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Evaluating the performance of PROSPECT in the retrieval of leaf traits across canopy throughout the growing season

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ABSTRACT

Leaf traits and subsequently leaf spectral properties depend on the leaf phenological stage and light conditions within a canopy. The PROSPECT radiative transfer model has been extensively and successfully used to retrieve leaf traits for mature, sunlit leaves at peak vegetation growth, i.e. summer. However, research on the quantification of leaf traits using PROSPECT across the canopy vertical profile throughout the growing season is still lacking. Therefore, this study aims at examining the effect of leaf position on the performance of the PROSPECT model in modelling leaf optical properties and retrieving leaf chlorophyll content (C_{ab}), equivalent water thickness (EWT), and leaf mass per area (LMA) throughout the growing season. To achieve this objective, we collected 588 leaf samples from the upper and lower canopies of deciduous stands over three seasons (i.e., spring, summer and autumn) in Bavaria Forest National Park, Germany. Leaf traits including C_{ab}, EWT and LMA, were measured for all the samples, and their reflectance spectra were obtained using an ASD FieldSpec-3 Pro FR spectroradiometer coupled with an Integrating Sphere. We initially assessed the performance of the PROSPECT model by comparing reflectance spectra generated in forward mode against reflectance spectra measured on leaf samples collected in the field. We subsequently inverted the PROSPECT model to retrieve C_{ab}, EWT and LMA using the look-up-table (LUT) approach. Our results consistently demonstrated that the measured reflectance of leaf samples collected from the lower canopy had a stronger match with PROSPECT simulated reflectance spectra, especially in the NIR spectrum compared to leaf samples collected from the upper canopy throughout the growing season. This observation concurred with the pattern of C_{ab} and EWT retrieval accuracies across the canopy i.e. the retrieval accuracy for the lower canopy was consistently higher (NRMSE = 0.1-0.2 for C_{ab}; NRMSE = 0.125-0.16 for EWT) when compared to the upper canopy (NRMSE = 0.122 - 0.269 for C_{ab}; NRMSE = 0.162 -0.0.258 for EWT) across all seasons. In contrast, LMA retrieval accuracies for the upper canopy (NRMSE = 0.146 - 0.184) were higher compared to the lower canopy (NRMSE = 0.162 - 0.239) for all seasons except for the spring season. For all the leaf traits examined in this study, the range in retrieval accuracy between the upper and lower canopy was greater in summer (compared to other seasons). We report for the first time that although the PROSPECT model provides reasonable retrieval accuracy of C_{ab}, EWT and LMA, variations in leaf biochemistry and morphology through the vertical canopy profile affects the performance of the model over the growing season. Findings of this study have important implications on field sampling protocols and upscaling leaf traits to canopy and landscape level using multi-layered physical models coupled with PROSPECT.

1. Introduction

Plant traits, such as leaf chlorophyll content (C_{ab}), leaf mass per area (LMA) and equivalent water thickness (EWT) play an important role in understanding ecosystem functional processes, such as primary productivity and nutrient cycling. Specifically, C_{ab} is a key bio-indicator of plant health and photosynthetic capacity (Evans and Poorter, 2001; Lichtenthaler et al., 1996), while LMA reflects the plant economic spectrum strategy with regard to nutrients uptake, light harvesting and carbon sequestration (Poorter et al., 2009). EWT, on the other hand,

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provides information on plant water status (Yao et al., 2014). Consequently, routine measurement of leaf traits is valuable to assess progress towards the Aichi Biodiversity Targets set by the Convention on Biological Diversity (CBD) (Pereira et al., 2013; Skidmore et al., 2015).

Leaf traits and their leaf spectral properties are strongly controlled by leaf phenological stage and light conditions within a canopy (Yang et al., 2016). Leaf traits are known to change as a function of time during the growing season within a year (Behrman et al., 2015). Moreover, changes in abiotic factors, such as temperature, rainfall and photo-period result in changes in the leaf physiological, biochemical and morphological traits (Coble et al., 2016). However, leaf traits do not only exhibit seasonal changes but also changes as a result of different light conditions such as between the sunlit, upper and shaded lower canopy (Gara et al., 2018a). Illuminated upper canopy leaves display higher nutrient stoichiometry when compared to shaded lower canopy leaves (Weerasinghe et al., 2014). For example, Yang et al. (2016) demonstrated that shaded leaves display lower C_{ab}, nitrogen and LMA when compared to sunlit leaves. The variation in leaf traits across the canopy vertical profile is important in maintaining an equilibrium between the ribulose-1.5-bisphosphate (RuBP) - rate of carboxylation and the electron transport - limited rate of carboxylation (Chen et al., 1993). These intrinsic mechanisms result in marked effects on leaf morphological, chemical as well as physiological traits across the canopy vertical profile and subsequently result in variations in leaf optical properties (Qiu et al., 2018). Plants are also known to translocate foliar nutrients as they age, moving nutrients from lower canopy leaves to the upper canopy leaves for protein repair and maintenance of a metabolic balance (Hikosaka, 2005). In this regard, capturing seasonal variations in leaf traits throughout the vertical canopy profile is critical for understanding dynamics in terrestrial ecosystem structure and functioning.

Several leaf traits databases aimed at improving our understanding of forest structure and functioning have been established based on *in situ* and *in vivo* trait measurements (Kattge et al., 2011; Poschlod et al., 2003). Although these conventional methods provide accurate measurements, they are expensive, time-consuming and particularly challenging for quick and repeated measurements. Field spectroscopy, on the other hand, has a capacity to augment conventional methods by indirectly retrieving leaf traits from spectral measurements (Carvalho et al., 2013). This approach is cost-effective and allows repeated assessments over time with a capacity to upscale to airborne and satellite imagery. Essentially two approaches, empirical (statistical) and physical models (radiative transfer models-RTM) are employed to establish a relationship between leaf traits and spectral measurements (Verrelst et al., 2015). Empirical models explore the parametric and non-parametric statistical relationship between leaf traits and vegetation spectra or derivatives such as vegetation indices (Darvishzadeh et al., 2012). Although statistical models are relatively easy to calibrate, they are difficult to transfer because in most instances the spectra-trait relationship is sensor, site, time, and biome dependent (Verrelst et al., 2014). Moreover the performance of statistical models can be affected by the representativeness of the set of reference samples used for calibration (Pasolli et al., 2015). The development of physical models or radiative transfer models (RTMs) on the other hand, has improved our understanding of the interaction between radiation and foliage material. Physical models, rigorously simulate light absorption and scattering based on radiation transfer theory and are thus transferable across sites and biomes (Homolová et al., 2013). However, the main challenge of physical models is that they often require a number of inputs for parameterization, which subsequently result in computation and model inversion sophistication (Zhang and Wang, 2015).

A number of RTMs have been developed to model leaf spectral properties and subsequently retrieve leaf traits through inversion. These models include PROSPECT (PROpriétés SPECTrales) (Feret et al., 2008; Jacquemoud and Baret, 1990; Jacquemoud et al., 1996), LIBERTY (Leaf Incorporating Biochemistry Exhibiting Reflectance and Transmittance Yields) (Dawson et al., 1998), N flux models (Allen and Richardson, 1968), ray tracing models (Govaerts and Verstraete, 1998) and stochastic models (Maier et al., 1999). Most of these physical models, except PROSPECT, have received relatively limited use within the vegetation spectroscopy community. This is mainly because they require a large number of input variables that are laborious and time consuming to measure and subsequently pose a challenge in model inversion. The PROSPECT model has been widely used to retrieve leaf traits from simulated hemispherical reflectance and transmittance spectra in different vegetation communities (Malenovský et al., 2006; Renzullo et al., 2006; Zhang et al., 2007; Barry et al., 2009). One advantage of the PROSPECT model is that it can be intricately coupled with canopy radiative models, such as SAILH to retrieve leaf traits at canopy and landscape level (Verhoef, 1984; Si et al., 2012; Tripathi et al., 2012). In spite of its popularity, robustness and transferability, studies that have examined the effect of leaf position on the performance of PROSPECT in modelling leaf spectral properties and retrieval of leaf traits throughout the growing season are lacking. Although an attempt to retrieve C_{ab} through the vertical canopy profile using the PROSPECT model was demonstrated by Demarez (1999) and Zhang et al. (2007), very little is known on how the PROSPECT model performs with regard to retrieval of other key radiation absorbers, i.e. LMA and EWT across the canopy and throughout the growing season. More specifically, no study has attempted to evaluate the effect of leaf position within a canopy on the modelling of leaf spectral properties across a growing season using PROSPECT. Previous studies have mainly focused on the retrieval of leaf traits for mature, sunlit leaves at peak vegetation growth, i.e. summer (Ali et al., 2016; Wang et al., 2015b). Therefore, this study sought to examine the effect of leaf position within a canopy on the performance of the PROSPECT model in modelling leaf optical properties and retrieval of leaf traits, specifically chlorophyll content (C_{ab}), equivalent water thickness (EWT) and leaf mass per area (LMA) across throughout the growing season.

2. Materials and methods

2.1. Study area and field data collection

To examine the effect of leaf position within a canopy on the performance of PROSPECT for modelling leaf spectral properties and retrieval of leaf traits across the canopy throughout the growing season, we collected leaf samples from Bavarian Forest National Park (Fig. 1). The Park is part of the Bohemian forest ecosystem and is located in south-eastern Germany (49°31′19″N and 13°12′9″N). The Park covers a total area of approximately 24 218 ha. Elevation stretches from 600 to 1453 m (Heurich et al., 2010). The climate is temperate with annual precipitation ranging from 1200 to 1800 mm (of which approximately 50% is snow), and a mean annual temperature of between 3 and 6° C. The Park is characterized by acidic and poor nutrient soil. The dominated tree species in the park are mainly the evergreen Norway spruce (*Picea abies*) (67%) and deciduous European beech (*Fagus sylvatica*) (24.5%). Other less dominant species include white fir (*Abies abies*) (2.6%), sycamore maple (*Acer pseudoplatanus*) (1.2%), and mountain ash (*Sorbus aucuparia*) (3.1%) (Cailleret et al., 2014).

