discerning the initial litter compounds and those generated via decay. Fiber analysis is undertaken to yield the content of solubles, hemicellulose, cellulose, and lignin, whereas NaOH extractions are used to examine humic substances. Each variable is tested against a data set of reflectance/transmittance measurements to determine if any compound(s) explain the spectral evolution of litter.

2.1. Sample collection and processing

The sample data set included two types of grass leaves, naturally decayed and artificially decayed (Table 1). Naturally decayed samples had senesced, and undergone decay in the field prior to harvest. As field decay was heterogeneous, individual leaves varied in their decay state. Leaves were visually sorted into decay stages, ranging from partial to strong decay. In contrast, artificially-decayed leaves were harvested post-senescence, and subjected to moist room temperature conditions to permit decomposition. Samples were collected from various locations between October and November 2014. These leaves were collected prior to any visible decay. Decomposition was induced by storage in moist conditions at room temperature for a period ranging between 3