



Estimation of photosynthesis traits from leaf reflectance spectra: Correlation to nitrogen content as the dominant mechanism



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ABSTRACT

Numerous studies have investigated reflectance-based estimations of physico-chemical leaf traits such as the contents of light absorbing pigments, leaf mass per area, or carbon and nitrogen contents. Only few studies, however, attempted to estimate leaf traits that are more directly linked to photosynthesis. We tested the feasibility of estimating two important photosynthesis traits, the maximum carboxylation capacity ($V_{cmax,25}$) and the maximum electron transport rate ($J_{max,25}$), from in-situ leaf reflectance spectra using approaches that are applicable also on larger spatial scales. We conducted measurements of reflectance, CO_2 response curves, leaf mass per area (LMA), and nitrogen content per area (N_a) for 37 temperate deciduous tree species and a total of 242 leaves from widely differing light environments. Partial least squares (PLS) regression was used to estimate $V_{cmax,25}$, $J_{max,25}$, LMA , and N_a from reflectance spectra.

The results showed that both $V_{cmax,25}$ and $J_{max,25}$ can be estimated from leaf reflectance measurements with good accuracy ($R^2 = 0.64$ for $V_{cmax,25}$, $R^2 = 0.70$ for $J_{max,25}$) even for a large number of tree species and varying light environments. Detailed analysis of reflectance-based PLS and linear regression models with regard to prediction performances and regression coefficients led to the conclusion that the correlation to N_a was the dominating mechanism on which the $V_{cmax,25}$ and $J_{max,25}$ PLS models were based. The PLS regression coefficients of N_a , $V_{cmax,25}$ and $J_{max,25}$ showed clear signatures of nitrogen-related absorption features.

The finding that $V_{cmax,25}$ and $J_{max,25}$ estimations from leaf reflectance are predominantly based on their relationships to N_a has important implications for large scale estimations of these photosynthesis parameters. We suggest that future studies should focus more on large scale estimation of N_a from remote sensing and estimate $V_{cmax,25}$ and $J_{max,25}$ in a separate step using their respective relationships to N_a .

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1. Introduction

Many researchers tried to improve the estimates of terrestrial gross primary production (GPP) (Beer et al., 2010) in order to minimize uncertainty in global carbon cycle models. A combination of remote sensing data and either statistical upscaling using machine learning methods (Jung et al., 2011; Papale et al., 2015) or process-based modelling (Bonan et al., 2011; Turner et al., 2004) was mostly used as there is currently no measurement technique that is able to provide GPP estimates on areas larger than the typical footprint of an Eddy Covariance tower, which is approximately 1 km^2 . In order to improve the performance of process-based models, spatially and temporally resolved

information on plant photosynthetic capacity is required. To our knowledge, only a few studies have tried to estimate the maximum carboxylation capacity, V_{cmax} , and the maximum electron transport rate, J_{max} , directly from leaf reflectance measurements (Ainsworth et al., 2014; Doughty et al., 2011; Serbin et al., 2012). Doughty et al. (2011) obtained poor results ($R^2 \leq 0.5$) for 11 tropical tree species, while Serbin and colleagues obtained very good results ($R^2 = 0.9$) for three species (Ainsworth et al., 2014; Serbin et al., 2012). Serbin et al. (2015) also obtained very good results ($R^2 = 0.9$) for nine crop species using airborne canopy measurements. The strong divergence of the results at the leaf scale leads to the question whether the number or type of species included might affect the results in a negative way, which would be disadvantageous for large scale use of the models. Furthermore, shade leaves were not considered in the studies by Doughty et al. (2011), Serbin et al. (2012) and Ainsworth et al. (2014). Plant traits, however, are known to respond to different light environments, which can result in different

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relationships between traits (e.g. Keenan and Niinemets, 2016; Seemann et al., 1987). This can also potentially affect the relationship between leaf reflectance and photosynthesis traits. The results of the canopy scale estimation for crop species (Serbin et al., 2015) seem promising but it is not clear if the method would work equally well for more heterogeneous natural vegetation. Serbin et al. (2012, 2015) raised the question whether there might be a direct link between apparent leaf reflectance (Kim et al., 1993) and V_{cmax} as well as J_{max} via Rubisco or chlorophyll fluorescence.