Field data were collected for three seasons, i.e. spring, summer and autumn of 2017. Spring data were collected between mid-May and mid-June, while summer field data were collected from mid-July to mid-August, and the autumn field data were collected between mid-September and mid-October. Sampling sites were randomly generated in deciduous and mixed vegetation stands based on the vegetation map provided by the Department of Conservation and Research, Bavarian Forest National Park (Silveyra Gonzalez et al., 2018). Most of the sample plots were located along the permanent transects designed for Biodiversity Research (Fig. 1). In the field, we used a hand-held Global Positioning System with an error of ± 5 m to navigate to the sampling sites. At each sampling site, a north-oriented plot of 30 m × 30 m was

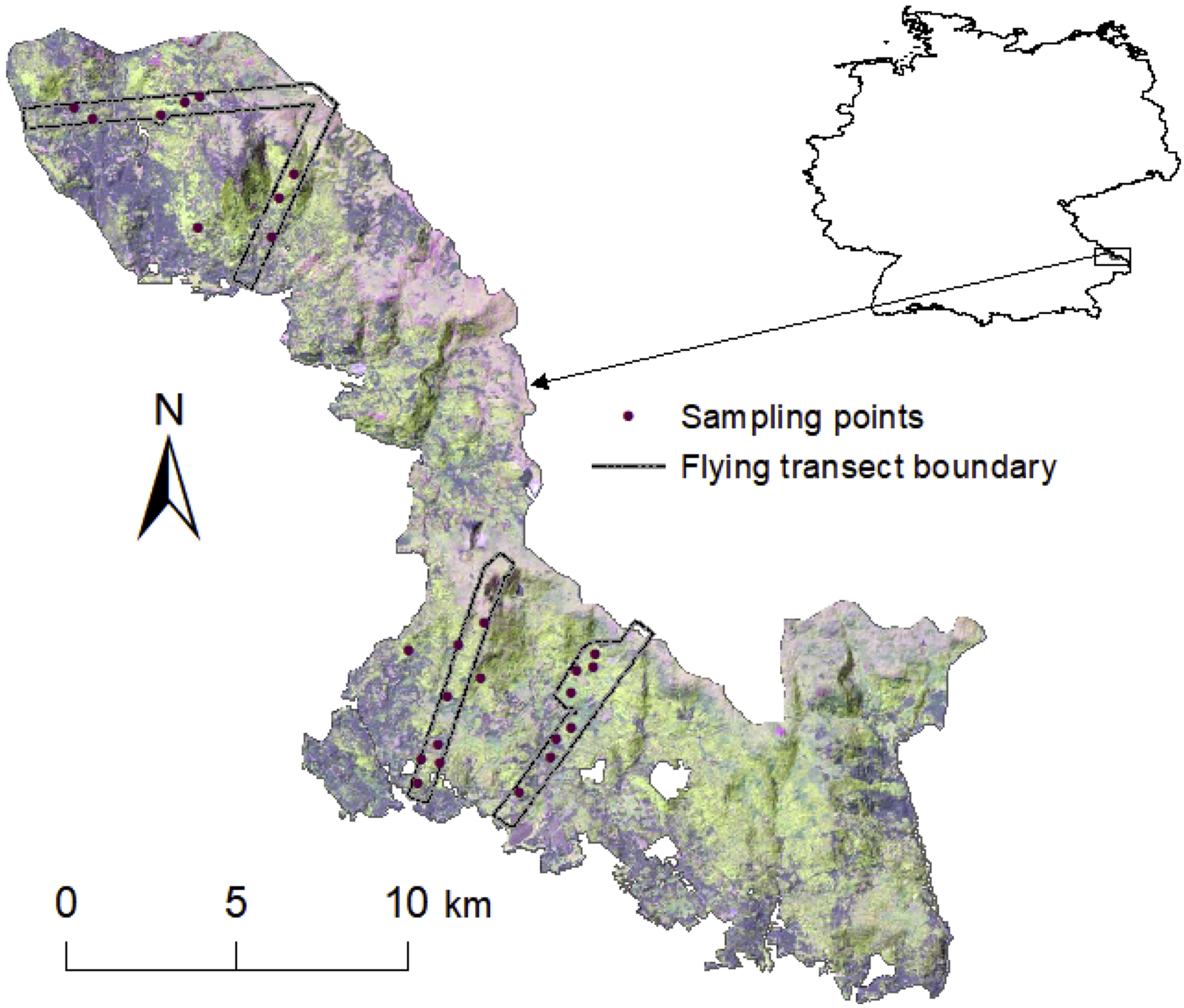

Fig. 1. Map of the Bavaria Forest National park and the location of the park in Germany. Sampling points are overlaid on a natural colour composite of Sentinel-2 satellite imagery of 13 July 2017. Black lines are the permanent flying transects boundaries designed for biodiversity research.

demarcated using a tape measure. We also recorded the centre location of each plot, using a Leica GPS 1200 (at an accuracy of less than 1 m after post-processing).

In total 588 leaf samples were collected from twenty-six deciduous and mixed vegetation sample plots across the three seasons. Species name and sample sizes for each season are shown in Table 1. Leaf samples were separately collected from the upper (n = 294) and lower canopy (n = 294) of each sampled tree. The average height of sampled trees was 24.4 ± 7.52 m (measured using a Nikon Forestry 550 hypsometer). Leaf samples from the sunlit, upper canopy were shot from the top one meter canopy using a crossbow, whilst leaf samples from the lower canopy were collected from the shaded, lowest living branch of the canopy using an extendable pair of secateurs (Atherton et al., 2017; Arellano et al., 2017). Sampling was performed on three to five trees with a diameter at breast height greater than 10 cm. A marker was placed on each sampled tree to facilitate tree identification for subsequent seasonal field measurements. Collected leaf samples were immediately measured for C_{ab}, using CCM -300 chlorophyll content meter (Opti-Sciences, 2011). The leaf samples were then wrapped with moist paper towels and zip-locked in polythene bags. The leaf samples were then transported in a cooler with ice packs within 6 h to the laboratory for further measurements (Atherton et al., 2017). Although the composition of our samples were heavily skewed to the European beech (92.86%), analysis with or without the other collected species (constituting 7.14%) did not alter the pattern in leaf traits retrieval accuracy across the canopy throughout the growing season (Appendix 1: Table A1). Therefore, all analyses were performed including all the species.

Table 1
Distribution of collected samples by species across the three seasons.

Species	Scientific name	Spring	Summer	Autumn	Total
European beech	*Fagus sylvatica*	156	194	196	546
Sycamore maple	*Acer pseudoplatanus*	6	12	12	30
Elm *spp*	*Ulmus minor*	2	2	2	6
Common rowan	*Sorbus aucuparia*	2	2	2	6
Total		**166**	**210**	**212**	**588**

2.2. *Laboratory measurement*

2.2.1. *Leaf trait measurements*

The following leaf traits were measured in the laboratory; fresh weight (Fw g), dry weight (Dw g) and leaf surface area (LA). Fresh weight for each sample was determined, using a high precision digital scale at an accuracy of 0.01 g. The leaf samples were then scanned, using AMH 350 area meter to determine the leaf surface area (ADC-BioScientific, 2013). The leaf samples were oven dried at 65^{O}C until a constant weight was attained after approximately 72 h, and then their dry weight was measured (Gara et al., 2018b). Subsequently, EWT and LMA were calculated using the following formula:

