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A double-digitising method for building 3D virtual trees with non-planar leaves: application to the morphology and light-capture properties of young beech trees (*Fagus sylvatica*)

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4 (*Fagus sylvatica*).

5

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16

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21 **Abstract**

22 We developed a double-digitizing method combining a hand-held electromagnetic digitizer
23 and a non-contact three-dimensional (3D) laser scanner. The former was used to record the
24 positions of all leaves in a tree and orientation angles of their lamina. The latter served to
25 obtain the morphology of leaves sampled in the tree. As the scanner outputs a cloud of points,
26 software was developed to reconstruct non-planar (NP) leaves composed of triangles, and to
27 compute numerical shape parameters: midrib curvature, torsion and transversal curvature of
28 the lamina. Combination of both methods allowed building 3D virtual trees with NP leaves.
29 The method was applied to young beech trees (*Fagus sylvatica*) selected in different sunlight
30 environments (from 1 to 100% of incident light) in forest of central France. Leaf morphology
31 responded to light availability, with more bent shape in well lit leaves. Light interception at
32 the leaf scale by NP leaves was decreased from 4 to 10%, for shaded and sunlit leaves
33 compared to planar leaves. At the tree scale, light interception by trees made of NP leaves was
34 decreased by 1 to 3% for 100% to 1% light, respectively.

35

36 **Keywords:** Virtual plants, laser scanner, electromagnetic digitizing

37 **Introduction**

38 Most trees have a strong ability for structural modification in response to light availability. At
39 the plant scale, leaf distribution has been reported to be more regular and more clumped in
40 shaded and sunny environments, respectively (Planchais and Sinoquet 1998; Farque *et al.*
41 2001). Leaf attributes may also change, e.g. inclination and rolling angles of the whole lamina
42 show significant changes with regard to irradiance level (Begg 1980; Niklas and Owens 1989;
43 Heckathorn and DeLucia 1991; Midgley *et al.* 1992; Planchais and Sinoquet 1998). For
44 example, in a recent study on *Fagus sylvatica* data showed that leaf number, mean leaf angle
45 and leaf dry matter content per unit area increased with light availability (Balandier *et al.*
46 2007). In addition, several species may show structural changes affecting the leaf
47 morphology, such as lamina folding or curling (Innes 1992; Muraoka *et al.* 1998; Fleck *et al.*
48 2003; Niinemets 2007). These multiple ways for changing the tree geometry has
49 consequences for the plant's ability to intercept light, and usually allows plants to maximize
50 light capture in low light and protect themselves against photo inhibition of photosynthesis in
51 excess light (Percy *et al.* 2005).

52 Three-dimensional (3D) virtual tree modelling (Prusinkiewicz and Lindenmayer 1990; Weber
53 and Penn 1995; Lintermann and Deussen 1998, Godin and Sinoquet 2005) has become a
54 promising tool for quantifying structural responses in relation with both the geometry and the
55 spatial distribution of the tree organs. In combination with radiation transfer models or foliage
56 projection model, the quantification of light interception at tree scale has been widely
57 addressed using virtual tree mock-ups constructed from measurements (e.g. Sinoquet and
58 Rivet 1997, Sinoquet *et al.* 1998, Sonohat *et al.* 2006). Measurements are presently
59 considered to be the most accurate approach to quantitatively represent the 3D tree
60 architecture, because the actual features of tree geometry are taken into account. These
61 processes are typically composed of two steps: an acquisition step consisting of capturing the

62 geometrical features of the tree organs using a suitable digitizing device (e.g. Hanan and
63 Room 2002), and a reconstruction step in which the resulting data are converted to a suitable
64 3D computer mock-up.

65 Hand-held electromagnetic digitizers (HHEMD) provide a robust way for quantifying the tree
66 geometry in a systematic manner especially the capture of the spatial position and orientation
67 of stems and leaves (Sinoquet and Rivet 1997; Sinoquet *et al.* 1998; Sonohat *et al.* 2006).
68 However, HHEMD are tedious, time-consuming and often not enough precise for accurately
69 capture the detailed leaf geometry, e.g. measuring the leaf edges (see Rakocevic *et al.* 2000
70 for white clover digitizing). This is the reason why most plant mock-ups constructed from
71 HHEMD do not integrate the non-planar (NP) leaf structure. Indeed leaf shape is often
72 reduced to planar polygons, *de facto* neglecting a potential influence of leaf curvature or leaf
73 torsion on the whole-plant light interception.

74 Conversely, other emerging 3D capture devices such as non-contact laser scan digitizers
75 (NCLSD) have been used for various plant measurement and reconstruction (e.g. Tanaka *et*
76 *al.* 1998; Kaminuma 2004; Rice *et al.* 2005; Dornbusch *et al.* 2007). Indeed, NCLSD are able
77 to rapidly quantify the surface of an object under investigation as a dense set of points and
78 consequently they seem potentially useful for modelling 3D virtual trees at a fine scale. A
79 drawback of this type of device is that organs that are overlaid are not "viewed" by the
80 scanner, e.g. a twig under a leaf, and thus not considered. Other drawback is the segmentation
81 task which is needed to clearly distinguish subsets of points related to the plant organs such as
82 leaves and stems. In practice automatic segmentation remains an open problem due to holes,
83 spikes, hidden parts, and data points that do not belong to the scanned tree (Hanan *et al.*
84 2004). Therefore the segmentation task must in most cases be manually achieved (Dornbusch
85 *et al.* 2007) through numerous fastidious interactive manipulations.

86 The present work was an attempt to combine the advantages of HHEMD and NCLSD for
87 building 3D virtual trees composed by NP leaves. In this goal, a four-step reconstruction
88 protocol was investigated: i) a 3Space Fastrack Polhemus HHEMD (www.polhemus.com)
89 was used to describe the location and orientation of all leaves in the tree, and the maximum
90 width and length of each leaf was manually measured with a ruler; ii) a Konica VIVID 910
91 NCLSD (www.konicaminolta.com) was used for capturing the geometry of a sample of
92 leaves leading for each digitized leaf to a dense set of 3D points; iii) each set of leaf points
93 was processed to extract numerical parameters featuring the leaf 3D morphology, and derive a
94 normalized triangulated leaf model by fitting a set of triangles onto the 3D leaf data points; iv)
95 the HHEMD data were combined with the triangulated leaves in order to get 3D tree mock-
96 ups with NP leaves. This framework was applied on young European beech trees (*Fagus*
97 *sylvatica*) selected in different sunlight environments in forest in central France, in order to
98 investigate how morphological leaf parameters change with light availability and the
99 consequences on light capture ability.

100

101 **Material and methods**

102 *Tree selection in a light gradient*

103 Eleven young beech trees were selected in the Chaîne des Puys, a mid-elevation volcanic
104 mountain range situated in the Auvergne region of France (45°42' N, 2°58' E). All trees
105 except one were located in a forest dominated by *Pinus sylvestris*. Light availability for each
106 sapling was estimated as follows. A digital fisheye camera fixed in a self-levelling device was
107 positioned just above the sapling, with the camera objective perpendicular to the soil surface.
108 The camera was connected to a PC for real-time photograph segmentation into sky and
109 vegetation pixels, and for analysis of light availability in percent of above canopy value
110 (%light) with software PiafPhotem (Adam *et al.* 2006). The trees were chosen in the range of

111 %light between 1 and 100%, i.e. from the limit of beech growth in the very shade to open
112 area. Trees were separated in four light classes (Table 1). Beech height ranged between 0.4
113 and 1.1 m, and included between 110 and 3400 leaves.

