

Quantifying vegetation indices using Terrestrial Laser Scanning: methodological complexities and ecological insights from a Mediterranean forest

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Abstract. Accurate measurement of vegetation density metrics including plant, wood and leaf area indices (PAI, WAI and LAI) is key to monitoring and modelling carbon storage and uptake in forests. Traditional passive sensor approaches, such as Digital Hemispherical Photography (DHP), cannot separate leaf and wood material, nor individual trees, and require many assumptions in processing. Terrestrial Laser Scanning (TLS) data offer new opportunities to improve understanding of tree and canopy structure. Multiple methods have been developed to derive PAI and LAI from TLS data, but there is little consensus on the best approach, nor are methods benchmarked as standard.

Using TLS data collected in 33 plots containing 2472 trees of five species in Mediterranean forests, we compare three TLS methods (*LiDAR Pulse*, *2D Intensity Image* and *Voxel-Based*) to derive PAI and compare with co-located DHP. We then separate leaf and wood in individual tree point clouds to calculate the ratio of wood to total plant area (α), a metric to correct for non-photosynthetic material in LAI estimates. We use individual tree TLS point clouds to estimate how α varies with species, tree height and stand density.

We find the *LiDAR Pulse* method agrees most closely with DHP, but is limited to single scan data so cannot determine individual tree properties, including α . The *Voxel-Based* method shows promise for ecological studies as it can be applied to individual tree point clouds. Using the *Voxel-Based* method, we show that species explain some variation in α , however, height and plot density were better predictors.

Our findings highlight the value of TLS data to improve fundamental understanding of tree form and function, but also the importance of rigorous testing of TLS data processing methods at a time when new approaches are being rapidly developed. New algorithms need to be compared against traditional methods, and existing algorithms, using common reference data. Whilst promising, our results show that metrics derived from TLS data are not yet reliably calibrated and validated to the extent they are ready to replace traditional approaches for large scale monitoring of PAI and LAI.

33 1 Introduction

34 ~~Terrestrial Laser Scanning (TLS) generates high resolution 3D measurements of whole forests and individual~~
35 ~~trees (Burt et al., 2018; Disney, 2018), leading to the development of completely new monitoring approaches to~~
36 ~~understand the structure and function of ecosystems (Lines et al., 2022). Unlike traditional passive sensors, TLS~~
37 ~~can estimate plant, wood and leaf area indices (PAI, WAI, LAI) for both whole plots and individual tree point~~
38 ~~clouds (Calders et al., 2018), and is unaffected by illumination conditions. This has led to the development of~~
39 ~~several methods for processing TLS data to extract the key metrics PAI, WAI and LAI (e.g. Hosoi and Omasa,~~
40 ~~2006; Jupp et al., 2008; Zheng et al., 2013). However, intercomparison studies of algorithms and processing~~
41 ~~approaches to derive the same metrics from different TLS methods are lacking.~~

42 Leaf Area Index (LAI), defined as half the amount of green leaf area per unit ground area (Chen and Black, 1992),
43 determines global evapotranspiration, phenological patterns and canopy photosynthesis, and is therefore an
44 essential climate variable (ECV), as well as a key input in dynamic global vegetation models (Sea et al., 2011;
45 Weiss et al., 2004). Accurate measurements of leaf, wood and plant area indices (LAI, WAI and PAI) have
46 historically been derived from labour intensive destructive sampling (Baret et al., 2013; Jonckheere et al., 2004),
47 so over large spatial or temporal scales these can only be measured indirectly, typically with remote sensing.
48 Large-scale remote sensing, using spaceborne and airborne instruments, has been widely used to estimate LAI
49 over large areas (Pfeifer et al., 2012), but requires calibration and validation using in situ measurements to
50 constrain information retrieval (Calders et al., 2018). Non-destructive in situ vegetation index estimates have
51 historically been made by measuring light transmission below the canopy and using simplifying assumptions
52 about canopy structure to estimate the amount of intercepting material (e.g. Beer-Lambert's law; Monsi and Saeki,
53 1953). The most common method, Digital Hemispherical Photography (DHP; Figure 1a), requires both model
54 assumptions and subjective user choices during data acquisition and processing in order to estimate both PAI and
55 LAI (Breda, 2003). DHP images are processed by separating sky from canopy, but not photosynthetic from non-
56 photosynthetic vegetative material, so additional assumptions are needed to calculate either LAI or WAI
57 (Jonckheere et al., 2004; Pfeifer et al., 2012). Separation of LAI from PAI can be achieved by removing or
58 masking branches and stems from hemispherical images (e.g. Sea et al., 2011; Woodgate et al., 2016), but is not
59 reliable when leaves are occluded by woody components (Hardwick et al., 2015). An alternative approach is to
60 take separate DHP measurements in both leaf on and leaf off conditions, and derive empirical wood to plant ratios
61 (WAI/PAI, α) (Leblanc and Chen, 2001), but this is not always practical, for example in evergreen forests. The
62 difficulty of separation means that studies often omit correcting for the effect of WAI on optical PAI
63 measurements altogether (Woodgate et al., 2016), but since woody components in the forest canopy can account
64 for more than 30% of PAI (Ma et al., 2016) this can introduce overestimation. Further, although DHP estimates
65 of LAI or PAI are valuable both for ecosystem monitoring and developing satellite LAI products (Hardwick et
66 al., 2015; Pfeifer et al., 2012), they are limited to sampling only at a neighbourhood or plot level (Weiss et al.,
67 2004), and cannot be used to measure individual tree LAI except for open grown trees (Béland et al., 2014).

68 The ratio of wood to total plant area, α , is known to be dynamic, changing in response to abiotic and biotic
69 conditions. For example, the Huber value (sapwood to leaf area ratio, a related measure to α) may vary according
70 to water availability (Carter and White, 2009). Leaf area may therefore be indicative of the drought tolerance level
71 of a tree, with more drought tolerant species displaying a lower leaf area, reducing the hydraulic conductance of

72 the whole tree and therefore increasing its drought tolerance (Niinemets and Valladares, 2006). α has been
73 hypothesised to increase with the size of a tree in response to the increased hydraulic demand associated with
74 greater hydraulic resistance of tall trees (Magnani et al., 2000) and higher transpiration rates of larger LAI
75 (Battaglia et al., 1998; Phillips et al., 2003). Stand density may also impact α (Long and Smith, 1988; Whitehead,
76 1978), as increased stand level water use scales linearly with LAI (Battaglia et al., 1998; Specht and Specht, 1989),
77 reducing water availability to individual trees competing for the same resources (Jump et al., 2017). Large scale
78 quantification of α or Huber value, however, is difficult as studies usually rely on a small number of destructively
79 sampled trees (e.g. Carter and White, 2009; Magnani et al., 2000), litterfall traps (e.g. Phillips et al., 2003) or
80 masking hemispherical images (e.g. Sea et al., 2011; Woodgate et al., 2016). These approaches are only applicable
81 on a small to medium scale, and in the case of image masking, cannot differentiate between individuals. Variation
82 in α , for example by species and or stand structure, is therefore largely unknown.

83 **1.12 TLS methods for calculating PAI, LAI and WAI**

84 Terrestrial Laser Scanning (TLS) generates high-resolution 3D measurements of whole forests and individual
85 trees (Burt et al., 2018; Disney, 2018), leading to the development of completely new monitoring approaches to
86 understand the structure and function of ecosystems (Lines et al., 2022). Unlike traditional passive sensors, TLS
87 can estimate plant, wood and leaf area indices (PAI, WAI, and LAI) for both whole plots and individual tree
88 point clouds (Calders et al., 2018), and is unaffected by illumination conditions. This has led to the development
89 of several methods for processing TLS data to extract the key metrics PAI, WAI and LAI (e.g. Hosoi and Omasa,
90 2006; Jupp et al., 2008; Zheng et al., 2013). However, intercomparison studies of algorithms and processing
91 approaches to derive the same metrics from different TLS methods are lacking.