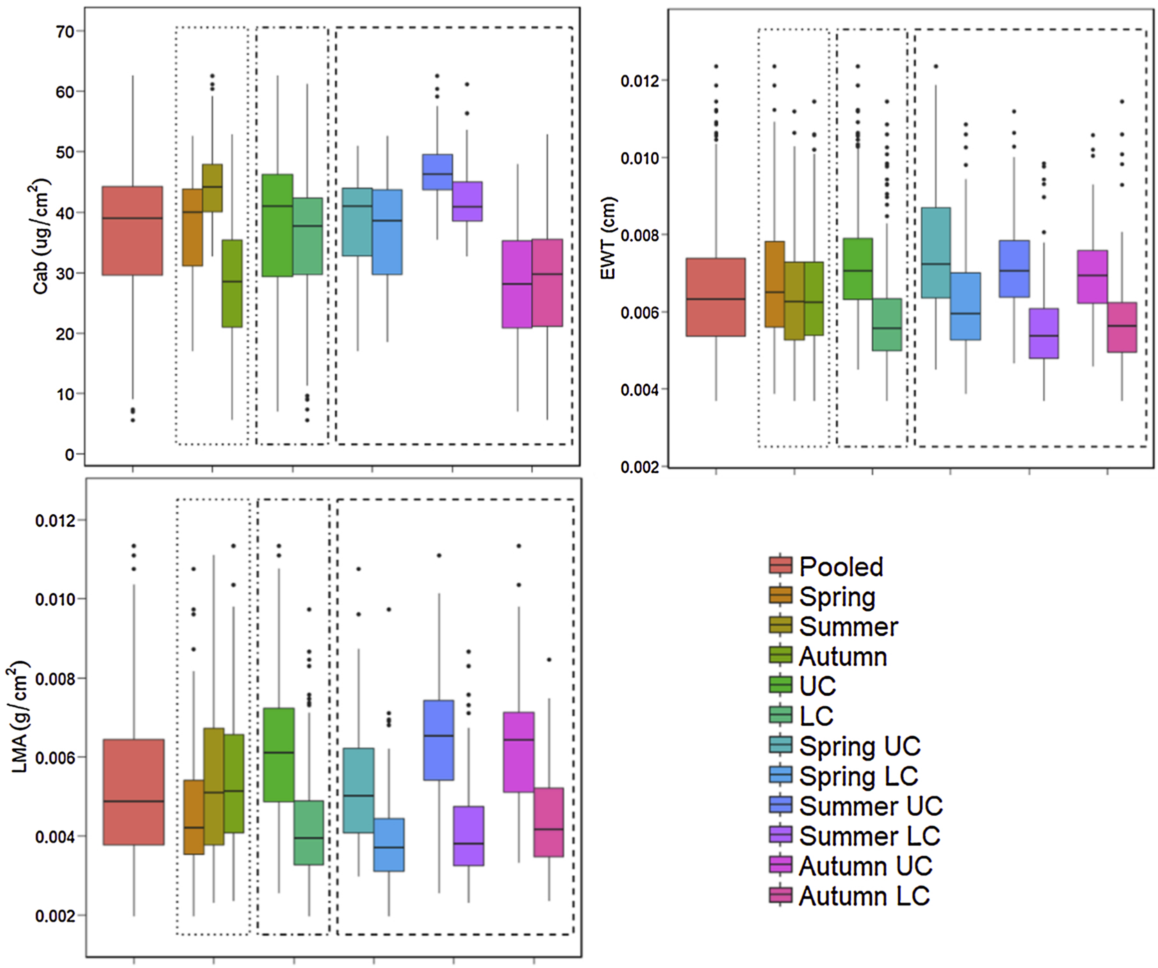

Fig. 2. Seasonal variation in measured C_{ab}, LMA and EWT across canopy positions (UC and LC represent upper and lower canopy respectively).

$$\text{EWT (cm)} = \text{Fw} - \text{Dw/LA} \tag{1}$$

$$\text{LMA (g/cm}^2) = \text{Fw /LA} \tag{2}$$

where: Dw, Fw and LA are the dry weight, fresh weight and leaf area of each sample, respectively. The summary and variation of measured traits are shown in Fig. 2.

2.2.2. Leaf reflectance spectra measurement

Leaf directional hemispherical reflectance from 350 to 2500 nm for each sample was measured, using an ASD FieldSpec-3 Pro FR spectroradiometer coupled with an ASD RTS-3ZC Integrating Sphere. To minimize spectral noise, the spectroradiometer was set to average two hundred scans into a single spectrum per each spectral measurement (Ali et al., 2016). Radiance measurements were converted to reflectance against scans of a calibrated white spectralon panel (with approximately 99% reflectance). During spectral measurements, care was taken to avoid leaf primary veins. The spectral reflectance measurements were corrected for dark current and stray light following the Integrating Sphere User Manual instructions (ASD, 2008). Spectral measurements of 5–10 leaves (depending on leaf size and weight) constituting a sample were averaged to a single spectrum to represent the sample. A moving second order Savitzky-Golay filter with a frame size of 11 was applied to each sample reflectance spectra to minimize instrument noise (Savitzky and Golay, 1964). Due to the low signal-to-noise ratio for wavelengths beyond 2200 nm as well as spectral bands before 400 nm, the reflectance spectra were cropped to 400–2200 nm range. Therefore, 1801 spectral bands were retained for further analysis. All required laboratory measurements were completed on the same day of sample collection.

2.3. Calibration of the PROSPECT model

The PROSPECT leaf optical properties model is a popularly used radiative transfer plate model for simulating leaf directional-hemispherical reflectance over the optical domain of 400–2500 nm (Jacquemoud and Baret, 1990). The model is widely used mainly because of its robustness, ease-of-use, availability and a reasonably low number of input parameters (Verrelst and Rivera, 2017). The PROSPECT model idealizes a leaf as elementary layers characterized by absorbing and scattering properties (Feret et al., 2008). The model requires four input parameters including leaf structure index (N_{struc}), leaf chlorophyll content (C_{ab}, μg/cm^2), leaf water content (EWT, cm) and leaf dry matter content (LMA, g/cm^2). PROSPECT has been widely validated for the retrieval of leaf traits across a variety of species especially for mature, sunlit leaf samples at peak vegetation growth, i.e. summer (Li and Wang, 2013; Malenovský et al., 2006; Ali et al., 2016; Wang et al., 2015a). However, in this study, we assess the effect of leaf position in the vertical canopy profile on the performance of PROSPECT for modelling leaf spectral properties and retrieval of leaf traits across canopy positions through a growing season. To achieved a higher accuracy in the retrieval of inputs parameters the dimension of the LUT has to be sufficiently large (Combal et al., 2003; Tang et al., 2007). We therefore used the improved (1 nm) and recalibrated PROSPECT 4 model (Feret et al., 2008) in forward mode to generate a LUT with 250 000 leaf spectral reflectance simulations. We used PROSPECT 4 instead of later versions because we did not measure leaf carotenoid and

Table 2
Ranges of the leaf variables used to build the LUT with the size of 250 000-reflectance spectra.

Parameter	unit	min	max	mean	SD
Leaf structure parameter (N)	–	1	2.22	1.52	0.15
Total leaf chlorophyll content (C_{ab})	$\mu g/cm^2$	2	67	36.57	10.6
Equivalent water thickness (Cw)	cm	0.0025	0.015	0.0015	0.0066
Leaf mass per area (Cm)	g/cm^2	0.0015	0.014	0.0016	0.0053

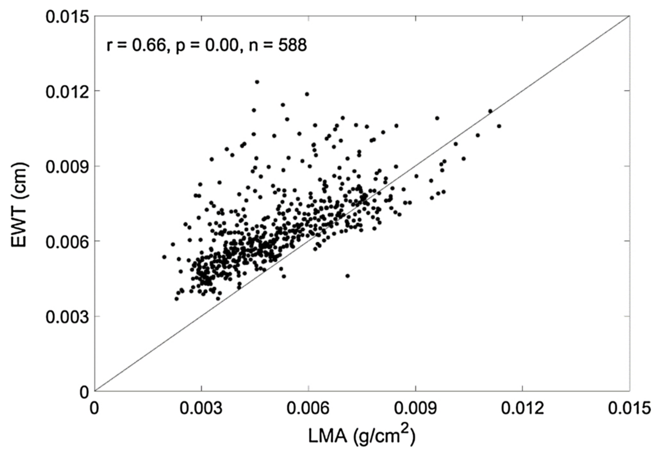

Fig. 3. Correlation between EWT and LMA for field-collected data.

anthocyanins content, which are input parameters in PROSPECT 5 and PROSPECT D (Féret et al., 2017; Feret et al., 2008). The ranges of the PROSPECT input variables (Table 2) were selected guided by prior information gathered from field-collected data. Specifically, the range of input parameters used for PROSPECT calibration were based on field collected data widened by 10% of their respective means. In order to preserve a strong relationship that existed between field-measured LMA and EWT (r = 0.66, p = 0.00, Fig. 3), the PROSPECT model was run by generating input variables (LMA and EWT) using a multivariate normal distribution function based on the mean and covariance matrix of their field measured values. For the N structure index, we used the same range presented by Ali et al. (2016) who retrieved N for similar species in the same study area. It is often a prerequisite to calibrate the physical and optical constants, such as refractive index and absorption coefficients of the PROSPECT model to the target experimental data. However, in this study, we validated the suitability of the original PROSPECT model to simulate field measured reflectance spectra by computing the RMSE between measured and simulated reflectance spectra generated in forward mode. The generated RMSE (Fig. 5a) was generally lower than reported in the literature (Feret et al., 2008; Sun et al., 2018). Therefore, we used the PROSPECT model without re-calibrating the physical and optical constants (Ali et al., 2016).

2.3.1. *Inversion of the PROSPECT model*

There are a number of inversion approaches that can be used to assess the performance of RTMs in modelling leaf spectral reflectance and retrieving leaf traits. The main inversion methods are iterative optimization, neural networks and look-up table (LUT) (Sun et al., 2018; Wang et al., 2015a). Optimization algorithms and neural networks search for the 'best fit' between measured and simulated spectra by successive input variable iteration (Verrelst et al., 2015). The overall performance of optimization algorithms depends on the initial guess (Preidl and Doktor, 2011). The main challenge with optimization algorithms is that they computationally demanding and time-consuming when inverting large look-up tables. The LUT inversion approach on other hand is based on querying the LUT using a merit function (Liang, 2007). The function essentially minimize the summed difference between measured and simulated spectra across the selected wavelength. The LUT approach has an advantage over other inversion methods because it is computationally efficient and guarantee finding global minima (Rivera et al., 2013, Sehgal et al., 2016). Previous studies have also demonstrated that the inversion technique has a minor influence on the inversion results (Buddenbaum and Hill, 2015; Kimes et al., 2000). The main factors that influence the performance of model inversion are the spectral range considered for target constituent and the signal to noise ratio of the spectra (Feret et al., 2008). In this study, we therefore used the widely used LUT approach to assess the performance of the PROSPECT model inversion in retrieving of leaf traits. The best match between simulated spectra to each measured reflectance spectra is determined by calculating and finding the lowest root mean square error (Eqn 3) of the unconstrained non-linear multivariate function (Darvishzadeh et al., 2012). In practice, model inversion involves finding the parameter vector $\theta = [N, C_{ab}, LMA, EWT]$ that minimizes the merit function $J(\theta)$.

$$J(\theta) = \sqrt{\frac{\sum_{\lambda} (\rho_{mes} - \rho_{sim})^2}{n}} \tag{3}$$

Where ρmes and ρsim are measured and simulated spectral reflectance respectively, n is the number of wavelengths (λ) i.e. 1801 used in this study. The selection of single best fitting spectra may not be the optimal strategy of inverting the LUT as this is prone to ill-poseness (Darvishzadeh et al., 2012, 2019). In this study, we observed that using a single best fitting spectral or multiple solutions (i.e. mean of the best 10, 50 and 100 solutions) did not affect the pattern of leaf traits retrieval accuracy (Appendix 1: Figs A1–A3).