114

115 *Tree mock-up reconstruction process*

116 We only considered leaves in this study. While petioles and branches participate to the
117 modification of canopy architecture and thus, indirectly, to light interception, leaf distribution
118 in space takes into account these features and the time for digitizing the tree (see below) is
119 accordingly reduced. A four-step 3D tree mock-up reconstruction method was developed.
120 First, the HHEMD was used to measure all leaf positions and orientation angles of each tree,
121 and the maximum width and length of each leaf was manually measured with ruler. This step
122 was realised in a non-destructive manner, by digitalizing and measuring the trees directly in
123 their natural environment. Second, 3D laser scans of nine individual leaves per tree (three
124 leaves in each of the lower, middle and upper part of the tree) were produced with the
125 NCLSD. The scans were realised on freshly harvested leaves which were transported (in
126 about one hour of travel) in plastic bag from the Chaîne des Puys to a scanning lab. Third,
127 each set of 3D scanner leaf points was computer processed to extract leaf shape parameters
128 and to produce a normalized triangulated leaf model. Fourth, the triangulated leaf models
129 were positioned in the tree structure according to leaf positions, orientations and dimensions
130 measured in step one.

131

132 *HHEMD for capturing leaf position and orientation (first step)*

133 A 3Space Fastrack Polhemus HHEMD (www.polhemus.com) was used to digitize all leaves
134 in each selected tree. This device is composed of a transmitter and a receiver connected to a

135 central unit. Both the transmitter and receiver contain a triad of electromagnetic coils. Those
136 in the transmitter are supplied with alternating voltage, so that they emit alternating magnetic
137 fields. When located in the magnetic fields, coils in the receiver show induced currents, the
138 value of them is related to the location and orientation of the receiver with regard to the
139 transmitter (Polhemus Inc. 1993). In practice, the transmitter must be placed near the target
140 tree for defining a global 3D Cartesian reference system (**O, X, Y, Z**). The receiver is inlayed
141 into a handle which allows an operator collecting/picking 3D points on the plant. The
142 accuracy of the device allows an approximate capture resolution of 0.8mm in a volume
143 depending on the magnetic source, here up to 3 m around the transmitter but acquisition is
144 possible up to 9 m with a more powerful transmitter. Each measurement produces 6 data,
145 namely a triplet of Cartesian coordinates locating the digitized point in the global reference
146 system, and the receiver orientation provided as Euler angle triplet i.e. azimuth, elevation and
147 roll angles. Data acquisition is driven by software PiafDigit (Donès *et al.* 2006) available at
148 <http://www2.clermont.inra.fr/piaf/eng/download/download.php> .

149 For leaf digitizing, the receiver was pointed at the proximal point of the lamina (i.e. the
150 junction between petiole and lamina) and oriented parallel to the midrib and to the mean plane
151 of the lamina (Fig. 1a). The receiver inclination was visually approximated by the leaf axis,
152 i.e. the line between the proximal and distal points of the midrib. With this orientation, the
153 Euler angles were the midrib azimuth, the midrib inclination and the roll angle of lamina
154 around the midrib (Sinoquet *et al.* 1998). During digitizing, leaf length and maximum leaf
155 width along the midrib were manually measured with a ruler, and the data were input in the
156 same software PiafDigit. The output of the HHEMD measurements was an ASCII file per
157 tree. Each file contained the list of tree leaves with their maximum width and length,
158 orientation angles and spatial coordinates. The related tree mock-ups with planar leaves were

159 visualized with the software VegeSTAR also available at
160 <http://www2.clermont.inra.fr/piaf/eng/download/download.php> (Adam *et al.* 2002) (Fig. 2a).

161

162 *NCLSD for capturing the leaf geometry (second step)*

163 A Konica Minolta VIVID 910 NCLSD (www.konicaminolta.com) was used to capture the
164 leaf geometry. This device is composed of a single parallelepiped unit presenting two circular
165 apertures hosting a laser emitting unit and a charge-coupled device (CCD) camera,
166 respectively (Fig. 1b).

167 The VIVID 910 uses a light-stripe method to acquire object geometry. This technique (Fig. 3)
168 consists of emitting a horizontal red laser ray through a cylindrical lens to the object and to
169 convert the reflected light into distance information by using an active triangulation principle.
170 The conversion is achieved through the CCD (here a 640*480 pixels) camera. The process is
171 repeated by scanning the light stripe vertically on the object surface using a rotating mirror.
172 The result is a dense set of 3D points outlining the part of the object which is visible for the
173 CCD. The VIVID 910 is provided with three interchangeable receiving lenses allowing an
174 angular field of view approximately covering 10 cm² to 1 m². The recommended scan distance
175 is between 0.6 m and 2.5 m and the scanner resolution, i.e. the distance between two digitized
176 points, varies from 0.039 mm to 0.090 mm according to the lens. An efficient embedded auto
177 focus technology allows automatically detection of the optimal scan distance for a given lens
178 and a given object. The number of digitized points varies with two resolution modes and the
179 ratio between the object size and the CCD field of view. In addition, a 24-bit colour image is
180 captured at the same time by the CCD camera. For our study, the VIVID 910 was driven from
181 the commercial software rapidform2006 (INUS Technology, Seoul, Korea). This industrial
182 software is widely used for computer-aided design issues, and provides a comprehensive suite

183 of tools designed to process real-world data, from 3D scanning devices control to parametric
184 surface reconstruction.

185 The smallest lens with the fine resolution mode (0.039 mm) was used for capturing the
186 geometry of 99 leaves, i.e. 9 leaves per beech tree. Three leaves were harvested in each of the
187 lower, middle and upper part of the tree. Each of the 99 leaves was positioned in front of the
188 VIVID so that the CCD camera viewed maximum projected area of the leaf (Fig. 1b). The
189 VIVID was levelled and the leaf axis was set vertically, i.e. parallel to the VIVID Y-axis.
190 Identification of the leaf axis in both the HHEMD and NCLSD data ensured the geometric
191 consistency between 3D data at tree and leaf scales. During our measurements, we overcame
192 segmentation problem related to the use of NCLSD since all digitised points belonged to the
193 scanned leaf. Each 3D digitized leaf included between 10,000 and 30,000 points depending on
194 leaf size. An image of the 3D data points for a digitized medium-sized leaf is given in Fig. 4a.