92 TLS methods for extracting PAI, LAI and WAI can be broadly categorised into two types: (1) LiDAR return
93 counting, using single scan data (e.g., the *LiDAR Pulse* method; Jupp et al., 2008, and *2D Intensity Image* method;
94 Zheng et al., 2013) and (2) point cloud voxelisation, usually using co-registered scans (e.g., the *Voxel-Based*
95 method; Hosoi and Omasa, 2006).

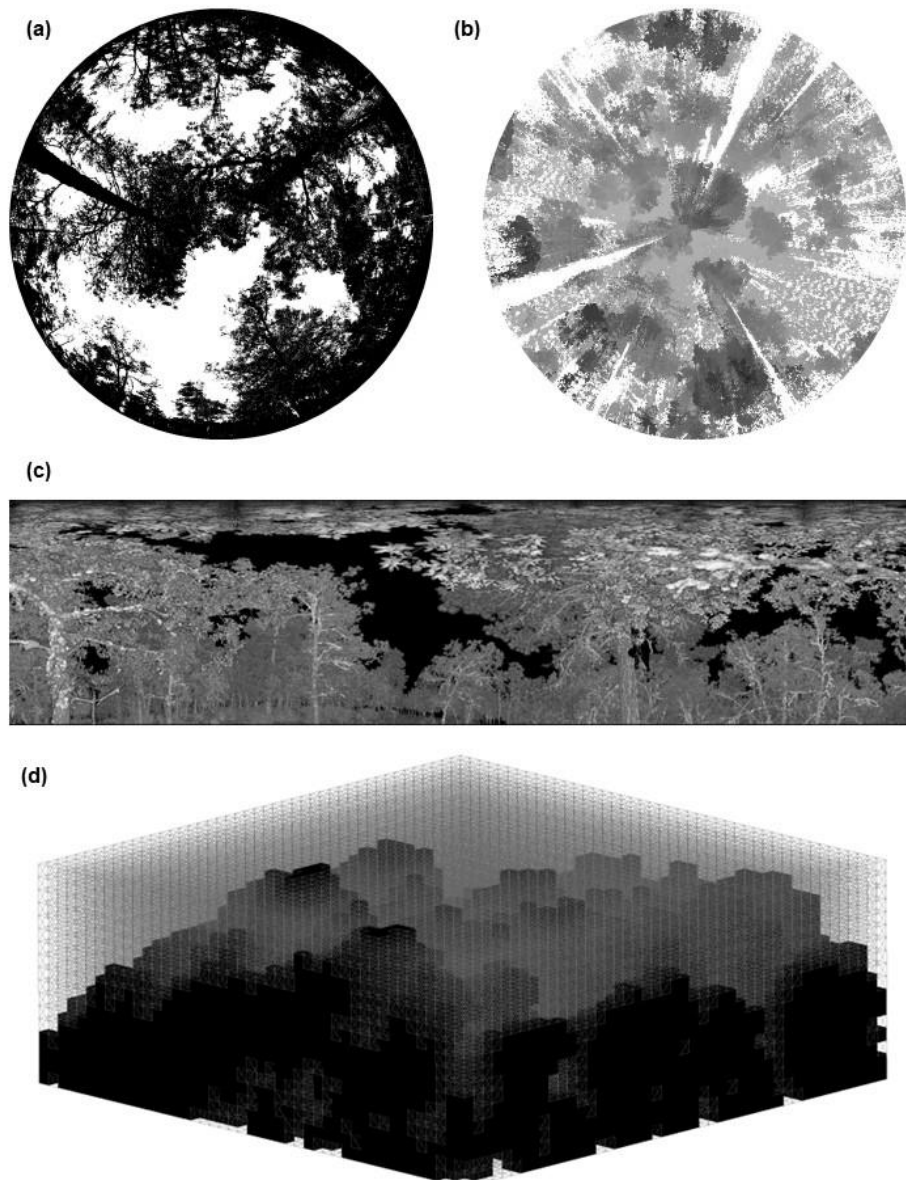
96 The *LiDAR Pulse* method (Jupp et al., 2008; Figure 1b) estimates gap fraction (P_{gap}) using single scan data, as a
97 function of the total number of outgoing LiDAR pulses from the sensor and the number of pulses that are
98 intercepted by the canopy. This method, which eliminates illumination impacts associated with the use of DHP
99 (Calders et al., 2014), has been implemented in the python module, *PyLidar* (www.pylidar.org) and the R package,
100 *rTLS* (Guzman, et al. 2021). Using the *LiDAR Pulse* method, Calderys et al. (2018) compared PAI estimates from
101 two ground-based passive sensors (LiCOR LAI-2000 and DHP) with TLS data collected with a RIEGL VZ-400
102 TLS in a deciduous woodland, and found the two passive sensors underestimated PAI values compared to TLS,
103 with differences dependent on DHP processing and leaf on/off conditions.

104 The *2D Intensity Image* method (Zheng et al., 2013; Figure 1c), also uses raw single scan TLS point clouds, but,
105 unlike the *LiDAR Pulse* method, converts LiDAR returns into 2D panoramas where pixel values represent return
106 intensity. PAI is estimated by classifying pixels as sky or vegetation, based on their intensity value, to estimate
107 P_{gap} , and then applying Beer-Lambert's law. Like the *LiDAR Pulse* method, this approach has been shown to
108 generate higher PAI estimates than DHP (Calderys et al., 2018; Woodgate et al., 2015; Grotti et al., 2020), with

109 differences attributed to the greater pixel resolution and viewing distance of TLS resolving more small canopy
110 details (Grotti et al., 2020).

111 The *Voxel-Based* method (Figure 1d) estimates PAI by segmenting a point cloud into voxels and either simulating
112 radiative transfer within each cube (Béland et al., 2014; Kamoske et al., 2019), or classifying voxels as either
113 containing vegetation or not, and dividing vegetation voxels by the total number of voxels (Hosoi and Omasa,
114 2006; Itakura and Hosoi, 2019; Li et al., 2017). Crucially, this method may be applied to multiple co-registered
115 scan point clouds and so can be used to calculate PAI for both whole plots and individual, segmented TLS trees.
116 However, PAI estimates derived using the voxel method are highly dependent on voxel size (Calders et al., 2020).
117 Using a radiative transfer approach, Béland et al. (2014) demonstrated that voxel size is dependent on canopy
118 clumping, radiative transfer model assumptions and occlusion effects, making a single, fixed choice of voxel size
119 for all ecosystem types-, scanners or datasets impossible. To test various approaches to selecting voxel size using
120 a voxel classification approach, Li et al. (2016) matched voxel size to point cloud resolution, individual tree leaf
121 size, and minimum beam distance and tested against destructive samples, finding that voxel size matched to point
122 cloud resolution had the closest PAI values to destructive samples.