2.3.2. *Assessing the performance of the PROSPECT model in forward mode*

To assess the performance of the PROSPECT model in simulating leaf spectral reflectance of leaf samples collected at different canopy positions, we examined the agreement between simulated reflectance spectra generated by the PROSPECT in forward mode against the reflectance spectra measured for the samples collected in the field using the root mean square error (RMSE). For this, we used the leaf traits content (C_{ab}, EWT and LMA) measured in the field for each sample to generate reflectance spectra (Feret et al., 2008). We initially used the N structure range presented by Ali et al. (2016) who retrieved N for similar tree species. We then inversely retrieved N to run the PROSPECT model in forward mode. The simulated spectra for each sample was then compared with the corresponding measured spectra using the RMSE for the lower and upper canopy across the growing season.

2.3.3. *Assessing the retrieval of leaf traits through PROSPECT model inversion*

The accuracy of retrieval of leaf traits across canopy and seasons were assessed by inverting the 250 000 LUT generated from the PROSPECT model as described in section 2.3.1. Specifically, we compared leaf traits retrieved from the PROSPECT model against the field-measured ones using the coefficient of determination (R^2), RMSE and normalized root mean square error (NRMSE = RMSE/range).

3. Results

3.1. *PROSPECT performance in reflectance spectra simulation across canopy positions throughout the growing season*

The effect of leaf position on the performance of the PROSPECT model was initially evaluated based on the agreement between simulated (generated in forward mode) and measured reflectance spectra. Generally, the PROSPECT model generated reflectance spectra that closely matched the measured spectra for both the upper and lower canopy across all seasons and throughout the entire spectrum (Fig. 4). However, some variation were observed, for example, there were

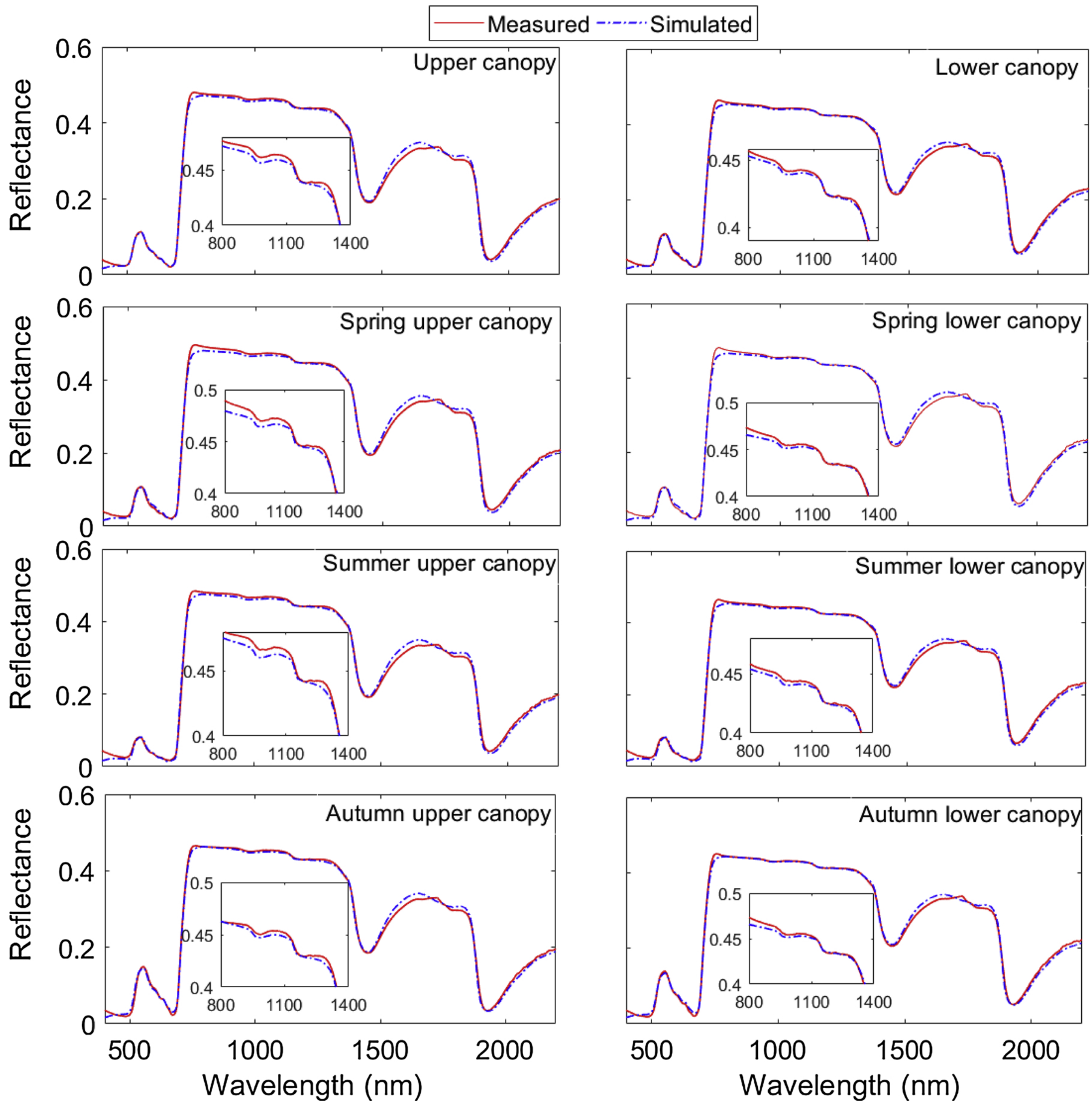

Fig. 4. Measured and simulated leaf reflectance spectra (generated in forward mode) for the upper and lower canopy for all samples used in the study. The spectral mismatch between measured and simulated reflectance is greater for the upper canopy compared to the lower canopy leaf samples for the pooled dataset and across all seasons (see inserts).

relatively higher peaks of spectra mismatch in wavelengths 490–530, 700–789 and 1500–1680 and 1880–1895 nm for the pooled dataset (Fig. 5 a). Across seasons and canopy positions, the peak in the 490–530 nm spectrum was observed for the autumn dataset. The RMSE peak in the 'red-edge' spectrum remains prominent for all the three seasons, with the highest RMSE observed for spring followed by summer and then autumn seasons. High errors in the 1500-to-1680 nm wavelengths were observed across all seasons. The RMSE in the NIR were lowest in autumn and highest in spring (Fig. 5b). The lower canopy demonstrated a better match between simulated and measured reflectance spectra compared to the upper canopy, especially in the NIR (800–1300 nm; Fig. 4, Fig. 5c) and SWIR across all seasons (Fig. 5d-f). Spectral disagreement in the 'red edge' between the upper and lower canopy was higher in the spring (Fig. 5d) and summer (Fig. 5e) when compared to autumn (Fig. 5f). A prominent spectral mismatch was observed in wavelengths centred at 515 nm for the autumn season, which is absent in spring and summer, respectively.

3.2. Retrieval of leaf traits across canopy positions throughout the growing season

Leaf traits retrieved via the PROSPECT model inversion were compared to leaf traits measured in the field. Results show that the retrieval accuracy for C_{ab} was higher for the lower canopy (NRMSE = 0.103) when compared to the upper canopy (NRMSE = 0.122) across all seasons (Fig. 6). The retrieval accuracy of C_{ab} for the lower canopy consistently outperformed that of the upper canopy for each season. The difference in C_{ab} retrieval accuracy between upper canopy and lower canopy was small in spring (NRMSE = 0.209 and NRMSE = 0.2 for lower and upper canopy respectively) when compared to summer (NRMSE = 0.269 and NRMSE = 0.199 for lower and upper canopy respectively) and autumn (NRMSE = 0.1 and NRMSE = 0.14 for lower and upper canopy respectively respectively). Across seasons, C_{ab} was retrieved with higher accuracy in autumn nRMSE (NRMSE = 0.112) when compared to spring (NRMSE = 0.195) and summer (NRMSE = 0.219).