195 *Leaf shape parameter extraction and leaf triangulation in 3D (third step)*

196 Three-dimensional data obtained from the NCLSD for each leaf were processed for both
197 extracting a set of numerical parameters featuring the leaf morphology and for constructing a
198 non-planar triangulated model of each harvested leaf. An application programming interface
199 which allows direct access to data structures and algorithms in rapidform2006 via the
200 Microsoft Visual C++ programming language was used to develop a rapidform2006 plug-in.
201 Extracted morphological parameters were midrib length L (mm), maximum leaf width W
202 (mm), leaf area A (mm^2), midrib curvature C (mm^{-1}), openness angle between two half-
203 laminas O ($^\circ$), lamina twirl T ($^\circ$), transversal curvature angle of lamina TC ($^\circ$) and symmetry
204 between the two half-laminas S , i.e. the ratio of the left leaf half width to the total leaf width
205 along its midrib. The extraction algorithm was based on a set of slicing free form NURBS
206 curves (Piegl and Tiller 1997) equidistantly subdividing the leaf along its midrib (Fig. 4b).
207 The set of 3D points for each leaf was transformed into an oriented set of curves: one curve

208 for modelling the midrib, and n curves for modelling the transversal shape of the lamina (Fig.
209 4b). The shape parameters were then extracted from the length and the curvature of the $(n+1)$
210 curves. The mean, minimal and maximal values of the shape parameters were computed for
211 each leaf from the values of the $(n+1)$ curves. Additional parameters were computed from A ,
212 L and W , namely the ratio W/L , and the allometric coefficient K defined as the ration between
213 A and the product $L W$. One can notice the difference between the quantification of the
214 midrib curvature, expressed in mm^{-1} , and the quantification of the transversal curvatures,
215 expressed in degrees ($^{\circ}$). The former is the mathematical differential curvature of the midrib
216 curve, i.e the inverse of the radius of the osculating circle (Piegl and Tiller 1997; Fig. 5). This
217 curvature has been proved efficient for quantifying the oscillations of the midrib because of
218 its low number of curvature variations. Conversely, practical evidences showed us that the
219 differential curvature was not a good solution for measuring the curvature of the transversal
220 NURBS curves because of their high number of local variations, often leading to null or
221 enormous curvature. For this reason, we preferred to measure the transversal curvature of the
222 leaf using an angle, which can be interpreted as the aperture angle of the half laminas (Fig. 5).
223 The quantity S is a ratio of two lengths which represents the level of symmetry of the leaf
224 along its midrib. This ratio is computed for each slicing curve. It is defined as the ratio
225 between the left half-lamina width (i.e. the length of the slicing curve from the left bound of
226 the leaf until the intersection with the midrib) and the total width of the leaf (i.e. the total
227 length of the slicing curve). S varies from 0.0 for a very dissymmetric piece of leaf until 0.5
228 for a perfectly symmetric piece of leaf. Note that the "left" direction is defined by the
229 direction of the negative abscissa (X^{-}) of the coordinate system linked to the laser scanner
230 (Fig 5).

231

232 A triangulated model of each leaf composed of $8n$ triangles was also constructed from the
233 $(n+1)$ curves (Fig. 4c). The triangulated leaves were normalized so that the distance between
234 the proximal and distal point of the lamina in the leaf model was 1. Here n was set to 9,
235 leading to 72 triangles per leaf. This value is a compromise between accuracy in the NP leaf
236 description and file size. Morphological parameters were exported to Microsoft Excel files
237 while the triangulated leaves were converted in VegeSTAR format as a set of triangles for
238 further visualization and light interception computation. We verified that the leaf surface
239 covered by the digitized points was equivalent to the one given by the triangulated leaf model
240 in VegeSTAR ($R^2 = 0.98$ with a 2% error between values given by the digitized and the
241 triangulated leaves).

242

243 *Replacing the planar hexagonal leaves by non-planar triangulated leaves (fourth*
244 *step)*

245 A specific computer program was developed for replacing the planar hexagonal leaves by the
246 NP triangulated leaves in the eleven tree mock-ups built from the HHEMD. For each planar
247 leaf in the tree, a normalized triangulated leaf model was randomly selected among those
248 owning to the same layer (upper, medium or lower) in the same tree. In order to support the
249 comparison of planar leaves with NP leaves, the selected normalized triangulated leaf model
250 was then scaled, rotated and translated in the tree structure according to the geometrical
251 attributes of the planar leaf i.e. L^2 , Euler angle triplet and Cartesian coordinates respectively.
252 The geometry of the 3D trees with NP leaves were saved as VegeSTAR files as a collection
253 of triangles for further visualization (Fig. 2b) and light interception computations.

254

255 *Computing light interception at leaf and tree scales*

256 Three-dimensional mock-ups of both, individual leaves and trees were used in software
257 VegeSTAR for light interception computations (Adam *et al.* 2002). In the software, the 3D
258 scene elements are geometrical primitives assigned with false colours. The principle of
259 VegeSTAR consists of taking a picture of the 3D scene from the sun (or any other light
260 source) direction Ω with a virtual orthographic camera (Sinoquet *et al.* 1998). The scene
261 elements seen on the picture are those lit from the view direction. The amount of projected
262 area intercepting light in direction Ω is then estimated from the coloured pixel counts in the
263 image. Light interception is finally characterized by the variable STAR (Silhouette to Total
264 Area Ratio; Carter and Smith 1985; Oker-blom and Smolander 1988), which is the ratio
265 between the projected area seen on the image and the total area contained in the scene. As
266 STAR depends on the incident direction Ω , the sky hemisphere was divided in 46 solid angle
267 sectors of equal measure, according to the Turtle sky proposed by Den Dulk (1989).
268 Directional STAR values were computed for the central direction of each solid angle sector.
269 Directional STAR values then were summed up over the sky hemisphere after weighting with
270 coefficients derived from the Standard OverCast distribution of sky radiance (Moon and
271 Spencer 1942). The resulting value STAR_{SKY} characterized light interception over the sky
272 vault. Both directional and hemispherical STAR values were computed at the individual leaf
273 scale for the 99 laser-scanned leaves displayed with horizontal leaf axis and null whole lamina
274 rolling. STAR values were also computed at the tree scale with planar leaves and NP leaves,
275 i.e. taking into account the size, orientation and location of each leaf in the tree. The use of the
276 STAR at tree level as an indicator of light interception efficiency was previously validated for
277 beech (Balandier *et al.* 2007); diameter growth (or biomass increment) of young beeches was
278 related to the combination of STAR, leaf area, and available light above the young beeches
279 with a good accuracy ($r^2 = 0.86$; $p < 0.0001$).

280

281 *Statistical data analysis*

282 The analysis of variance of leaf parameters (table 2) was determined using a mixed general
283 linear model, with the mixed procedure (Proc Mixed) in SAS version 8.2 (Christophe et al.
284 2006). The effects of individual plants were added as random effects in the error of the model,
285 using the repeated option in Proc Mixed. The variance–covariance matrix of the error was
286 specified by an autoregressive model. When data were analysed by regression (figures 7 to
287 10) differences in the slopes between different light classes were tested with an F test after
288 linearization if necessary.

289

290 **Results**

291 *Leaf morphology*

292 The leaf morphology depended on the light available above the plant. Shaded plants were
293 almost flat becoming more bent when exposed to increased light above the plant (Fig. 6). A
294 quantitative analysis of the leaf morphology parameters showed a significant effect of %light
295 on the following parameters (Table 2): minimal openness angle between the two half-laminas
296 (O_{\min}), maximal lamina twirl angle around the midrib (T_{\max}), minimal transversal curvature
297 angle (TC_{\min}), and allometric coefficient K. Midrib curvature C did not show any significant
298 change with %light, although it would contribute to strengthen the bent aspect of leaves. The
299 higher value of K in full light meant that the same leaf area was achieved with smaller leaf
300 length and leaf width (no significant change was found in the ratio W/L).

301

302 *Light interception at leaf scale*

303 A linear regression analysis between individual leaf area and its projection averaged over all
304 sky directions showed differences in light capture efficiency according to %light (Fig. 7;

305 slopes were statistically different at $P < 0.0001$). Higher light led to lower $STAR_{SKY}$, with
306 slope values of 0.96-0.97, 0.94 and 0.90 for plant irradiance between 1-15%, 30-40% and
307 100%, respectively. For any light class, $STAR_{SKY}$ values only showed little variations with
308 leaf size, since the coefficient R^2 was always very high.