Many leaf physiological studies have investigated relationships between leaf chemical and morphological traits on the one hand and $V_{cmax,25}$ and $J_{max,25}$ on the other hand (the subscript 25 in $V_{cmax,25}$ and $J_{max,25}$ denotes normalisation to a reference temperature of 25 °C). It is well known that the Rubisco content in the leaf is closely related to $V_{cmax,25}$ (Jacob et al., 1995; Makino et al., 1994; Onoda, 2005) and that cytochrome *f* content has a strong linear relationship to $J_{max,25}$ (Onoda, 2005; Sudo et al., 2003; Terashima and Evans, 1988). These links are not only of statistical nature but represent mechanistic relationships. $V_{cmax,25}$ represents the maximum capacity of carboxylation which is mechanistically linked to the Rubisco content of the leaf, as the Rubisco enzyme catalyses the carboxylation reaction (von Caemmerer, 2000). Cytochrome *f* is known to play an important part in electron transport between the two photosystems (Onoda, 2005). It is unclear, however, if Rubisco and cytochrome *f* content in leaves can be retrieved accurately from reflectance measurements in the range of 400–2500 nm. Their signal in the reflectance spectrum is expected to be very weak compared to dominant absorbers, as these proteins are present in the leaves only in small concentrations and, in contrast to chlorophyll, are not built to strongly absorb light in this part of the spectrum. Therefore, it seems likely that the information related to $V_{cmax,25}$ and $J_{max,25}$ in the reflectance spectra, is not directly related to Rubisco and cytochrome *f* contents but to other leaf traits which have both a stronger absorption signal in this part of the spectrum and a strong but less direct relationship to the target parameters. Potential candidates for these leaf traits are leaf mass per area, *LMA* and nitrogen per area, N_a , as well as phosphorus content, which are highly correlated to both $V_{cmax,25}$ and $J_{max,25}$ (Kattge et al., 2009; Walker et al., 2014). The strong link between N_a and $V_{cmax,25}$ was described in the semi-mechanistic model of Farquhar et al. (1980). Both empirical and mechanistic relationships between N_a and $V_{cmax,25}$ have been used in Earth System Models (Rogers, 2014). The candidate trait with the strongest signal in the reflectance spectrum is *LMA*, but the one with the strongest relationship to $V_{cmax,25}$ and $J_{max,25}$, which also has a relatively strong absorption signal, is N_a (Jacquemoud et al., 1996; Kattge et al., 2009). Phosphorus has been shown to increase the sensitivity of $V_{cmax,25}$ to N_a for high nitrogen contents (Walker et al., 2014). This effect, however, is expected to be rather weak in temperate ecosystems due to the dominance of nitrogen limitation and relatively abundant phosphorus (Elser et al., 2007). Furthermore, phosphorus has been estimated from reflectance with consistently lower accuracy and precision than nitrogen content (Asner et al., 2011, 2014). Based on the above reasoning, we hypothesise that the main mechanism behind reflectance-based $V_{cmax,25}$ and $J_{max,25}$ estimation is the relationship to N_a . We also expect the reflectance-based estimation of $V_{cmax,25}$ and $J_{max,25}$ to be feasible across species, as the relationship to N_a was shown to be valid for a large number of temperate broadleaf tree species (Kattge et al., 2009).

Here, we present the results from a study designed to examine if 1) the estimation of $V_{cmax,25}$ and $J_{max,25}$ from leaf reflectance is possible for many different broadleaf tree species and leaves from different light environments and 2) the mechanism behind the estimation is the correlation to N_a . We studied reflectance-based multivariate regression models to estimate $V_{cmax,25}$ and $J_{max,25}$ and inspected the corresponding regression coefficients closely. The prediction performances of these multivariate regression models were compared to linear regression models based on estimated N_a and *LMA*. We also restricted the range of the reflectance spectrum in order to locate the relevant information

contributing to the photosynthesis trait estimation. Furthermore, we inverted a leaf radiative transfer model to estimate chlorophyll, carotenoid and water contents in order to examine if these leaf traits also contributed to the multivariate regression models for $V_{cmax,25}$ and $J_{max,25}$.

2. Materials and methods

2.1. Study site and sampling

Measurements were conducted in the Arboretum of the University of Leipzig located in Großpösna, central Germany (51°15' N, 12°29' E, 150 m above sea level). The Arboretum has about 100 European deciduous and coniferous tree species in two different plantations. The main plantation has trees widely spaced with a minimum distance of three metres between trees, and a secondary plantation with minimum distances of 1 m. The trees in both plantations were planted as seedlings in 2012. Measurements were mostly conducted in the secondary plantation due to practical reasons. A total of 242 leaves of 103 trees were measured. For each leaf, the photosynthetic CO₂ response curve and leaf reflectance were measured and the nitrogen content and the dry leaf mass per area were determined destructively. Trees from 37 broadleaf species comprising 21 genera were sampled. Two species, *Morus alba* and *Prunus serotina*, were sampled more intensively with 29 and 42 leaves from 10 and 11 trees, respectively. 4.9 ± 2.6 leaves and 2.3 ± 0.9 trees were measured on average for each of the other 35 species. The list of the measured species including the exact number of leaves and trees per species is given in Table S1 of the supplementary material. The measurements were conducted mainly in August and early September of the year 2014. Observations were made throughout the day, normally between 9:00 CEST and 19:00 CEST.

The leaves were chosen to represent the widest possible range of light environments, from almost complete shade to direct sun light. This was done in order to obtain a wide range of values for the studied leaf traits and to test whether the relationships between leaf reflectance and photosynthesis traits would hold in different light environments. We attempted to cover the range of available light environments in cases where shading by nearby trees restricted the light environments of leaves to diffuse light. A classification of some of the sampled leaves into sun and shade leaves was done by a human observer based on the orientation and exposure to light throughout the day. Leaves exposed mostly to direct sunlight and top-of-canopy leaves exposed to diffuse light were classified as sun leaves, while strongly shaded leaves exposed only to diffuse light were classified as shade leaves.

2.2. Photosynthesis measurements and parameter estimation

2.2.1. In situ measurements

CO₂ response curves were measured in situ for each leaf, using portable Licor 6400 photosynthesis systems (Li-Cor Biosciences, Lincoln, NE, USA). Two of the photosynthesis systems were equipped with fluorescence chambers and one system had the standard blue/red LED light source chamber. All measurements were made with internal LED light sources and custom autoprogammes. Leaf temperature was always actively stabilized. A set point of 25° C was chosen for most response curves, but lower temperature set points between 20° and 25° C were used for some of the response curves for practical reasons. Relative humidity was not actively stabilized for the sake of higher stability of the photosynthesis and transpiration measurements. The systems with fluorescence chambers had a smaller volume of the sample cell and therefore the flow rate was set to a lower value than for the LED light source chamber in order to obtain measurements with a precision comparable to the measurements with the larger chamber. Each leaf was first adapted to the chamber light, humidity and temperature environment for about 6 min before a CO₂ response curve was measured at a constant photosynthetic photon flux density of 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ with external CO₂ concentrations in the following order in $\mu\text{mol mol}^{-1}$:

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