123 The *LiDAR Pulse* method and *2D Intensity Image* method both use single scan data. However, to generate robust
124 estimates of canopy properties that avoid errors from occlusion effects, multiple co-registered scans taken from
125 different locations are likely needed (Wilkes et al., 2017). Further, both these methods require raw unfiltered data
126 to accurately measure the ratio of pulses emitted from the scanner and number of pulses that are intercepted by
127 vegetation. This means “noisy” points caused by backscattered pulses (Wilkes et al., 2017) are included in
128 analyses, potentially leading to higher PAI estimates. However, the *LiDAR Pulse* and *2D Intensity Image* methods
129 may introduce fewer estimation errors compared to DHP, which is influenced by differences in sky illumination
130 conditions and camera exposure (Weiss et al., 2004).



131

132

133 **Figure 1: Visual representation of the four methods for PAI and WAI estimation used in this study: (a) a binarised**
134 **digital hemispherical photograph (DHP), (b) TLS raw single scan point cloud, for the *LiDAR Pulse* method (Jupp et**
135 **al., 2008). Image shows a top-down view of raw point cloud and greyscale represents low (grey) and high (black) Z**
136 **values, (c) TLS 2D intensity image for the *2D Intensity Image* method (Zheng et al., 2013), (d) Voxelised co-registered**
137 **whole plot point cloud for the *Voxel-Based* method (Hosoi and Omasa, 2006), showing a representative schematic of**

138 cube voxels with edge length of 1m, voxelised using the R package *VoxR* (Lecigne et al., 2018). Solid black voxels are
139 classified as containing vegetation (filled) and voxels outlined with grey lines are voxels classified as empty.

140 **1.23 Scope and aims**

141 The aims of this study are twofold: the first aim is to compare three TLS methods for estimating PAI with
142 traditional DHP. The second aim of this study is to use TLS to understand drivers of individual tree α variation.

143 In this study we use a dataset of 528 co-located DHP and high-resolution TLS scans from 33 forest plots to
144 compare DHP derived PAI (PAI_{DHP}) with estimates from three methods to estimate PAI from TLS data (PAI_{TLS}):
145 the *LiDAR Pulse* method; the *2D Intensity Image* method and the *Voxel-Based* method (Figure 1). We use a dataset
146 collected from a network of pine/oak forest plots in Spain (Owen et al., 2021) and ask (1) are the three TLS
147 methods able to reproduce PAI_{DHP} estimates at single scan and whole plot level? (2) does α , calculated from the
148 *Voxel-Based* method on individual tree point clouds, vary with species and tolerance to drought? and (3) does α
149 scale with height and stand density?

150 **2. Methods**

151 **2.1 Study site**

152 We collected TLS and DHP data from 29 plots in Alto Tajo Natural Park ([40°41'N, 02°03'W](#); FunDIV –
153 Functional Diversity plots; see Baeten et al. (2013) for a detailed description of the plots) and four plots in Cuellar
154 ([41°23'N 4°21'W](#)) in June - July 2018 (see Owen et al. (2021) for full details) (Figure A1). Plots contained two
155 oak species: semi-deciduous *Q. faginea* and evergreen *Q. ilex*, and three pine species: *P. nigra*, *P. pinaster* and *P.*
156 *sylvestris*. *P. sylvestris* is the least drought tolerant species, followed by *P. nigra*, *Q. faginea*, *Q. ilex*; shade
157 tolerance follows the same ranking (Niinemets and Valladares, 2006; Owen et al., 2021). Although not
158 quantitatively ranked, *P. pinaster* has been shown to be very drought tolerant, appearing in drier areas than the
159 other species (Madrigal-González et al., 2017). The area is characterised by a Mediterranean climate (altitudinal
160 range 840 – 1400 m.a.s.l.) (Jucker et al., 2014; Madrigal-González et al., 2017). In addition to the five main canopy
161 tree species, plots contained an understory of *Juniperus thurifera* and *Buxus sempervirens* (Kuusk et al., 2018).

162 **2.2 Field protocol**

163 In each of the 33 plots of size 30 x 30 m ~~plots~~ we collected TLS scans on a 10 m grid, making 16 scan locations
164 following Wilkes et al. (2017) to minimise occlusion effects associated with insufficient scans. We used a Leica
165 HDS6200 TLS set to super high resolution (3.1 x 3.1mm resolution at 10 m with a beam divergence of ≤ 5 mm at
166 50 m; scan time 6m 44 s; see Owen et al. (2021)). At each of the 528 scan locations and following the protocol
167 in Pfeifer et al. (2012), we captured co-located DHP images with three exposure settings (automatic and \pm one
168 stop exposure compensation), levelling a Canon EOS 6D full frame DSLR sensor with a Sigma EX DG F3.5
169 fisheye lens, mounted on a Vanguard Alta Pro 263AT tripod.

170 **2.3 Calculation of single scan and whole plot PAI using DHP data**

171 For each of the red-green-blue (RGB) DHP images we extracted the blue band for image thresholding, as this best
172 represents sky/vegetation contrast (Pfeifer et al., 2012). For each plot, we picked the exposure setting that best
173 represented sky/vegetation difference based on pixel brightness histograms of four sample locations indicative of
174 the plot. We carried out automatic image thresholding using the Ridler and Calvard method (1978), to create a

175 binary image of sky and vegetation, avoiding subjective user pixel classification (Jonckheere et al., 2005). We
176 calculated PAI from the binary image, limiting the field of view to a 5° band centred on the hinge angle of 57.5°
177 ($55^\circ - 60^\circ$). The hinge angle has a path length through the canopy twice the canopy height, so the band around it
178 is an area of significant spatial averaging taken as representative of canopy structure of the area (Calders et al.,
179 2018; Jupp et al., 2008). From the binarised hinge angle band we calculated P_{gap} as the number of sky pixels
180 divided by the total number of pixels and PAI using an inverse Beer-Lambert law equation (Monsi and Saeki,
181 1953). We calculated whole plot PAI as the arithmetic mean of the 16 plot scan location PAI estimates. As this
182 value does not correct for canopy clumping, it is better described as effective PAI, rather than true PAI (Woodgate
183 et al., 2015). However, as the TLS and DHP methods we apply here account for canopy clumping differently, we
184 compared effective values and here-on refer to effective PAI as PAI (Calders et al., 2018). DHP images used in
185 this study are freely available (see Flynn et al., 2023).

186 **2.4 Calculation of single scan and whole plot PAI from TLS data**

187 To calculate PAI using the *LiDAR Pulse* method (Jupp et al., 2008), we calculated P_{gap} for a single scan (Figure
188 1b) by summing all returned laser pulses and dividing by the number of total outgoing pulses, following Lovell et
189 al. (2011; see Eq. 7 in that study), and then estimated PAI following Jupp et al. (2008; see Eq. 18 in that study),
190 setting the sensor range to 5° around the hinge angle as before ($55^\circ - 60^\circ$). Single scan PAI was taken as the
191 cumulative sum of PAI values estimated by vertically dividing the hinge region into 0.25 m intervals (Calders et
192 al., 2014). We implemented the *LiDAR Pulse* method using the open-source *R* (R Core Team, 2020) package,
193 *rTLS* (Guzmán and Hernandez, 2021).