309 Directional STAR values showed high variation with the elevation angle h of the incident
310 beam direction (Fig. 8). The main source of variation was the angle between the beam
311 direction and the leaf normal, as directional STAR of a horizontal planar leaf is defined by the
312 sine function $\sin(h)$, i.e. STAR ranging from 0 to 1 for h between 0 and 90° . However,
313 directional STAR values of NP leaves showed some deviations with regard to that of a planar
314 leaf. For low elevation angles ($h < 20^\circ$), STAR values of NP leaves was slightly higher than
315 that of planar leaves, while STAR of NP leaves was lesser than that of planar leaves for
316 $h > 20^\circ$. The magnitude of the deviation for both low and high elevation angles was related to
317 %light, with greater deviations for more lighted plants (Fig. 8; $P = 0.009$).

318

319 *Light interception at tree scale*

320 $STAR_{SKY}$ values of the whole trees with NP leaves were also lower than those of trees with
321 planar leaves (Fig. 9; slope of the regression line statistically different from the 1:1 line at $P <$
322 0.0001). In contrast with the leaf scale, the tree $STAR_{SKY}$ decrease when tree was built with
323 NP leaves did not depend on %light, and the magnitude of STAR reduction was a maximum
324 of 3.2% for all light classes. Moreover the higher %light, the lower STAR value, leading to a
325 smaller effect of NP leaves on the absolute $STAR_{SKY}$ value at tree scale.

326 For %light below 40%, tree directional STAR increased with elevation angle (Fig. 10). For
327 low elevation angles, trees with %light below 40% showed similar values of directional
328 STAR around 0.21 without any differences between trees with planar leaves and trees with

329 NP leaves. For elevation angles above 20°, differences in directional STAR between %light
330 classes increased with elevation angles (slopes of the regression line after linearization
331 statistically different between %light classes at $P < 0.0001$), with higher STAR values for the
332 more shaded plants (Fig. 10). For that elevation angles higher than 20° STAR of trees with
333 NP leaves was always slightly lower than that of trees with planar leaves, with the maximum
334 differences being around 45-50° of elevation. The tree in full light showed a particular
335 behaviour with a small bell shaped curve of directional STAR with elevation and only a very
336 slight decrease in case of trees with NP leaves.

337 **Discussion**

338 *A double-digitizing method for 3D plant structure*

339 We developed a double-digitizing method to build 3D plants with non-planar leaves (NP
340 leaves). Indeed only one digitizing method would be insufficient for this purpose. Contact
341 digitizers (e.g. hand-held electromagnetic digitizer, HHEMD, used here) are not accurate
342 enough and only allow a rough description of the 3D leaf shape (e.g. Rakocevic et al. 2000).
343 Non-contact laser scan digitizers (NCLSD) are better suited for continuous surfaces (i.e. their
344 current use in industrial applications) than for plants where many small surfaces are
345 distributed in the vegetation volume. This is the reason why laser scanner applications to
346 building 3D plants deal with simple isolated plants with a few organs (Kaminuma et al. 2004;
347 barley, Dornbush et al. 2007) or isolated leaves (Loch 2004). The scan of a leaf is easy and
348 very rapid (less than 1 minute) in the lab where focus is easy to do with controlled light
349 conditions. The scan could be more complicated with *in situ* organs in the field conditions
350 with organs moved by the wind and none controlled light conditions leading to many artefacts
351 in the point cloud. Scanning in the field would obviously require plant protection, at least
352 from wind and light.

353 Scanner application to more complex whole plants is presently limited by the segmentation of
354 the 3D data set, as suitable automatic algorithms are for the moment unavailable. Moreover
355 scanner beams only hit the plant organs making the plant hull, preventing one to get
356 information inside the plant volume. This problem is emphasized in plants with high foliage
357 density. Dutilleul et al. (2008) used a computed-tomography (CT) scanner to get a full
358 description of the whole plant as a set of 3D data points, i.e. solving the masking effect. This
359 is a great improvement but this is limited to small plants (i.e. able to be inserted within the CT

360 scanner). Moreover algorithms for the segmentation of the 3D data points, i.e. point
361 assignation to plant organs, are also unavailable.

362 In consequence, the combination of HHEMD and NCLSD with suitable software turns out to
363 be a reliable approach for rapidly acquiring detailed plant architecture data. A constant
364 problem with such approaches is the validation of the built mock-up, and particularly of the
365 light intercepting surface, i.e. leaf area. What could be a method of reference to measure leaf
366 area, particularly for NP leaves? A flat-bed scanner is probably no more accurate than the
367 scanner laser and in case of discrepancy between both measurements it would be difficult to
368 say which is the "true" leaf area. The same problem is true at the tree scale. It was already
369 assessed by example by Drouet (2003) who compared direct measurements of maize
370 architecture with a 3D-digitization technique. The conclusion was that both techniques were
371 effective; the question is more linked to which resolution we want the spatial data.

372

373 *Effect of light availability on the leaf morphology and consequences on light capture*
374 *ability*

375 Non-planar leaf morphology is significantly dependent on light availability, with flatter leaves
376 in shaded environment. This is in agreement with the only study we found on this topic for
377 broad-leaves species (Fleck et al. 2003). In this previous study, the 3D leaf shape was
378 characterised by the average cross-sectional angle between the leaf halves, which was derived
379 from manual measurements. This angle is similar to the openness angle O used in the present
380 study. For beech leaves, Fleck et al. (2003) found a larger range in openness angles, i.e. 170°
381 to $90-100^\circ$ for shaded and full lit leaves, respectively. Of course, using the laser scanner
382 method allowed us a more detailed characterization of the 3D leaf shape, showing that several
383 parameters accounting for the 3D shape also responded to light availability (Table 2).

384 Light capture at both leaf and tree scales decreased when the 3D shape of leaves was
385 emphasised, i.e. for higher light availability. This is in agreement with the few previous
386 reported results. At the leaf scale, Fleck et al. (2003) showed lower interception for smaller
387 openness angles between leaf halves, and the decrease in light interception was higher for
388 direct than for diffuse radiation. Our results cannot be directly compared to those of Fleck et
389 al. (2003), because they dealt with direct and diffuse radiation at the daily scale. Rather we
390 showed that differences between planar leaves and NP leaves in directional light interception
391 is low for low elevation angles and markedly increases for higher elevation angles.

392 At the tree scale, the decrease in hemispherical interception ($STAR_{SKY}$) due to NP leaves was
393 a maximum of 3% mainly for the most shaded beeches (Fig. 9 & 10). The absence of strong
394 differences between light levels might be related to compensation from other structural
395 changes, and among other a higher leaf area density observed in sunny beech plants (e.g.
396 Planchais and Sinoquet 1998; Delagrange et al. 2005). A 3% decrease of light interception at
397 the tree scale may seem relatively low, but this is similar to the effect of other plant processes
398 on carbon acquisition, e.g. the spatial distribution of leaf nitrogen in tree canopies (Hollinger
399 1996) and heliotropism in cotton crops (Ehleringer and Hammond 1987). The competitive
400 advantage of such a decrease in light interception could be that NP leaves allow better
401 irradiance distribution over the tree leaf area and light penetration into deeper canopy leaves,
402 with positive consequences on the carbon gain by the plant (Niinemets 2007).

403

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407 d'Auvergne.

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515 **Tables**

516 Table 1. Distribution of eleven selected young *Fagus sylvatica* trees in four light classes in
517 forest stands of central France.