Results of the study show that EWT for the lower canopy was

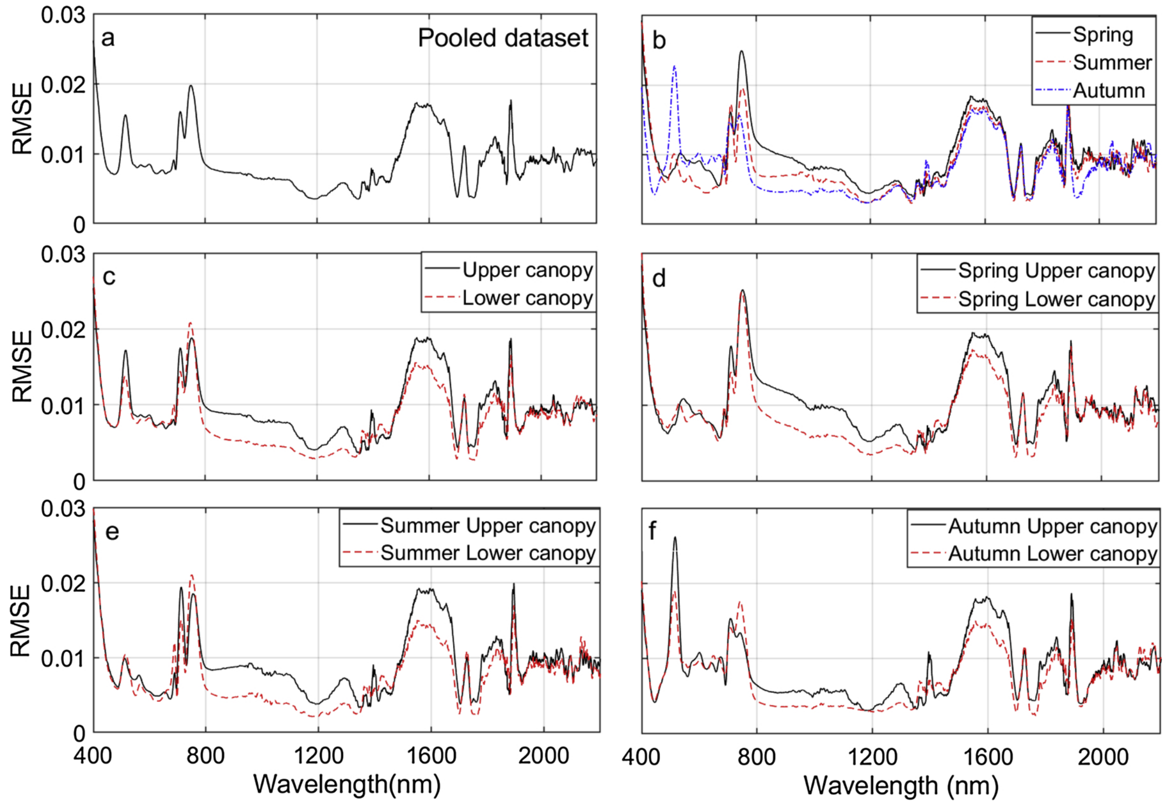

Fig. 5. Variation in RMSE between measured and simulated leaf reflectance for pooled dataset (a), seasons (b), leaf position (c); and leaf position for spring (d), summer (e) and autumn (f).

retrieved with higher accuracy (NRMSE = 0.125) when compared to the upper canopy (NRMSE = 0.188) across all seasons (Fig. 7). Upper

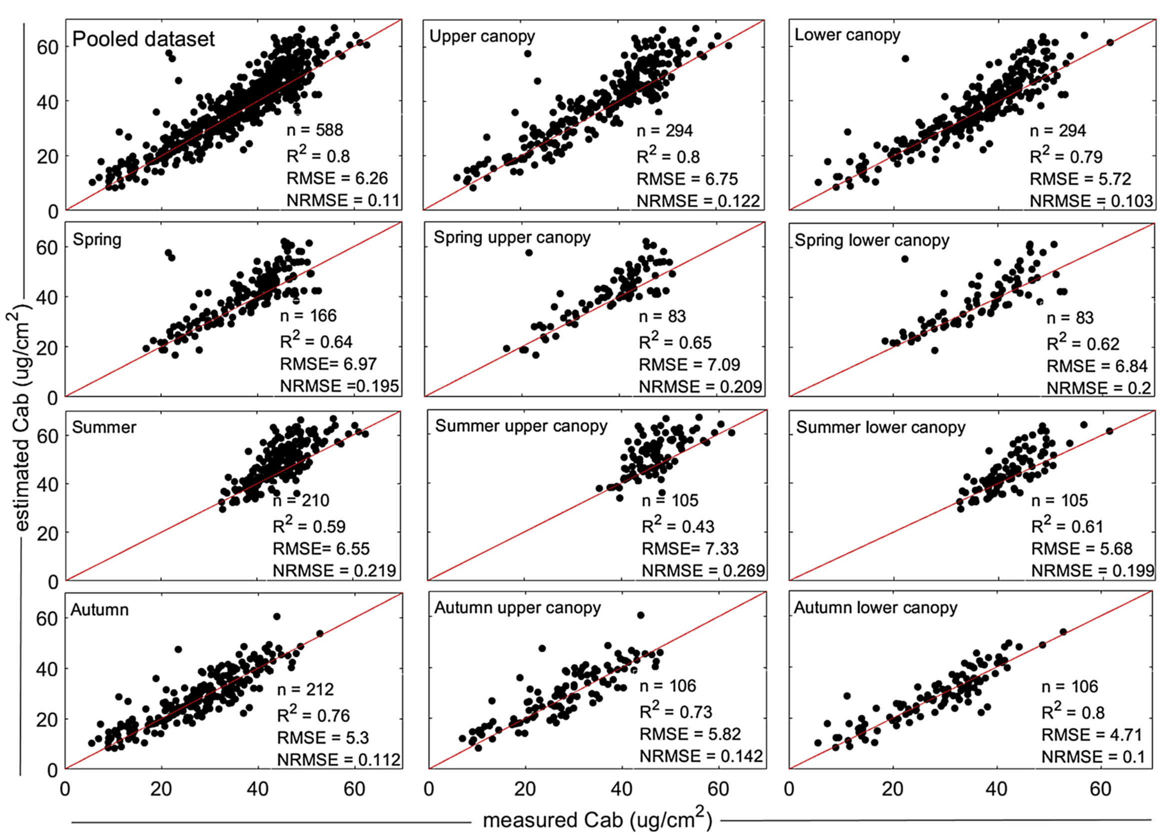

Fig. 6. Retrieval accuracies of the leaf chlorophyll content (C_{ab}) across canopy positions throughout the growing season.

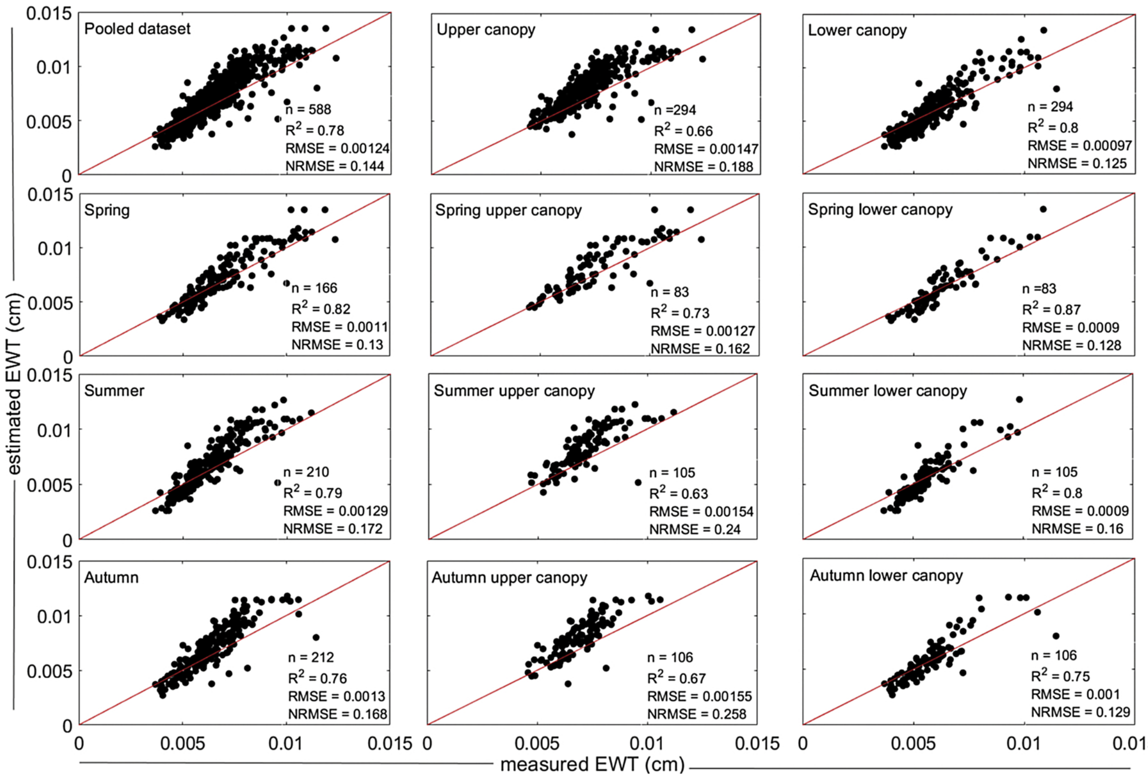

Fig. 7. Retrieval accuracies of EWT across canopy positions throughout the growing season.

canopy EWT was retrieved with low accuracy (NRMSE = 0.162 for spring, NRMSE = 0.24 for summer and NRMSE = 0.258 for autumn) when compared to low canopy (NRMSE = 0.128 spring, NRMSE 0.16 = summer and NRMSE = 0.129 autumn) across all seasons. The difference in EWT retrieval accuracy between the upper and lower canopy widens as the season progressed with a huge difference observed in summer. Generally the retrieval accuracy of EWT was high in spring (NRMSE = 0.13), compared to summer (NRMSE = 0.172) and autumn (NRMSE = 0.168). The pattern of EWT retrieval accuracy between the upper and lower canopy follows a similar trend observed for C_{ab}.

The retrieval accuracy for LMA was higher for the upper canopy (NRMSE = 0.154) compared to lower canopy (NRMSE = 0.176) across all seasons (Fig. 8). A similar trend was also observed for summer (NRMSE = 0.146 and NRMSE = 0.213) and autumn (NRMSE = 0.174 and NRMSE = 0.239). In contrast, lower canopy LMA for spring was retrieved with higher accuracy (NRMSE = 0.162) when compared to the upper canopy (NRMSE = 0.184) for the same season. The difference in LMA retrieval accuracy between the upper canopy and the lower canopy was wide in summer and autumn compared to spring. Generally, LMA was retrieved with higher accuracy in summer (NRMSE = 0.148) when compared to spring (NRMSE = 0.154) and autumn (NRMSE = 0.158). The difference in retrieval accuracy of LMA across seasons was small however the summer season exhibited a better fit (R^2 = 0.82).