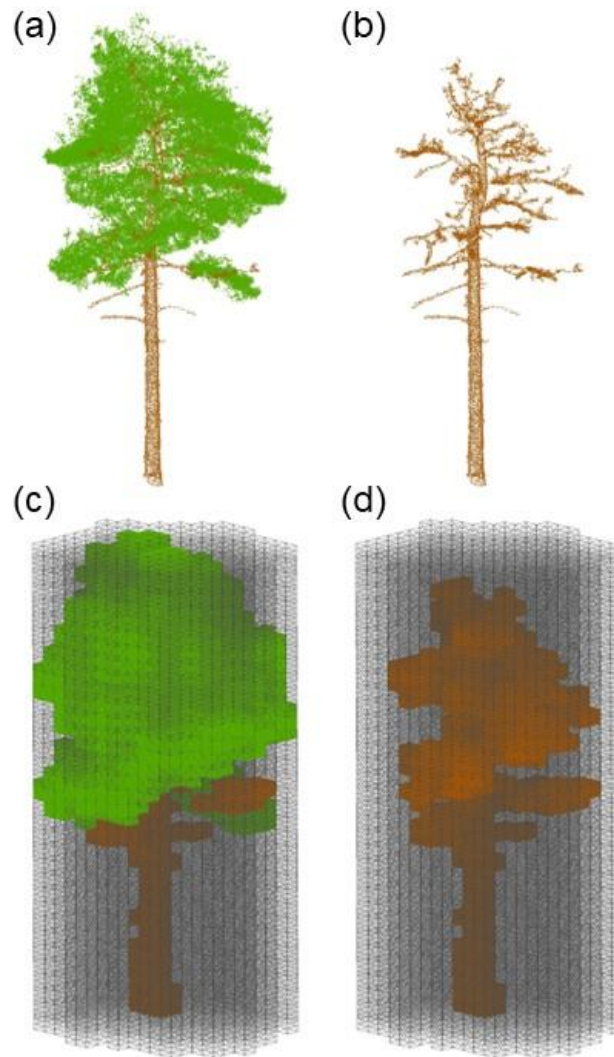
194 To calculate PAI using the *2D Intensity Image* method (Zheng et al., 2013), we converted 3D TLS point cloud
195 data from all 528 scan locations into polar coordinates, scaled intensity values to cover the full 0-255 range (Figure
196 1c) and rasterised into a 2D intensity image using the open-source *R* package, *raster* (Hijmans, 2022). We cut the
197 2D intensity image to a 5° band around the hinge angle ($55^\circ - 60^\circ$) and classified sky and vegetation pixels in each
198 image using the Ridler and Calvard method (1978). We calculated P_{gap} as the number of pixels classified as sky
199 divided by the total number of pixels and derived PAI with an inverse Beer-Lambert law equation (Monsi and
200 Saeki, 1953).

201 Following the same approach as applied to our DHP data, we calculated whole plot PAI for the *LiDAR Pulse* and
202 *2D Intensity Image* methods as the arithmetic mean of the 16 plot scan location PAI estimates.

203 To calculate PAI using the *Voxel-Based* method, we followed a voxel classification approach (Hosoi and Omasa,
204 2006), downsampling the point cloud to 0.05 m to aid computation time and matching the voxel size to the
205 resolution of the point cloud, following Li et al. (2016), who showed that matching the voxel size to the point
206 cloud point to point minimum distance (resolution) increases accuracy as small canopy gaps are not included in
207 voxels classified as vegetation. We chose to use a voxel classification approach (rather than a radiative transfer
208 based one) as this method is widely applicable to a range of TLS systems and levels of processing, as well as
209 providing explicit guidance on voxel size selection, which is known to impact derived PAI estimates (Li et al.,
210 2016). We re-combined individually segmented trees, filtered for noise using a height-dependent statistical filter
211 (see Owen et al., 2021) back into whole plot point clouds and voxelised them using the open source *R* package,
212 *VoxR* (Lecigne et al., 2018), with a full grid covering the minimum to maximum XYZ ranges of the plot. We

213 classified any voxel containing > 0 points as vegetation (“filled”), and empty voxels as gaps. We then split the
 214 voxelised point cloud vertically into slices one voxel high. Within each slice, the contact frequency is calculated
 215 as the fraction of filled to total number of voxels. We then multiplied the contact frequency by a correction factor
 216 for leaf inclination, set at 1.1 (Li et al., 2017), and whole plot PAI was calculated as the sum of all slices’ contact
 217 frequencies.

218 **2.5 Calculation of individual tree PAI, WAI and α using the voxel-based method**



219 **Figure 2: Visualisation of the workflow for applying the Voxel-Based method to estimate individual-tree PAI, WAI and**
 220 **α . (a) Individual tree point cloud; (b) separated leaf off (wood) individual tree point cloud; (c) voxelised individual tree**
 221 **point cloud; (d) voxelised wood cloud. Coloured voxels (green represents leaf and brown represents wood) are filled**
 222 **voxels and grey lines are empty voxels. Empty voxels occupy the space within the projected crown area of the tree.**
 223 **Image shows schematic of point cloud voxelised with cube voxels with edge length of 0.5 m. Panels (a) and (b) show**
 224 **wood and leaf separation of an example *P. sylvestris*, carried out using *TLSeparation* (Vicari et al., 2019). Point cloud**
 225 **voxelisation was carried out using modified functions from R package *VoxR* (Lecigne et al., 2018). Note that our method**
 226 **used voxel sizes at the resolution of the cloud (0.05 em), but here we present an image with larger voxels to ease visual**
 227 **interpretation.**

228 As the only method using multiple co-registered scans, the *Voxel-Based* method is only method compared in this
 229 study capable of deriving PAI, WAI and LAI of segmented individual tree point clouds. We estimated PAI and
 230 WAI for 2472 individual trees segmented from co-registered point clouds following a similar method to the whole

231 plot point cloud. We used individual tree point clouds downsampled to 0.05 m, to aid computation time, and
232 segmented using the automated tree segmentation program *treeseq* (Burt et al., 2019), implemented in C++, by
233 Owen et al., (2021) for that study. Individual segmented tree data used in this study are freely available (see Owen
234 et al., 2022).

235 To estimate PAI, WAI and α for each tree, we used individual tree point clouds wood – leaf separated by Owen
236 et al., (2021) using the open source Python library *TLSeparation* (Vicari et al., 2019), and then used the separated
237 wood point clouds to calculate WAI. *TLSeparation* assigns points as either leaf or wood, iteratively looking at a
238 predetermined number of nearest neighbours (*knn*). The *knn* of each iteration is directly dependent on point cloud
239 density, since high density point clouds will require higher a *knn* (Vicari et al., 2019). The utility package in
240 *TLSeparation* was used to automatically detect the optimum *knn* for each tree point cloud.

241 To voxelise individual tree complete (Figure 2a) and wood only (Figure 2b) point clouds, we used a modified
242 approach based on Lecigne et al., (2018), voxelising within the projected crown area of the whole tree point cloud
243 (Figure 2c) to calculate PAI. In the same way as for PAI, we calculated WAI using the separated wood point cloud
244 within the projected crown area of the whole tree (Figure 2d; using the whole crown and not just the wood point
245 cloud), and derived α for each tree as WAI/PAI , allowing a comparison with existing literature estimating α for a
246 range of ecosystems, (Sea et al., 2011; Woodgate et al., 2016).

247 2.6 Statistical Analyses

248 We tested the relationships between PAI_{TLS} and PAI_{DHP} estimates using Standardised Major Axis (SMA) using
249 the open source *R* (R Core Team, 2020) package, *smatr* (Warton et al., 2012). SMA is an approach to estimating
250 a line of best fit where we are not able to predict one variable from another (Warton et al., 2006); we chose SMA
251 because we do not have a ‘true’ validation dataset, so avoid assuming either DHP or any of the TLS methods
252 produces the most accurate results. For each TLS method, we assessed the relationship with DHP using the
253 coefficient of determination and RMSE. We chose to compare PAI values rather than WAI or LAI as to do so
254 would mean an additional correction for non-photosynthetic elements, which each method does in different ways,
255 so introducing further source of uncertainty and limiting our ability to fairly compare processing approaches. To
256 further understand observed drivers of variance in PAI, we tested the relationship between PAI and whole plot
257 crown area index, CAI, a proxy measure of stand density and local competition (Caspersen et al., 2011; Coomes
258 et al., 2012). We calculated CAI as the sum of TLS-derived projected crown area, divided by the plot area (Owen
259 et al., 2021).