Light class	Class bounds (%light)	Number of trees
1	1 – 5%	4
2	7 – 15 %	3
3	30 – 40%	3
4	100%	1

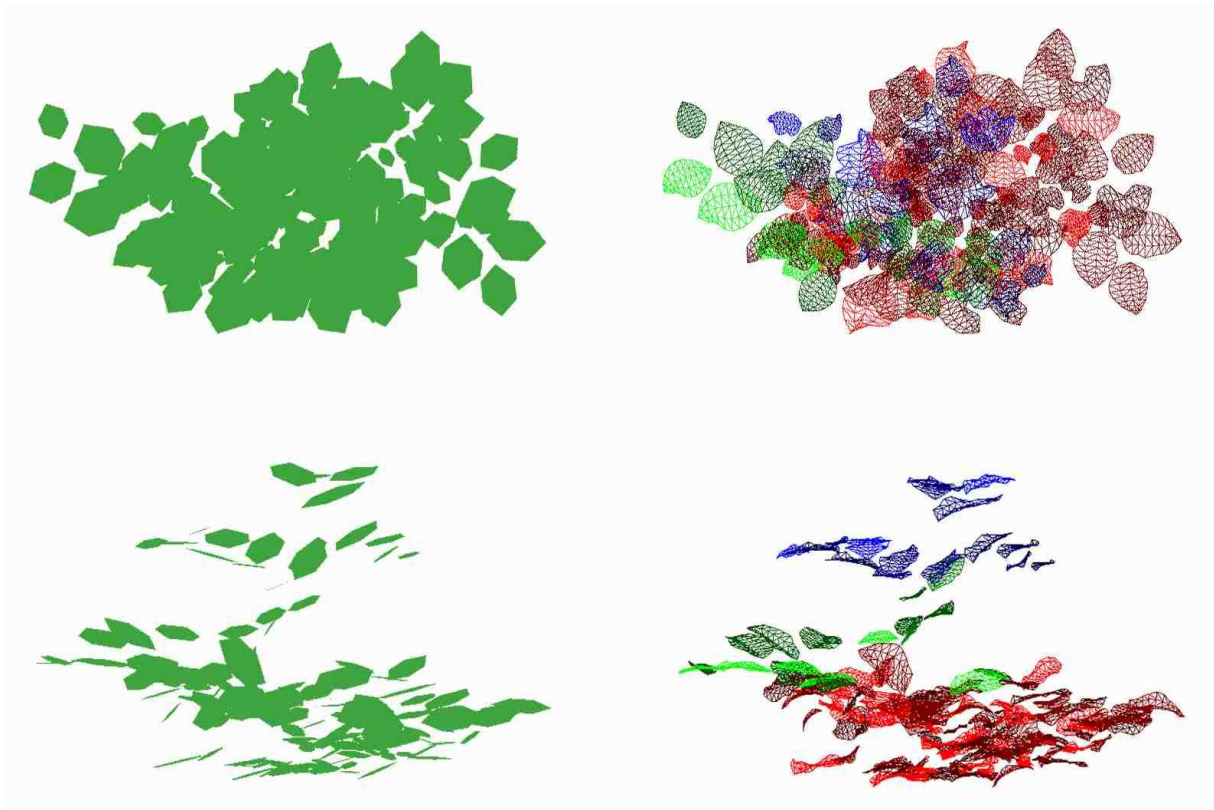
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519 Table 2. *Fagus sylvatica* leaf morphology parameters per light class, and significance of
 520 differences between light classes (P < 0.001 ***, P < 0.01 **, P < 0.05 *, and P > 0.05 Ns).

Parameters		Light class				P
		1-5%	7-15%	30-40%	100%	
Leaf area A (mm ²)		1398	1412	1380	2258	Ns
Midrib length L (mm)		55	54	55	65	Ns
Leaf width W (mm)		35	36	34	47	Ns
W/L		0.63	0.68	0.64	0.72	Ns
Midrib curvature C (mm ⁻¹)	mean	0.01	0.02	0.02	0.02	Ns
	max	0.05	0.06	0.06	0.06	Ns
	min	-0.01	-0.01	-0.02	-0.02	Ns
Openess angle O (°)	mean	164.0	165.9	163.6	148.5	Ns
	max	174.7	176.8	176.8	174.3	Ns
	min	150.2	150.2	146.3	113.3	**
Lamina twirl T (°)	mean	8.3	8.5	14.2	14.4	*
	max	18.0	17.9	35.3	41.5	*
	min	3.9	3.9	4.5	3.5	Ns
Allometric coefficient K	K	0.70	0.71	0.70	0.74	*
	Kdist	0.65	0.68	0.66	0.71	Ns
	Kprox	0.74	0.75	0.76	0.74	Ns
Transversal curvature TC (°)	mean	170.1	174.3	170.0	167.5	Ns
	max	179.1	179.2	179.1	178.3	Ns
	min	152.6	154.7	144.5	135.7	*
Symmetry S	mean	0.49	0.52	0.50	0.52	Ns
	max	0.55	0.59	0.55	0.55	Ns
	min	0.42	0.44	0.41	0.42	Ns



521 **Fig. 1.** Illustration of two digitizing methods: a) Leaf digitizing in a tree with a hand-held
522 electromagnetic digitizer 3Space Fastrack Polhemus; the pointer is set parallel to the midrib
523 and the mean plane of the lamina and points the junction between petiole and lamina. b) Leaf
524 digitizing with a non-contact laser scan digitizer Konica Vi-910 on detached leaves. The light
525 red triangle mimics the emitted laser plane.



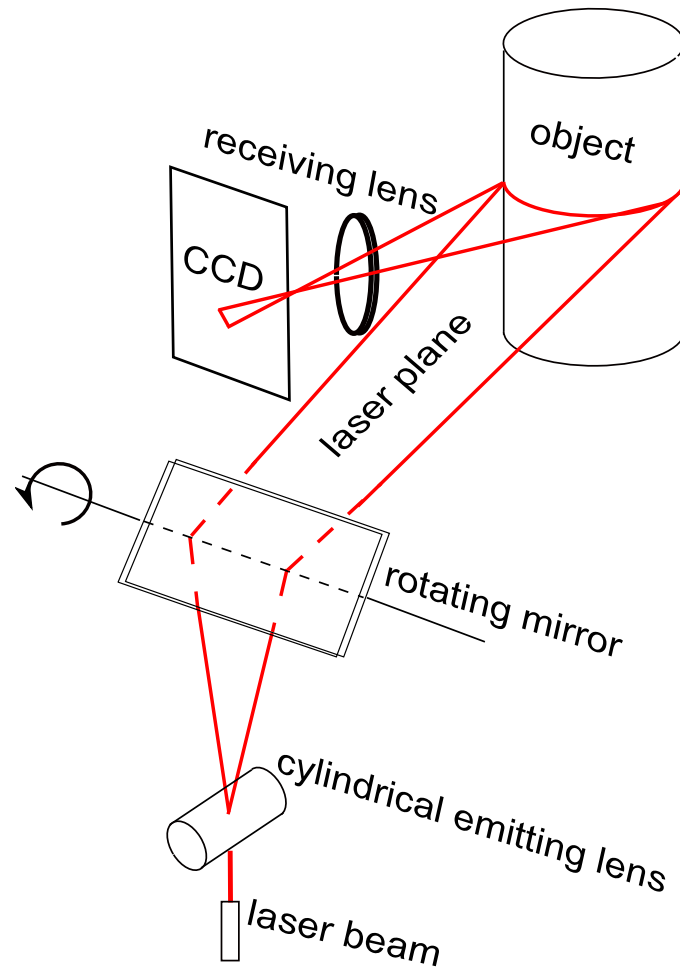
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a)

b)