4. Discussion

4.1. Does the position of a leaf within a vertical canopy profile affects modelling leaf spectral reflectance throughout the growing season?

The PROSPECT model exhibited the capability to reconstruct leaf reflectance spectra across the canopy throughout the growing season. The stronger agreement between measured and simulated reflectance spectra observed for the lower canopy leaves compared to the upper canopy leaves (Fig. 4 and 5) can be attributed to difference in leaf morphological traits, such as specific leaf area (SLA) and LMA between leaf samples collected from the two canopy layers. These morphological differences have been reported to complicate the modelling of leaf optical properties and subsequent retrieval of leaf traits (Qiu et al., 2018). Field data used in this study evidently demonstrated high SLA values for leaf samples collected from the lower canopy when compared to the upper canopy leaf samples throughout the growing season (Fig. 9), implying that generally upper canopy leaves are thicker compared to lower canopy leaves. Leaf reflectance, especially in the NIR, increases when a leaf thickens due to the increase in the quantity of materials that scatters radiation (Zhang et al., 2007).

The relatively high RMSE between measured and simulated leaf reflectance in wavebands centred around 510, 740 and 1590 and 1885 nm across seasons and canopy positions, imply that these wavebands are either not well measured or modelled by the PROSPECT model. The spectral mismatch in these wavebands has been observed even for re-calibrated PROSPECT models. For example, Li and Wang (2011) observed RMSE of up to 0.06 in the 'red edge' and SWIR spectral regions after recalibrating the PROSPECT 4 model. The lower RMSEs between measured and simulated leaf reflectance in the 'red edge' spectrum for autumn in comparison to spring and summer can be ascribed to the sensitivity of the 'red edge' spectrum when the distribution of foliar nutrients within the leaf volume become uniform during senescence in the autumn season (Maillard et al., 2015). This observation reflects the subtle sensitivity of the PROSPECT model to variation in chlorophyll content at peak vegetation growth, which potentially has an effect on retrieval accuracy of C_{ab} during the summer season. To the best of our knowledge, our study provides the first preliminary understanding on the effect of leaf position within a vertical canopy profile on the performance of PROSPECT model by inspecting the spectral match between measured and simulated leaf reflectance spectra throughout the growing season.

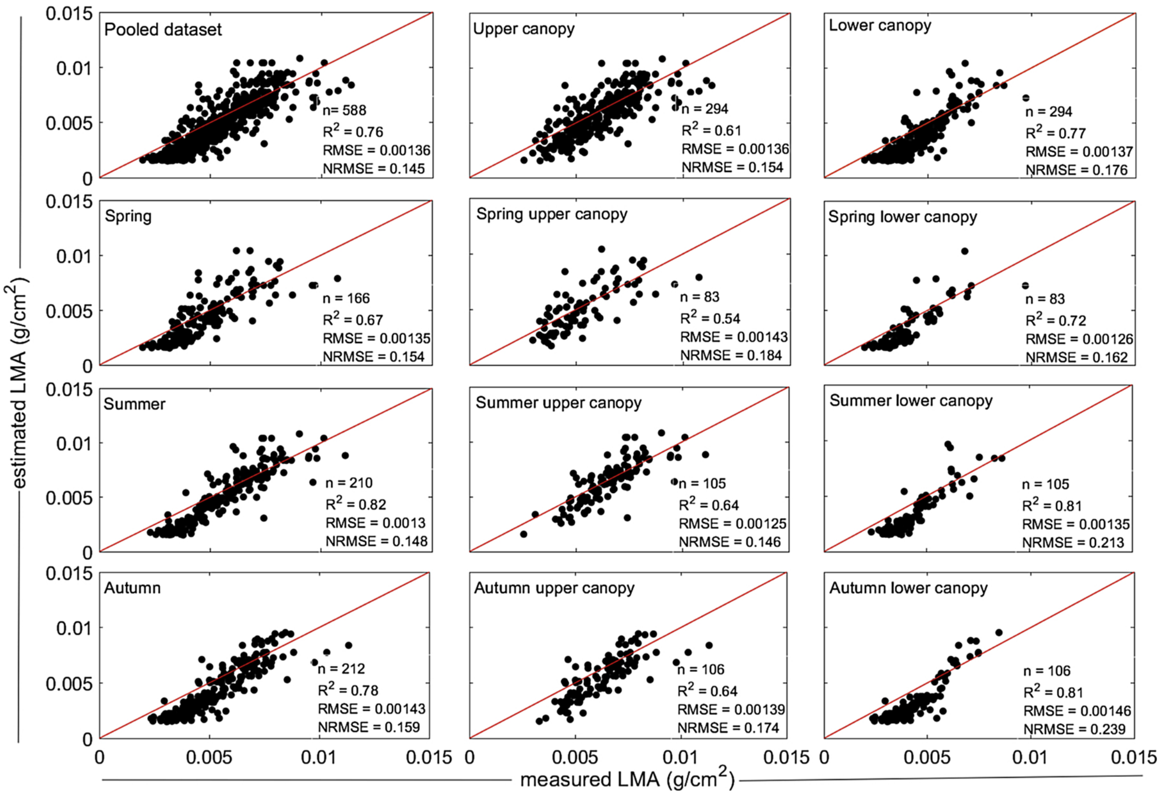

Fig. 8. Retrieval accuracies of the leaf mass per area (LMA) across canopy positions throughout the three growing seasons.

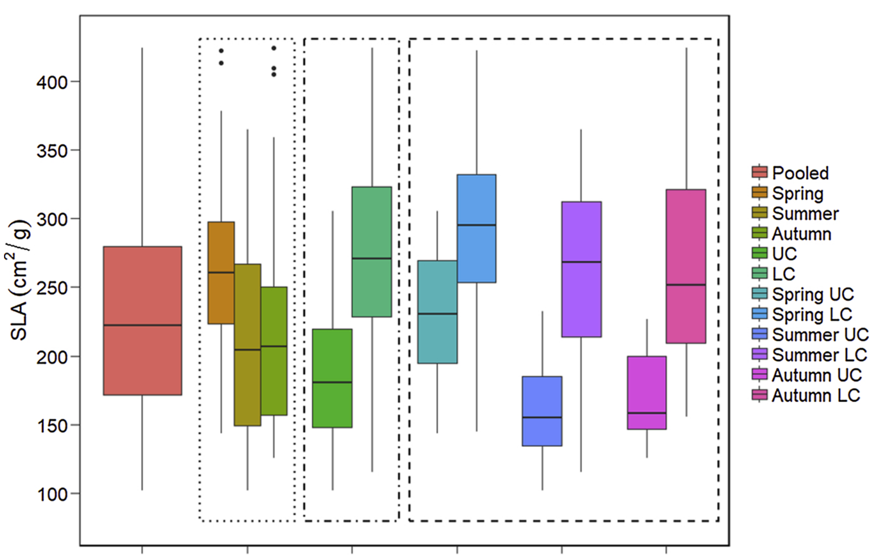

Fig. 9. Variation in SLA across canopy positions throughout the growing season. (UC and LC represent upper and lower canopy respectively).

4.2. *Effect of leaf position on the retrieval accuracy of leaf traits throughout the growing season*

The higher accuracy of retrieval of C_{ab} obtained for leaf samples collected from the lower canopy compared to the upper canopy throughout the growing season (Fig. 6) can be attributed to the distribution of chloroplasts within a leaf that affects absorption and transmittance of radiation by leaf chlorophyll pigments. Most of the chloroplasts for upper sunlit leaves are clumped in the palisade layer whilst for shaded leaves, the chloroplasts are evenly distributed between the palisade and spongy mesophyll layer (Adds et al., 1997). We speculate that the evenly distributed chloroplast in shaded lower canopy leaves improves the sensitivity and interaction of radiation and chlorophyll pigments. The widest differences in C_{ab} retrieval accuracy between upper and lower canopy coincided with the period of maximum leaf chlorophyll content (Fig. 2). This observation can be attributed to the manifestation of the shadow effect on the lower canopy resulting in a reduction in photosynthetically active radiation (PAR) reaching to the lower canopy. The position of a leaf across the canopy vertical profile is a key determinant of its pigment content and subsequently photosynthetic capacity (Arellano et al., 2017). The illuminated upper canopies are known to display high pigment content to commensurate the high relative irradiance received. The least retrieval accuracy of C_{ab} across all seasons (i.e. summer (NRMSE = 0.219) coincided with the season of high leaf chlorophyll content (Fig. 2). This observation is in agreement with the findings of Zhang et al. (2007) who obtained the lowest accuracy in the retrieval of C_{ab} in summer, using the PROSPECT model in sugar maple stands. The seasonal distribution of chlorophyll pigments within a leaf can be linked to poor leaf chlorophyll retrievals obtained in summer. During peak vegetation growth, chlorophyll and other nutrients are confined in chloroplast cells, and these cells are organized in a clumped manner. As leaves senescence, chloroplast degrades, and the chlorophyll pigments together with other nutrients like leaf protein are released in remobilizable form and become uniformly distributed across the leaf volume (Carrión et al., 2014). This phenomenon, therefore, improves the interaction between radiation and leaf nutrients that are freely and uniformly distributed across the leaf volume. However, it is worthwhile to note that Yang et al. (2016) estimated chlorophyll with high accuracy in summer in comparison to other seasons using partial least squares regression (PLSR) in two temperate deciduous forests in the northeastern United States.

