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## Mechanisms behind the estimation of photosynthesis traits from leaf reflectance observations

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Many studies have investigated the reflectance-based estimation of leaf chlorophyll, water and dry matter contents of plants. Only few studies focused on photosynthesis traits, however. The maximum potential uptake of carbon dioxide under given environmental conditions is determined mainly by RuBisCO activity, limiting carboxylation, or the speed of photosynthetic electron transport. These two main limitations are represented by the maximum carboxylation capacity,  $V_{cmax,25}$ , and the maximum electron transport rate,  $J_{max,25}$ . These traits were estimated from leaf reflectance before but the mechanisms underlying the estimation remain rather speculative. The aim of this study was therefore to reveal the mechanisms behind reflectance-based estimation of  $V_{cmax,25}$  and  $J_{max,25}$ .

Leaf reflectance, photosynthetic response curves as well as nitrogen content per area,  $N_{area}$ , and leaf mass per area,  $LMA$ , were measured on 37 deciduous tree species.  $V_{cmax,25}$  and  $J_{max,25}$  were determined from the response curves. Partial Least Squares (PLS) regression models for the two photosynthesis traits  $V_{cmax,25}$  and  $J_{max,25}$  as well as  $N_{area}$  and  $LMA$  were studied using a cross-validation approach. Analyses of linear regression models based on  $N_{area}$  and other leaf traits estimated via PROSPECT inversion, PLS regression coefficients and model residuals were conducted in order to reveal the mechanisms behind the reflectance-based estimation.

We found that  $V_{cmax,25}$  and  $J_{max,25}$  can be estimated from leaf reflectance with good to moderate accuracy for a large number of species and different light conditions. The dominant mechanism behind the estimations was the strong relationship between photosynthesis traits and leaf nitrogen content. This was concluded from very strong relationships between PLS regression coefficients, the model residuals as well as the prediction performance of  $N_{area}$ -based linear regression models compared to PLS regression models. While the PLS regression model for  $V_{cmax,25}$  was fully based on the correlation to  $N_{area}$ , the PLS regression model for  $J_{max,25}$  was not entirely based on it. Analyses of the contributions of different parts of the reflectance spectrum revealed that the information contributing to the  $J_{max,25}$  PLS regression model in addition to the main source of information,  $N_{area}$ , was mainly located in the visible part of the spectrum (500-900 nm). Estimated chlorophyll content could be excluded as potential source of this extra information. The PLS regression coefficients of the  $J_{max,25}$  model indicated possible contributions from chlorophyll fluorescence and cytochrome f content.

In summary, we found that the main mechanism behind the estimation of  $V_{cmax,25}$  and  $J_{max,25}$  from leaf reflectance observations is the correlation to  $N_{area}$  but that there is additional information related to  $J_{max,25}$  mainly in the visible part of the spectrum.