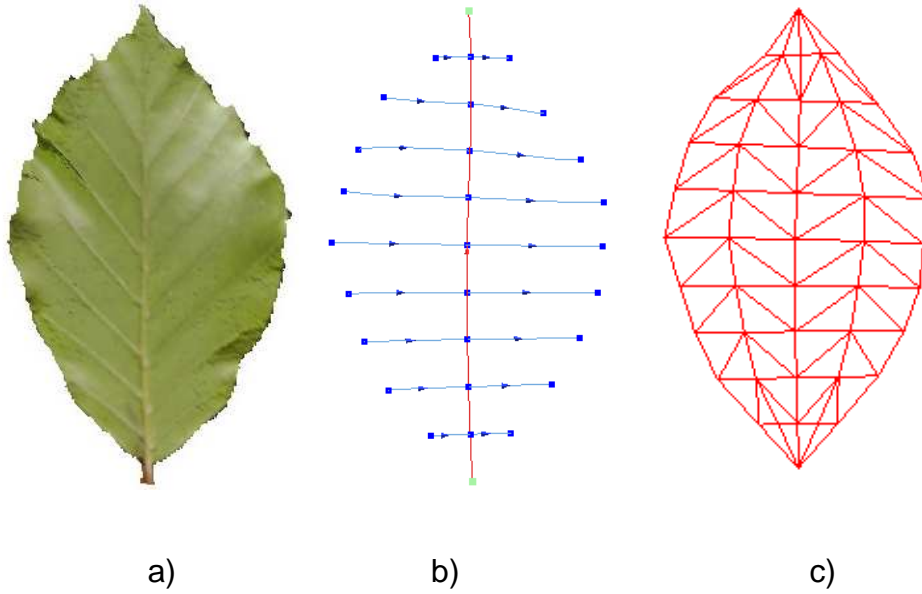
528 **Fig. 2.** Images of three-dimensional plant mock-ups of the same tree (*Fagus sylvatica*) at 9%
529 light viewed from the top (first line) or laterally (second line). a) Three-dimensional mock-up
530 made of planar hexagonal leaves. b) Three-dimensional mock-up made of non-planar
531 triangulated leaves. Blue, green and red false colours are assigned to non-planar leaves in top,
532 medium and bottom canopy layers.



533

534

535 **Fig. 3.** Illustration of the light stripe method used in the Konica Vi-910 scanner: a red laser
536 beam is emitted through a cylindrical lens in order to generate a laser plane. The laser plane is
537 sent to a rotating mirror in order to scan the object. Reflected light by the object is converted
538 into distance information by using an active triangulation principle. The conversion is
539 achieved through a charge-coupled device camera.

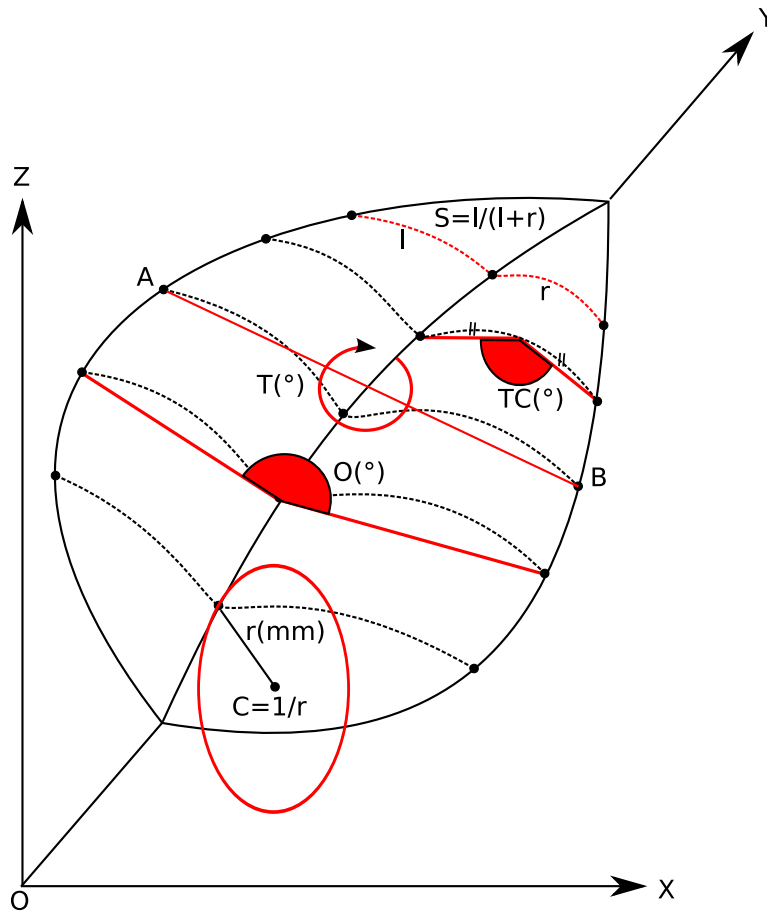


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541

542 **Fig. 4.** Processing of the three-dimensional leaf point cloud acquired with a non-contact laser
543 scan digitizer (Konica Vi-910) to extract morphological parameters and obtain a non-planar
544 leaf model made of 72 triangles: a) Scanned *Fagus sylvatica* leaf made of 18927 coloured
545 points; b) Nine slicing NURBS (Non Uniform Rational B-Spline) curves devoted to the
546 extraction of leaf morphological parameters and the construction of a triangulated leaf model;
547 c) Resulting triangulated leaf model composed of 72 triangles.