260

261 To test if α differs by species, we used linear mixed models (LMMs) in the *R* package, *lme4* (Bates et al., 2015).
262 We included an intercept only random plot effect to account for local effects on α :

263

$$264 \alpha_{i,sj} = \varphi\alpha_s + Plot_j, \quad (1)$$

265

266 here, α_i is α of an individual of species s , in plot j , and $\varphi\alpha_s$ is the parameter to be fit. To test the effect of stand
 267 structure and tree height on α , we fit relationships separately for each species, again including a random plot
 268 effect:

269

$$270 \quad \alpha_{i,sj} = \varphi\alpha_s + b_s H_i + c_s CAI_j + Plot_{sj}. \quad (2)$$

271

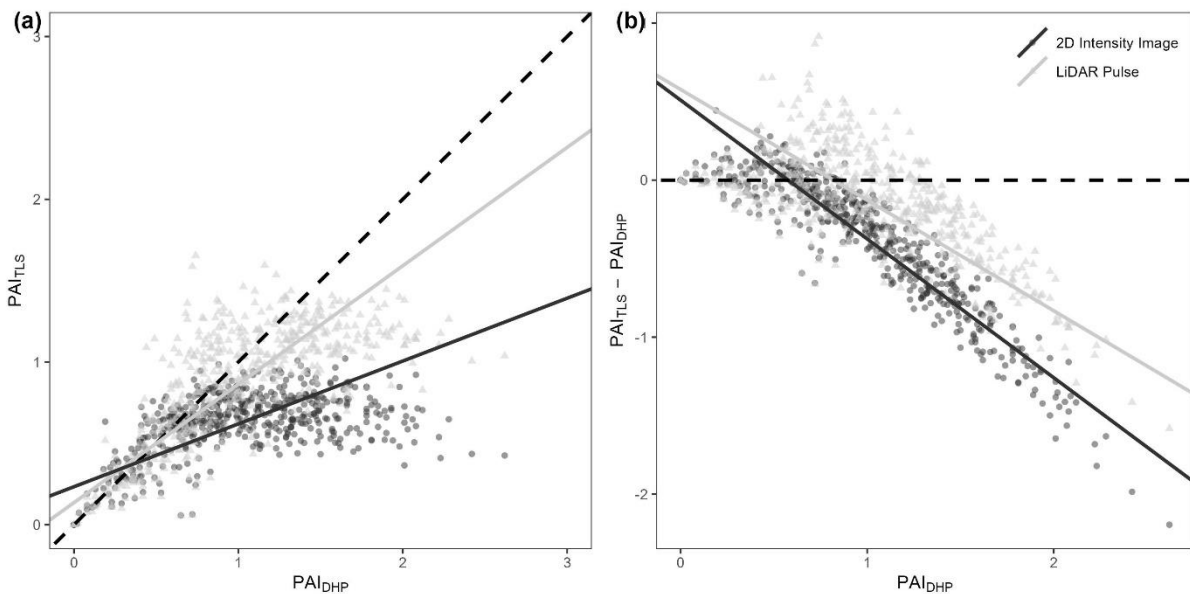
272 here H_i is the height of the tree, CAI_j is the crown area index for the plot, with other parameters as before.

273 For each species' model (equation 2), we calculated the intra-class correlation coefficient (ICC). The ICC, similar
 274 to coefficient of determination, quantifies the amount of variance explained by the random effect in a linear mixed
 275 model (Nakagawa et al., 2017).

276 3. Results

277 3.1 Comparison of plant area index estimated by DHP and single scan TLS

278 Of the two single scan TLS methods tested (*LiDAR Pulse* method and *2D Intensity Image* method), we found that
 279 the relationship between PAI estimated using the *LiDAR Pulse* method and PAI_{DHP} , had a higher R^2 than the *2D*
 280 *Intensity Image* method (SMA; *LiDAR Pulse* method $R^2 = 0.50$, slope = 0.73, $p < 0.001$, RMSE = 0.14, and *2D*
 281 *Intensity Image* method $R^2 = 0.22$, slope = 0.38, $p < 0.001$, RMSE = 0.39, respectively, Figure 3a). At larger PAI
 282 values, both TLS methods underestimated PAI relative to DHP (Figure 3b). We found statistically significant
 283 negative correlations between residuals and DHP for both methods (SMA; *2D Intensity Image* method residuals
 284 $R^2 = 0.85$, slope = -0.88 , $p < 0.01$; *LiDAR Pulse* method residuals $R^2 = 0.47$, slope = -0.70 , $p < 0.01$; Figure 3b).
 285 The *2D Intensity Image* method showed larger underestimation at higher PAI_{DHP} values, suggesting this method
 286 may saturate sooner for higher PAI values than either DHP or the *LiDAR Pulse* method (Figure 3b).



287

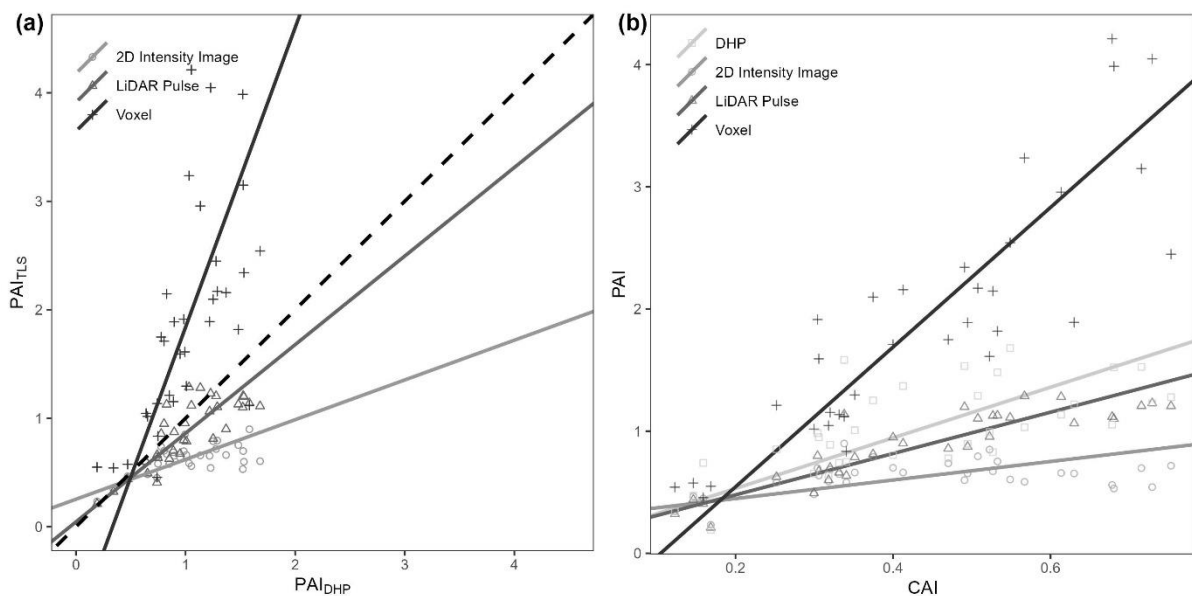
288 **Figure 3: Comparison of single scan PAI_{TLS} and PAI_{DHP} estimates, for all 528 scan locations (16 per plot). (a) The**
 289 **correlation between DHP derived PAI with PAI derived using the 2D Intensity Image method $R^2 = 0.22$, slope = 0.38,**
 290 **$p < 0.001$, RMSE = 0.39 (circles), and LiDAR Pulse method $R^2 = 0.50$, slope = 0.73, $p < 0.001$, RMSE = 0.14 (triangles).**
 291 **Dashed line in panel (a) represents 1:1 relationship. (b) The difference between PAI_{TLS} and PAI_{DHP} estimates for the**
 292 **2D Intensity Image method, and LiDAR Pulse method. Dashed line in panel (b) represents 0. Solid lines show**
 293 **statistically significant relationships fitted using SMA ($p < 0.01$).**