Results of our study demonstrate contrasting patterns in seasonal retrieval accuracies of LMA and EWT across canopy positions. We expected LMA and EWT to display similar seasonal retrieval patterns across the canopy, mainly because these two traits co-vary on the leaf economic spectrum, i.e. EWT facilitates transportation of nutrients and is a key regulator of photosynthesis and subsequently the amount of dry matter content accumulated in a leaf (Asbjornsen et al., 2011; Waring and Landsberg, 2011). Statistically, LMA and EWT demonstrated a positive co-variance and strong correlation ($r = 0.66$, $p = 0.00$, Fig. 3). Previous studies reported that EWT is probably easier to retrieve via PROSPECT inversion due to its dominance and well-elaborated specific absorption features compared to LMA (Jiang et al., 2018, Wang et al., 2011; Feret et al., 2008). The high EWT retrieval accuracies obtained for the lower canopy in comparison to the upper canopy throughout the growing season conform to the variation in spectral matching between measured and simulated reflectance spectra for the two canopy layers especially in key water absorption wavebands [970, 1200 and 1400 nm (Curran, 1989)]. The pattern in EWT retrieval accuracy across canopy positions and seasons can be explained by the high wax-cuticle load that characterize upper canopy leaves in a bid to prevent photo-damage, especially at peak vegetative growing season that is characterized by increased radiation amounts (Jacoby et al., 1990; Bouzoubaâ et al., 2006). High wax-cuticle load conceal the interaction between radiation and leaf biochemical constituents especially in the NIR/SWIR optical domain resulting in complex relationship with reflected light (Féret et al., 2018; Barry et al., 2009).

Contrary to the pattern of EWT retrieval accuracy across seasons and canopy positions, we observed that the retrieval accuracy of LMA for the upper canopy outperformed that of the lower canopy for all the seasons except the spring season. This observation does not reflect the pattern of spectral matching between measured and PROSPECT simulated reflectance spectra observed in Fig. 4 and 5 for the upper and lower canopy samples. We expected to retrieve LMA for the lower canopy with higher accuracy mainly because reflectance spectra simulated by the PROSPECT model in forward model closely matched the measured reflectance spectra for lower canopy in comparison to the upper canopy. This was especially evident in the NIR and SWIR spectrum -known to be sensitive to variations in LMA (Feret et al., 2008; Baret and Fourty, 1997). Several reasons can be attributed to the mismatch between the pattern of LMA retrieval accuracy and spectral matching across the canopy throughout the growing season. Firstly, LMA is often retrieved with relatively low accuracy because the high specific absorption coefficients of water which conceal the effect of LMA spectral response (Jacquemoud et al., 1996; Riano et al., 2005). Secondly, LMA consists of a wide range of constituents, such as protein, lignin, cellulose, starch, sugar and lipids (Qiu et al., 2018). The specific absorption coefficient spectrum used in the PROSPECT model is considered a weighted average of the molecular absorption spectra of these constitutes (Jacquemoud et al., 1996). This approach is likely to induce increased uncertainties, especially in wavelengths of high LMA absorption as different components of these constituents can yield different specific absorption coefficients of LMA. Thirdly, thicker leaves or leaves of higher LMA values tend to have denser tissues and less air space, which results in diverse leaf internal structure and complex light scattering (Demarez, 1999). Finally, although it has been demonstrated earlier that the SWIR (especially between 2100–2300 nm) is more sensitive to LMA (Wang et al., 2011), our spectral reflectance data had low signal to noise ratio in this spectrum.

Although retrieval of LMA did not show similar patterns to C_{ab} and EWT retrieval across the canopy, it was generally retrieved with higher accuracy (NRMSE = 0.145 for the pooled dataset) compared to previous studies that used the PROSPECT model in the same ecosystem. For example, Ali et al. (2016) reported an NRMSE of 0.23 while Wang et al. (2015a) reported an NRMSE of 0.22 for LMA retrieved using the PROSPECT inversion based on 53 sunlit leaf samples collected in summer. The relatively lower accuracy reported in these studies could be ascribed to a small sample size ($n = 53$ compared to 588 samples in this study) used for model validation. To our knowledge, our work provides the first attempt to examine the effect of leaf position within a vertical canopy profile on the performance of the PROSPECT model when retrieving leaf traits throughout a growing season.

4.2.1. *Implications on plant traits spectroscopy*

Results presented in this study have implications on modelling leaf optical properties and retrieval of foliar traits especially using multi-layer canopy radiative models (Kuusk, 2001). The conventional approach of sampling foliar material exclusively from the sunlit upper canopy has recently become a contentious approach in remote sensing vegetation canopies. Recent studies demonstrate that the vertical heterogeneity in leaf chlorophyll, water and dry matter content have a significant effect on canopy reflectance measured by remote sensing instruments (Yang et al., 2017; Wang and Li, 2013; Zhao et al., 2017). The vertical heterogeneity in leaf traits is known to affect re-absorption and scattering of radiation within vegetation canopies, and subsequently, the top of canopy reflectance measured by remote sensing instruments (Verhoef and Bach, 2007). Our previous study (Gara et al., 2018b) also demonstrated that incorporating leaf traits from the shaded lower canopy improve the modelling accuracy of dry matter related canopy traits such as canopy LMA, nitrogen and carbon using in-situ hyperspectral measurements. Results presented in the current study demonstrate that the position of a leaf affects the performance of the PROSPECT model and the retrieval of its input parameters. This observation implies that failure to account for the vertical heterogeneity in leaf traits between sunlit upper and shaded lower leaves together with their optical properties might introduce significant uncertainties in the modelling canopy reflectance and retrieval of canopy traits(Yang et al., 2017; Li et al., 2018). These results are particularly relevant to the vegetation spectroscopy community considering that the PROSPECT model is coupled with widely used canopy RTMs such as INFORM (Schlerf and Atzberger, 2006) and SAILH (Jacquemoud et al., 2009).

5. Conclusion

Our results demonstrated a strong agreement between the measured and PROSPECT simulated reflectance spectra for leaves from the lower canopy compared to the upper canopy, especially in the NIR spectral region, throughout the growing season. This pattern concurred with the higher retrieval accuracy of C_{ab} and EWT for the lower canopy compared to the upper canopy throughout the growing. Variations in C_{ab} and EWT retrieval accuracy across the canopy vertical profile can be linked to seasonal changes in leaf biochemistry and morphology, especially SLA. On the contrary, the LMA retrieval accuracy pattern did not reflect the spectral match observed between the upper and lower canopy. This implies that there is further need to separate and model respective constituents of LMA to improve PROSPECT stability and credibility. We conclude that the PROSPECT model provides reasonable retrieval accuracies for C_{ab}, EWT and LMA from reflectance spectra across canopy position throughout the growing season. However, our results for the first time demonstrated seasonal variation in retrieval accuracy of leaf traits via PROSPECT model inversion through a vertical canopy profile. Our results point out the potential source of uncertainties in the retrieval of leaf traits using the widely used PROSPECT model.

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Appendix 1

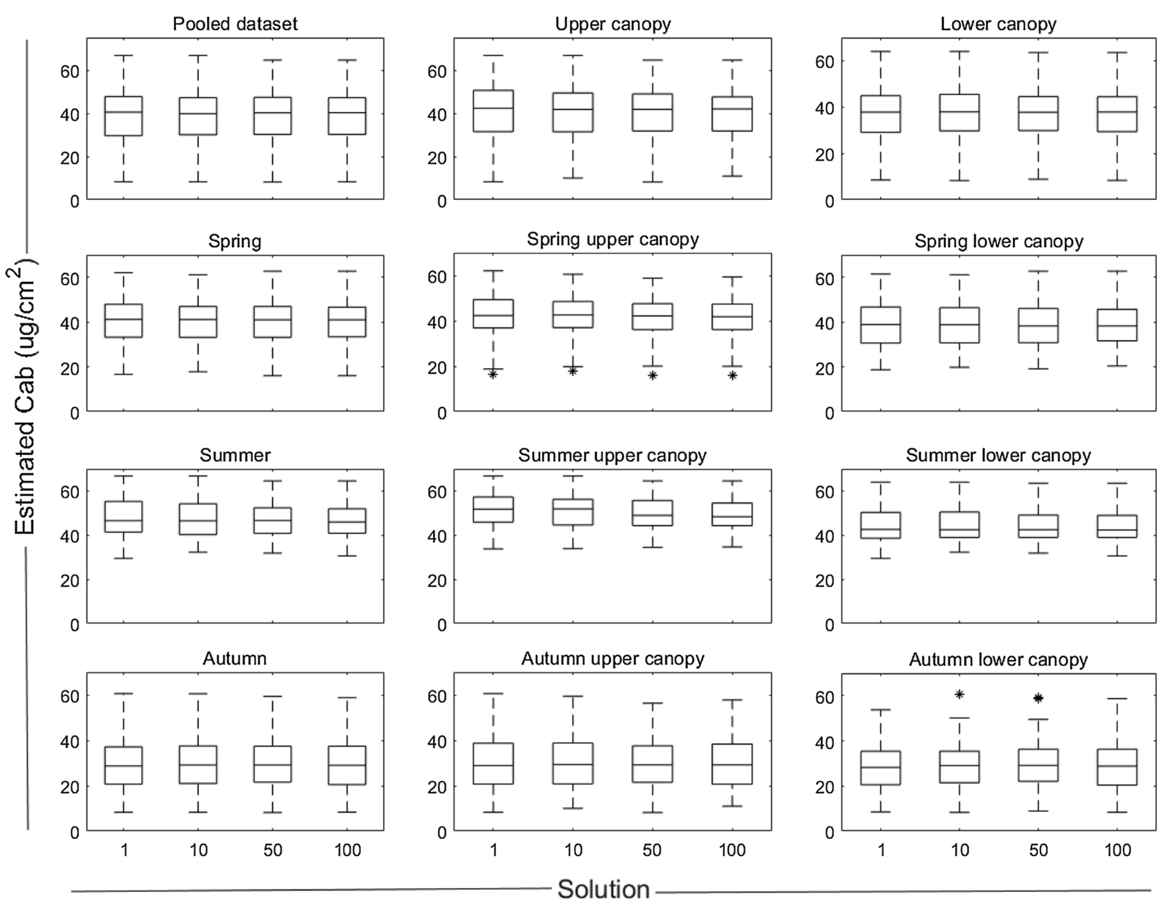

Fig. A1. Distribution of retrieved C_{ab} based on different solutions across the canopy throughout the growing season.