548



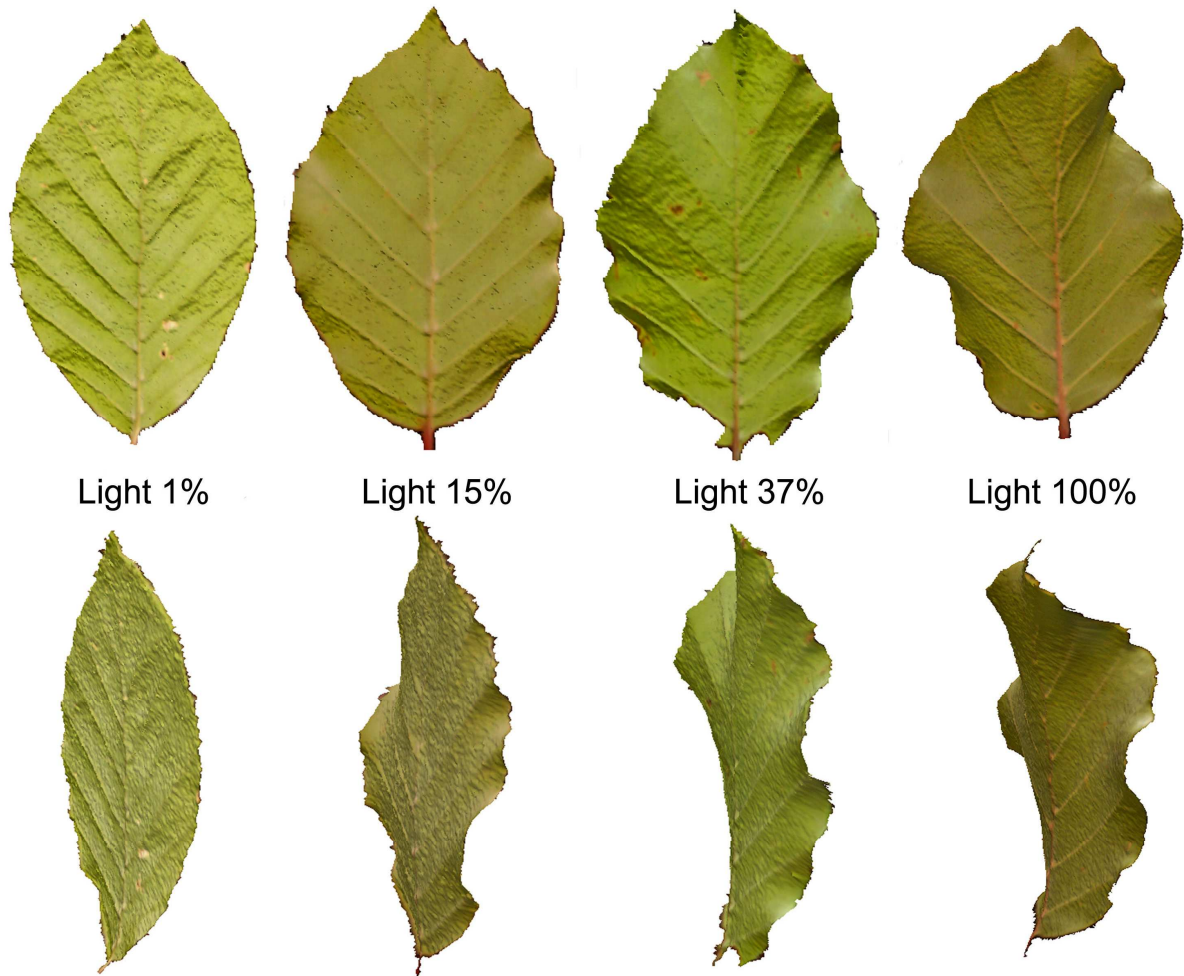
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550 **Fig. 5.** Illustration of five morphological parameters of a *Fagus sylvatica* leaf, namely midrib
 551 curvature C , openness angle between two-half laminas O , lamina twirl T , transversal
 552 curvature angle of lamina TC and symmetry between the two half-laminas S . First slicing
 553 curve, illustration of C (mm^{-1}) i.e. the inverse of the osculating circle radius; second slicing
 554 curve, O ($^\circ$); third slicing curve, T ($^\circ$), defined as the rotation angle of the segment AB around
 555 the Y axe; fourth slicing curve, TC ($^\circ$); fifth slicing curve, S .

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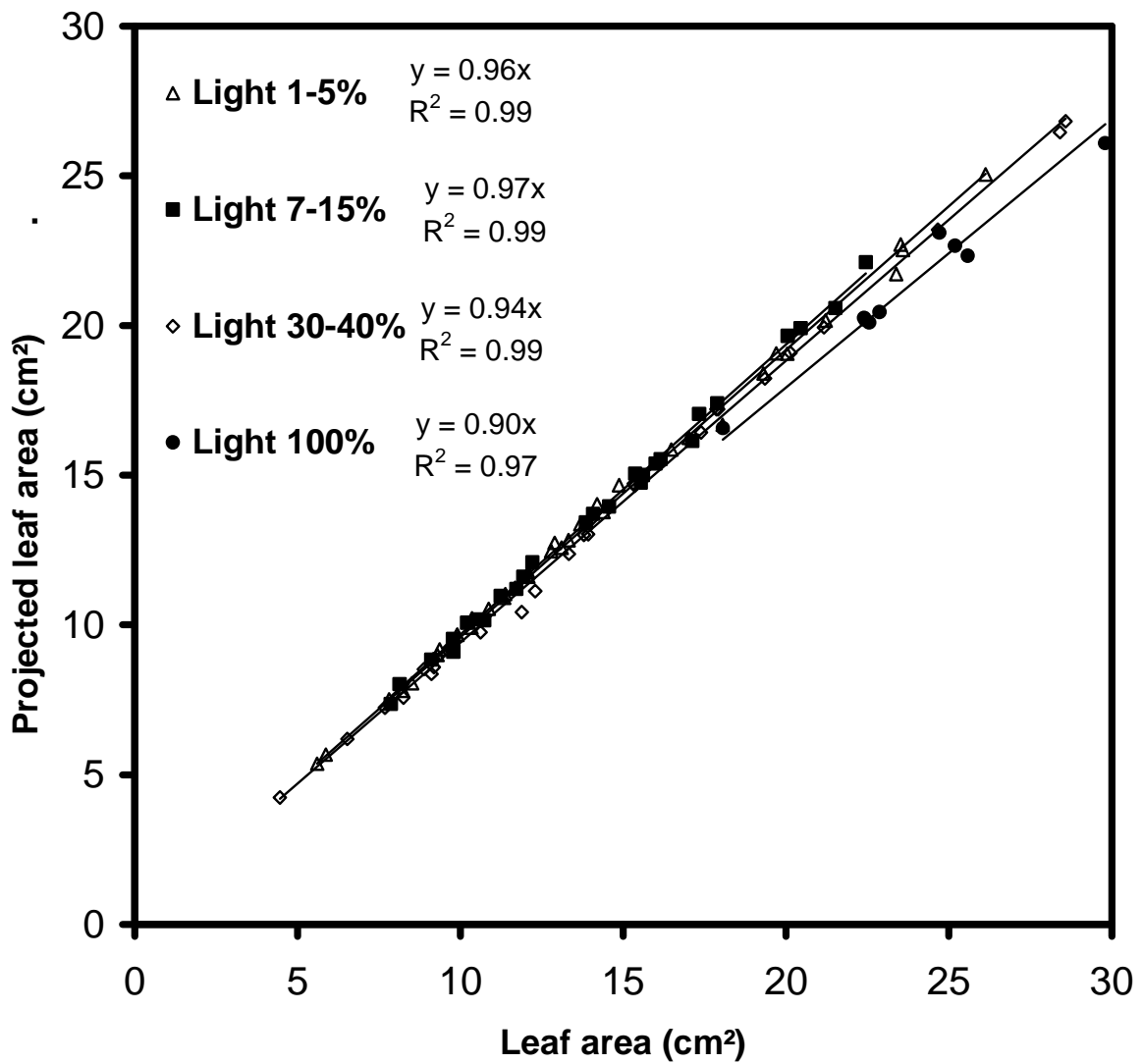
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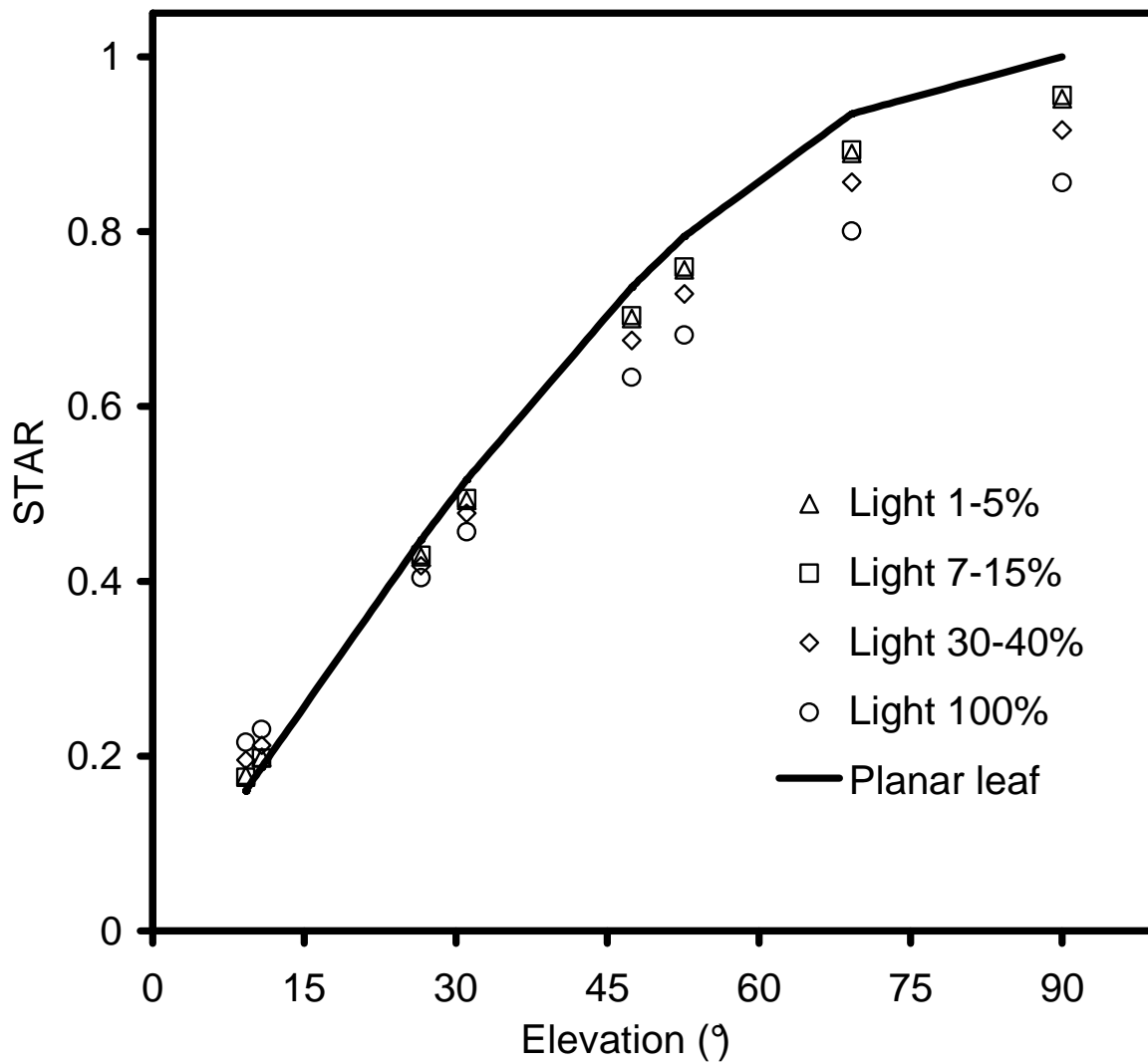
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560 **Fig. 6.** *Fagus sylvatica* leaves as a point cloud originated from the laser scanner (Konica Vi-
561 910) for some young trees sampled under different light availabilities. Top panel:
562 perpendicular view to the main leaf plane. Bottom panel: parallel view to the main leaf plane