294 3.2 Comparison of whole plot plant area index estimated using TLS and DHP and the effect of plot structure 295 on PAI

296 We found statistically significant correlations between whole plot PAI_{TLS} values and PAI_{DHP} for all three TLS
 297 methods (Figure 4). As for single scans, the *LiDAR Pulse* method showed the closest agreement to PAI_{DHP}, here
 298 compared to both the *Voxel-Based* and *2D Intensity Image* methods (SMA; *LiDAR Pulse* method $R^2 = 0.66$, slope
 299 = 0.82, $p < 0.01$, RMSE = 0.14; *Voxel-Based* method $R^2 = 0.39$, slope = 2.76, $p < 0.01$, RMSE = 0.88; *2D Intensity*
 300 *Image* method $R^2 = 0.35$, slope = 0.36, $p < 0.01$, RMSE = 0.39, respectively; Figure 4a). The *2D Intensity Image*
 301 method and *LiDAR Pulse* method consistently underestimated PAI compared to DHP, whilst the *Voxel-Based*
 302 method underestimated in plots with lower PAI_{DHP} and overestimated in plots with higher PAI_{DHP}. The *Voxel-*
 303 *Based* method's high PAI values compared to other methods is likely due to its use of multiple co-registered scans
 304 reducing occlusion effects prevalent in single scan data.

305 To assess the effect of plot structure on variation in TLS derived PAI, we compared PAI_{TLS} estimates to ~~TLS~~
 306 ~~estimated crown area index (CAI, m² projected crown area per m² ground area, CAI~~ (Figure 4b). We found a
 307 significant positive relationship between CAI and PAI estimated using each of the *LiDAR Pulse* method, the
 308 *Voxel-Based* method, and DHP (SMA; *LiDAR Pulse* method $R^2 = 0.79$, slope = 1.69, $p < 0.01$; *Voxel-Based*
 309 method $R^2 = 0.76$, slope = 5.72, $p < 0.01$; *2D Intensity Image* method $R^2 = 0.15$, slope = 0.76, $p < 0.05$; DHP R^2
 310 = 0.46, slope = 2.07, $p < 0.01$, respectively; Figure 4b), where the *2D Intensity Image* method shows signs of
 311 saturation at medium CAI values (Figure 4b).

312

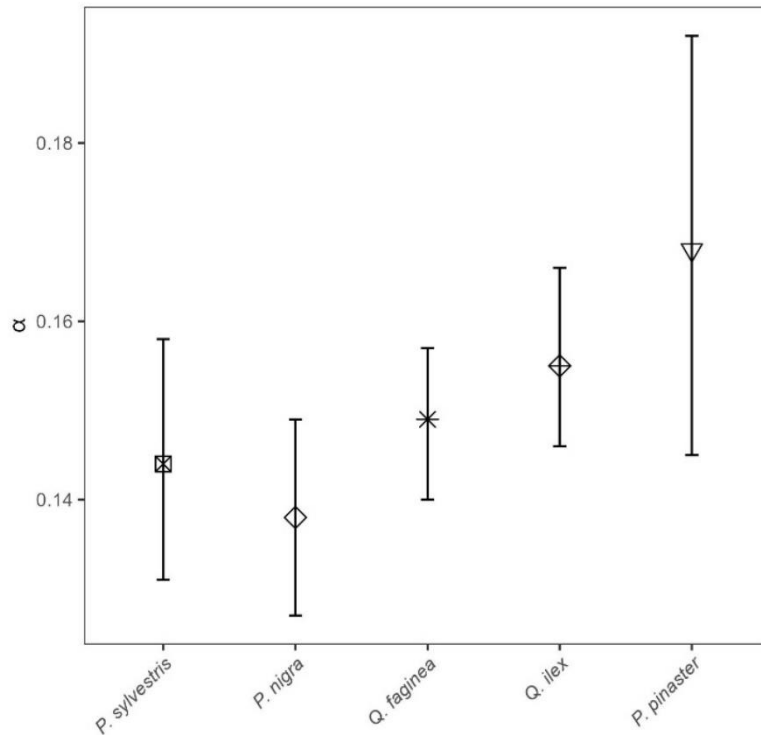


313 **Figure 4: Comparison of plot level PAI_{TLS} vs PAI_{DHP}, and CAI vs PAI estimates for all 33 plots. (a) The correlation**
 314 **between DHP derived PAI and PAI derived using 2D Intensity Image $R^2 = 0.35$, slope = 0.36, $p < 0.01$, RMSE = 0.39**

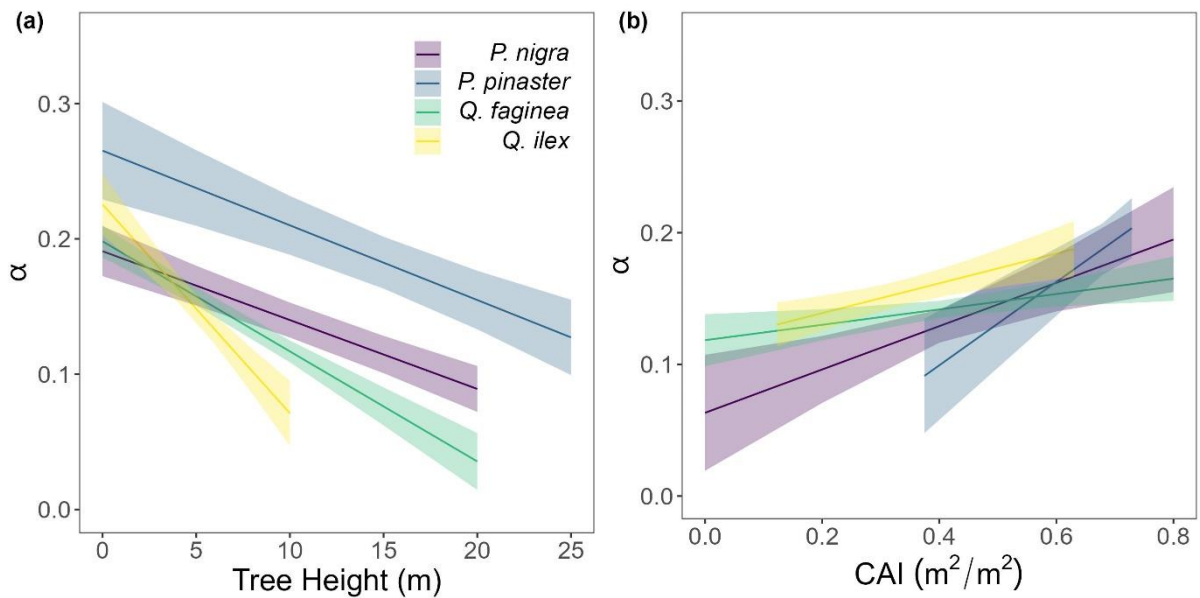
315 (circle), LiDAR Pulse $R^2 = 0.66$, slope = 0.82, $p < 0.01$, RMSE = 0.14 (triangle) and Voxel-Based $R^2 = 0.39$, slope = 2.76,
316 $p < 0.01$, RMSE = 0.88 (cross) methods (b) The correlation between TLS derived CAI and PAI derived using DHP R^2
317 = 0.46, slope = 2.07, $p < 0.01$ (square), 2D Intensity Image $R^2 = 0.15$, slope = 0.76, $p < 0.05$ (circle) LiDAR Pulse $R^2 =$
318 0.79, slope = 1.69, $p < 0.01$ (triangle) and Voxel-Based $R^2 = 0.76$, slope = 5.72, $p < 0.01$ (cross) methods. Lines show
319 statistically significant relationships fitted using SMA ($p < 0.01$). Dashed line in panel (a) represents 1:1 relationship.