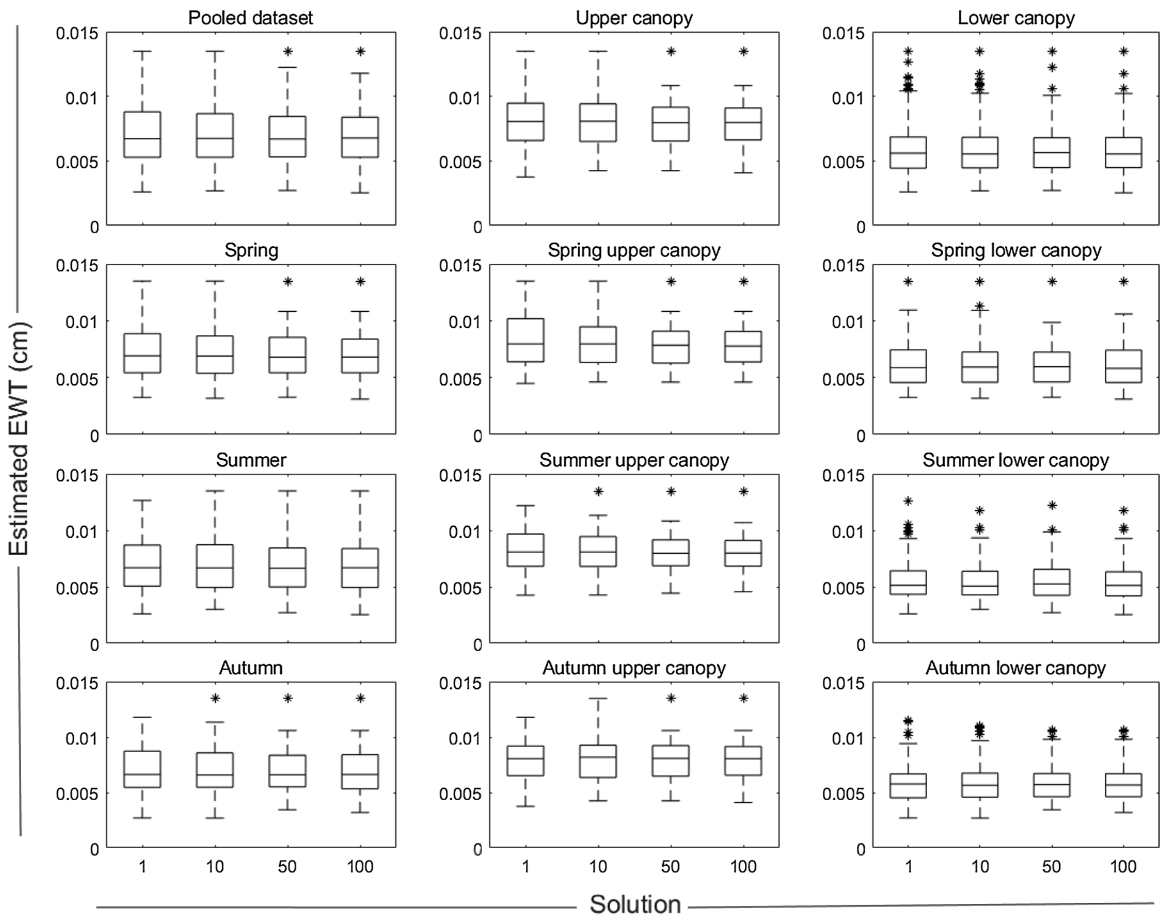

Fig. A2. Distribution of retrieved EWT based on different solutions across the canopy throughout the growing season.

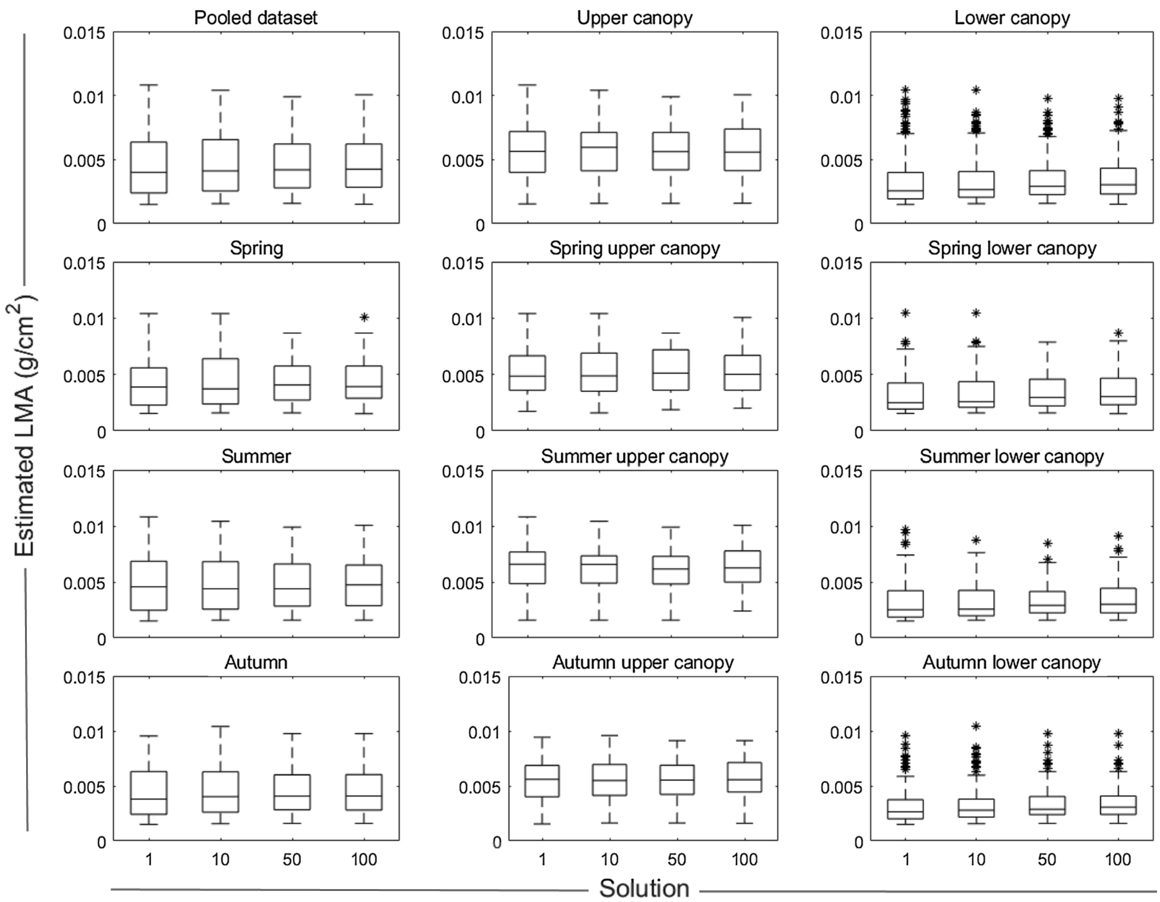

Fig. A3. Distribution of retrieved LMA based on different solutions across the canopy throughout the growing season.

Table A1
: Retrieval accuracies of leaf traits across canopy positions throughout the growing season for European beech only.

		Cab			LMA			EWT		
Category	n	R^2	RMSE	nRMSE	R^2	RMSE	nRMSE	R^2	RMSE	nRMSE
Pooled	546	0.83	5.78	0.115	0.78	0.00132	0.14	0.77	0.00121	0.14
Spring	156	0.76	5.61	0.157	0.68	0.00128	0.146	0.8	0.0011	0.128
Summer	194	0.59	6.68	0.287	0.85	0.00124	0.141	0.79	0.00129	0.172
Autumn	196	0.79	4.89	0.116	0.8	0.00143	0.159	0.78	0.00123	0.178
UC	273	0.83	6.42	0.131	0.63	0.00132	0.16	0.63	0.00145	0.185
LC	273	0.82	5.06	0.108	0.79	0.00133	0.171	0.8	0.00091	0.131
Spring UC	78	0.78	5.79	0.17	0.53	0.00136	0.182	0.71	0.00126	0.161
Spring LC	78	0.76	5.42	0.159	0.74	0.00119	0.154	0.84	0.00086	0.135
Summer UC	97	0.43	7.55	0.368	0.66	0.00119	0.149	0.61	0.00155	0.238
Summer LC	97	0.55	5.68	0.344	0.86	0.00129	0.2	0.79	0.00096	0.219
Autumn UC	98	0.75	5.64	0.138	0.66	0.00139	0.18	0.64	0.00149	0.25
Autumn LC	98	0.85	3.99	0.103	0.81	0.00147	0.24	0.78	0.00089	0.129

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