320 3.4 Influence of species, tree height and CAI on α

321 To understand drivers of variance in α , we used individual tree PAI and WAI, calculated using the *Voxel-Based*
322 method to test the relationship between species and α , and height/ CAI and α . We found that more drought tolerant
323 species generally had higher α values than less drought tolerant species (Table B1; Figure 5), however, confidence
324 intervals were wide and overlapping, suggesting that species is not a strong predictor of variation in α . We found
325 a statistically significant negative effect of height ($p < 0.001$; Table B2; Figure 6a) and positive effect of CAI (p
326 $< 0.01 - 0.05$; Table B2; Figure 6b) on α for all species apart from *P. sylvestris*. α decreased more rapidly with
327 height and increased less rapidly with CAI for oaks than pines. Statistically significant ICC values were higher
328 for *P. nigra* (ICC = 0.211; Table B2) than *P. pinaster*, *Q. faginea* and *Q. ilex* (ICC = 0.036; 0.060; 0.070,
329 respectively), showing that more α variation is explained by the random plot effect in *P. nigra* than the other
330 species. *P. pinaster* has a wider confidence interval (Figure 5), possibly explained by its lower sample size. To
331 understand drivers of variance in WAI we carried out additional analysis to test the relationship between WAI
332 and species, height, CAI, and PAI, and presented these results in Appendix C (Figure C3; Tables C3, C4).



333 Figure 5: Linear mixed model derived α values (Eq. 1) for all 2472 individual trees of species *P. sylvestris*, *P.*
 334 *nigra*, *Q. faginea*, *Q. ilex* and *P. pinaster*. Error bars represent 95% confidence intervals. Species are listed left to right
 335 from low – high drought tolerance, with the exception of *P. pinaster*, for which drought tolerance index has not been
 336 calculated in the literature. Drought tolerance rankings are taken from Nünemets and Valladares, (2006).



337 Figure 6: Variation in α for each species: *Pinus nigra*, *P. pinaster*, *Q. faginea* and *Q. ilex* with (a) height and (b) plot
 338 CAI. Lines represent statistically significant linear mixed models (equation 2; significance levels from $p < 0.001$ to $p <$
 339 0.05). Ribbons represent 95% confidence intervals. The model for *P. sylvestris* was not statistically significant.

340
 341
 342

343 4. Discussion

344 4.1 Comparison of approaches to deriving PAI from remote sensed data

345 We found substantial differences in PAI values estimated from TLS and DHP and from different TLS processing
346 methods (Figures 3 and 4). Further, differences between TLS methods varied across plot structure ~~(CAI)~~, with the
347 greatest differences between methods in plots with high CAI, and therefore high canopy density. Although
348 previous studies have presented TLS as an improvement over DHP due to its independence of illumination and
349 sky conditions during the data acquisition phase, and ability to resolve fine-scale canopy elements and gaps
350 (Calders et al., 2018; Grotti et al., 2020; Zhu et al., 2018), we have shown that there is large variability between
351 TLS processing methods in Mediterranean forests. Rigorous intercomparison of approaches, ideally using
352 standard benchmarking TLS datasets, and destructive sampling, would improve trust and reliability of TLS
353 algorithms.

354 We found the *LiDAR Pulse* method (Jupp et al., 2008) to have the best agreement with DHP for both whole plot
355 and single scan PAI estimates. In contrast to previous studies comparing PAI_{TLS} with PAI_{DHP} (Calders et al.,
356 2018; Grotti et al., 2020; Woodgate et al., 2015), we found that the *LiDAR Pulse* and *2D Intensity Image* methods
357 underestimated PAI compared to DHP, except at very low PAI values ($PAI_{TLS} < 0.5$). Quantification of PAI from
358 DHP may introduce additional sources of error, for example, its relatively lower resolution compared to TLS
359 could lead to mixed pixels that have a greater chance of misclassification of sky as vegetation (Jonckheere et al.,
360 2004). This effect could be enhanced in a Mediterranean forest as trees in drier climates tend to have smaller
361 leaves (Peppe et al., 2011), leading to more small canopy gaps that TLS may resolve where DHP cannot. Further,
362 although we took steps to reduce the error introduced at DHP data acquisition and processing steps, including
363 using automatic thresholding and collecting images with multiple exposures, DHP processing requires both model
364 and user assumptions that can impact results. For example, PAI_{DHP} estimates are highly sensitive to camera
365 exposure; increasing one stop of exposure can result in 3 – 28% difference in PAI and use of automatic exposure
366 can result in up to 70% error (Zhang et al., 2005).

367 We found the *Voxel-Based* method overestimated PAI values compared to the other methods at the whole plot
368 level. This is likely due to the method's use of co-registered scans, rather than averaged single scan PAI values,
369 since co-registered scans will reduce occlusion effects prevalent in single scan data that could lead to an
370 underestimation of PAI (Wilkes et al., 2017). The *Voxel-Based* method is, however, sensitive to voxel size (Li et
371 al., 2016), and larger voxels lead to larger PAI estimates as they ~~are unable to capture all of the intricate details of~~
372 ~~canopy structure-fill small canopy gaps~~; we chose a voxel size of 0.05 m to match the minimum distance between
373 points in our downsampled dataset. However, the *Voxel-Based* method is a memory intensive approach to
374 calculating PAI, and smaller voxels have higher memory requirements. We picked this data resolution, and
375 therefore voxel size, to balance the need to capture fine-scale canopy details against memory requirements for
376 running the method on many large plot point clouds. Voxel size could have been chosen based on estimates'
377 match to DHP, but this would assume (1) that DHP estimates are most accurate, and (2) that DHP data are always
378 available, limiting the wider applicability of our findings. Understanding which method is over- or
379 underestimating would require a destructively sampled dataset for validation, which was not possible for this
380 study (or most ecosystems). However, other studies using voxel approaches have found that although these
381 produce high LAI values for individual trees, these are underestimates compared with destructive samples (Li et

382 al., 2016). Regardless, PAI and LAI estimates using a *Voxel-Based* approach are highly dependent on voxel size
383 (Li et al., 2016), and future work should test the influence of voxel size on PAI estimates, using destructive
384 samples in a range of environments.

385 The relationship between the *LiDAR Pulse* method and TLS derived CAI had the highest R^2 , demonstrating that
386 the method is well suited to measuring PAI across the range of plot CAI values used in this study. Although the
387 *2D Intensity Image* method can tackle the significant challenges presented by edge effects and partial beam
388 interceptions, particularly present in phase-shift systems (Grotti et al., 2020), our results suggest this method has
389 a lower performance ability, with saturation occurring sooner than all other methods in dense forests (Figures 3
390 and 4). The *2D Intensity Image* method uses the same raw single scan data as the *LiDAR Pulse* method, so the
391 better performance from the latter is likely due to the method's use of vertically resolved gap fraction; both the
392 *LiDAR Pulse* method and *Voxel-Based* method account for the vertical structure of the canopy by summing
393 vertical slices through the canopy.

394 **4.2 α variation between species and plot**

395 We used the *Voxel-Based* method to investigate individual tree α variation between species and across structure,
396 as this was the only approach we compared that could be applied to single tree point clouds which are leaf-wood
397 separated. We found α values obtained were within the range of values obtained from destructive approaches (0.1
398 – 0.6, Gower et al., 1997). The drought and shade intolerant *P. nigra* showed stronger variability in α across plots
399 (higher ICC value, Table B2) than other species, suggesting its wood – leaf ratio may be more sensitive to site
400 factors. However, as the plots measured in this study vary in both abiotic conditions (altitude, aspect, slope,
401 wetness) as well as species composition, stem density and canopy cover, there may be other drivers of variation
402 in α values.

403 We found some evidence that species with higher drought tolerance had higher α values (Figure 5; Table B1),
404 however, confidence intervals were wide, suggesting a weak relationship. There is evidence that trees that tolerate
405 water limited environments have a lower leaf area (Battaglia et al., 1998; Mencuccini and Grace, 1995), so higher
406 α values may reflect maintenance of homeostasis of leaf water use through adjustment of wood to leaf area ratio
407 (Carter and White, 2009; Gazal et al., 2006). The potential for a tree to lose water is mostly regulated through leaf
408 traits including stomatal conductance and leaf area, and both stand (Battaglia et al., 1998; Specht and Specht,
409 1989) and individual tree (Mencuccini, 2003) water use have been found to scale linearly with LAI, with drought
410 often mitigated through leaf shedding (López et al., 2021).

411 **4.3 Tree stature and stand density drives α variation**

412 Although species had a weak relationship with α , tree height and plot CAI had a statistically significant
413 relationship with α ($p < 0.001$ – $p < 0.05$) for all species, showing the importance of local stand structure on leaf
414 and woody allocation. We found that α scaled negatively with height for all species apart from *P. sylvestris*,
415 suggesting that in this environment, taller trees generally have a lower proportion of wood to plant area index than
416 shorter ones. *P. sylvestris*, which is at the edge of its geographical range and physiological limits (Castro-Díez et
417 al., 1997; Owen et al., 2021), showed no significant relationship between height and α . We found that α scaled
418 positively with plot level CAI for all species apart from *P. sylvestris*, that is, trees growing in denser plots have a
419 higher α . This supports theory that trees growing in dense forests are competing for resources, reducing individual

420 tree leaf area (Jump et al., 2017). The negative relationships between height and α and positive relationships
421 between CAI and α relationships in our model suggest that trees may initially invest in vertical growth to reach
422 the canopy level, and once there invest in lateral growth, with more leaf area, to increase light capture. This
423 supports theory that trees grow to outcompete neighbouring individuals for light capture (Purves and Pacala, 2008)
424 and evidence that both lateral growth and LAI are reduced beneath closed canopies (Beaudet and Messier, 1998;
425 Canham, 1988).

426 Wood may be harder to accurately classify than leaves in TLS data (Vicari et al., 2019), resulting in a higher
427 occurrence of false positives in wood clouds, potentially leading to an overestimation in WAI, and therefore
428 underestimation of α , especially in trees with small leaves which are prevalent in dry, Mediterranean environments
429 (Peppe et al., 2011). The problem of misclassification will increase in taller trees due to TLS beam divergence,
430 occlusion and larger beam footprint at further distances (Vicari et al., 2019), suggesting that WAI overestimation
431 could be more pronounced in tall trees. Although our dense scanning strategy (Owen et al., 2021) was designed
432 to mitigate some of these effects, these effects mean our findings may underestimate the slope of the negative
433 relationship between α and tree height. Conversely, the increasing leaf-to-wood ratio could potentially be
434 explained by a greater number of empty voxels caused by occlusion in large trees. However, we took significant
435 steps to reduce occlusion, employing a 10 m scanning strategy that was developed in a dense tropical forest
436 (Wilkes et al., 2017).

437 **4.4 Correcting for non-photosynthetic elements in LAI estimates using TLS**

438 The value of TLS data to estimate individual tree PAI, WAI and subsequently α , demonstrates their potential to
439 corrective factors for non-photosynthetic components in ground based remote sensing measurements of LAI.
440 Properly correcting for WAI in LAI estimates is of global importance as small errors in ground based
441 measurements propagate through to large scale satellite observations generating large errors in global vegetation
442 models (Calders et al., 2018). The work presented here provides a foundation for future work combining multi-
443 source and multi-scale remote sensing datasets to correct largescale LAI products. Our results echo others' in
444 finding that the prevalence of woody material in the tree canopy, and therefore α , is dynamic and varies by species
445 as well as senescence, crown health and, in the case of deciduous forests, leaf phenology (Gower et al., 1999).
446 The use of single α value in a plot or region (Olivas et al., 2013; Woodgate et al., 2016), invariant of species, size
447 and forest structure, to convert PAI to LAI is therefore problematic (Niu et al., 2021). Our study demonstrates the
448 importance of taking species mix and structural variation into account when correcting for non-photosynthetic
449 material in ground-based LAI estimates.

450 **5. Conclusions**

451 We tested three methods for estimating PAI using Terrestrial Laser Scanning data and compared these against
452 traditional DHP measurements. We found large variation between PAI values estimated from each TLS method
453 and DHP, demonstrating that care should be taken when deriving PAI from ground based remote sensing methods.
454 Although the *LiDAR Pulse* method was found to have the best agreement with both single scan and whole plot
455 PAI values measured by DHP, the *Voxel-Based* method allowed separate analysis of the key metric used to correct
456 for the effect of WAI in LAI measurements, α , in individual trees. We recommend the *LiDAR Pulse* method as a
457 fast and effective method for PAI estimation independent of illumination conditions. Whilst the *Voxel-Based*

458 method may be used to analyse individual tree α and determine ecological drivers of variation, work remains to
459 determine the validity of these approaches, in particular correct voxel size choice. We found that α varies by
460 species, height and stand density, showing the importance of accurately correcting for WAI on the individual tree
461 level and the utility of TLS to do so.

462 The variation in our results for the different methods used to derive PAI from TLS data show that there is some
463 way to go before TLS derived vegetation indices can be interpreted as robust and reliable. Validation using
464 destructive samples and further intercomparison studies of methods are needed to demonstrate the advantages of
465 TLS, and use of benchmarking datasets should be standard. DHP is a faster, cheaper and more widely accessible
466 method for PAI estimation, and while TLS promises to alleviate potential bias in DHP estimates, results are highly
467 methods dependent. Our results demonstrate the challenges that stand in the way of large scale adoption of TLS
468 for vegetation indices monitoring.

469 **6. Code availability**

470 See https://github.com/will-flynn/tls_dhp_pai.git for all processing and modelling code.

471 **7. Data availability**

472 See Owen et al.; (2022) for individual segmented tree data and Flynn et al.; (2023) for thresholded DHP images.

473 **8. Author contribution**

474 All authors designed the study. HJFO and WRMF collected and processed TLS and DHP data; WRMF performed
475 formal analysis with guidance from all authors. WRMF led the writing with input from all authors. All authors
476 contributed critically to drafts and gave final approval for publication.

477 **9. Competing interests**

478 The authors declare that they have no conflict of interest.

479 **7. Acknowledgements**

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