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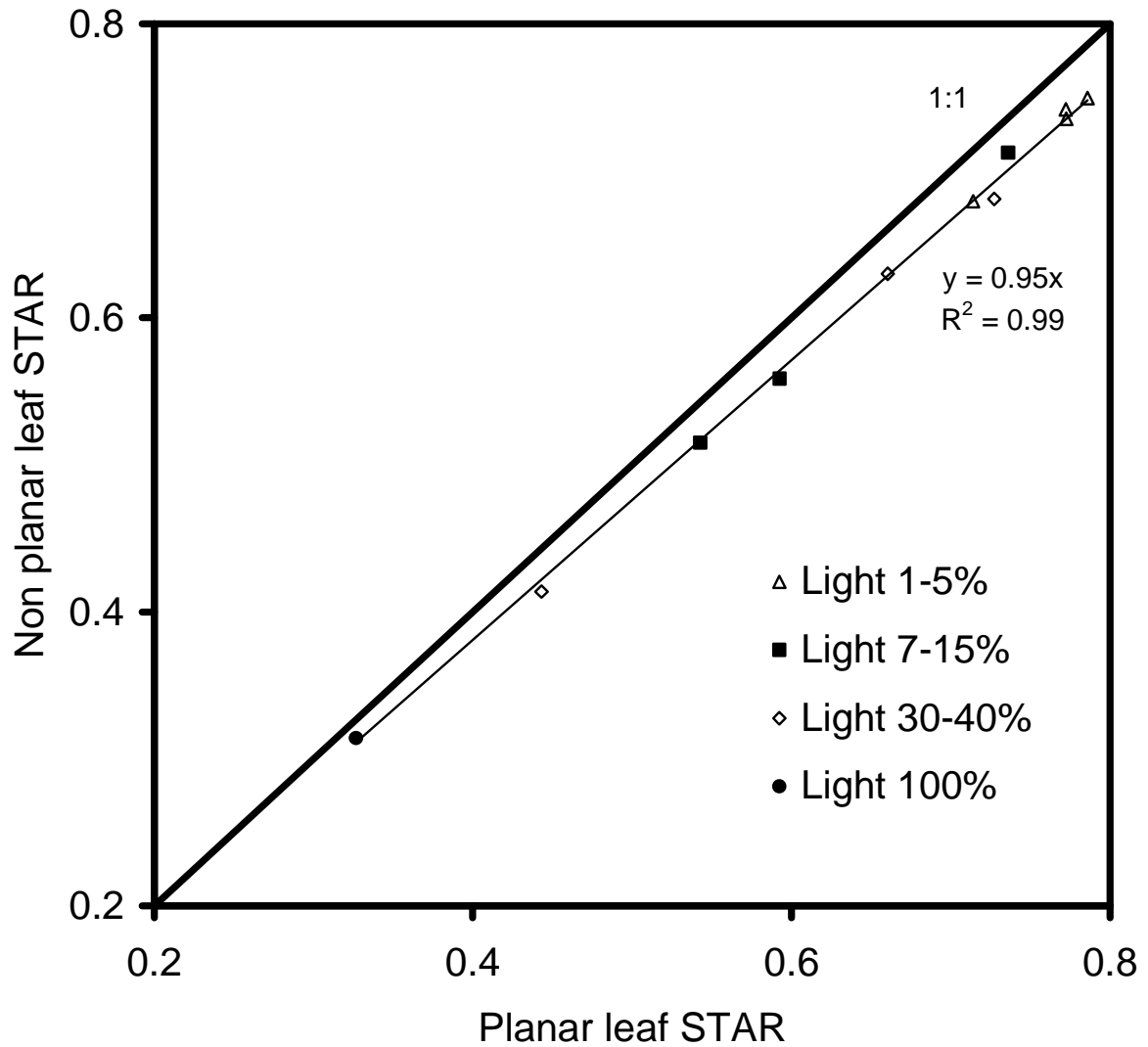
564 **Fig. 7.** Silhouette to total leaf area ratio integrated on the whole sky, STAR_{SKY}, of individual
565 non-planar leaves of *Fagus sylvatica* in central France under different light availabilities,
566 shown as a scatter plot between individual leaf area and projected leaf area averaged over all
567 sky directions.



568

569 **Fig. 8.** Directional STAR (Silhouette to Total leaf Area ratio) as a function of elevation angle
570 of individual non-planar leaves of *Fagus sylvatica* under different light availabilities in
571 Central France and in comparison with planar leaves (dark line).

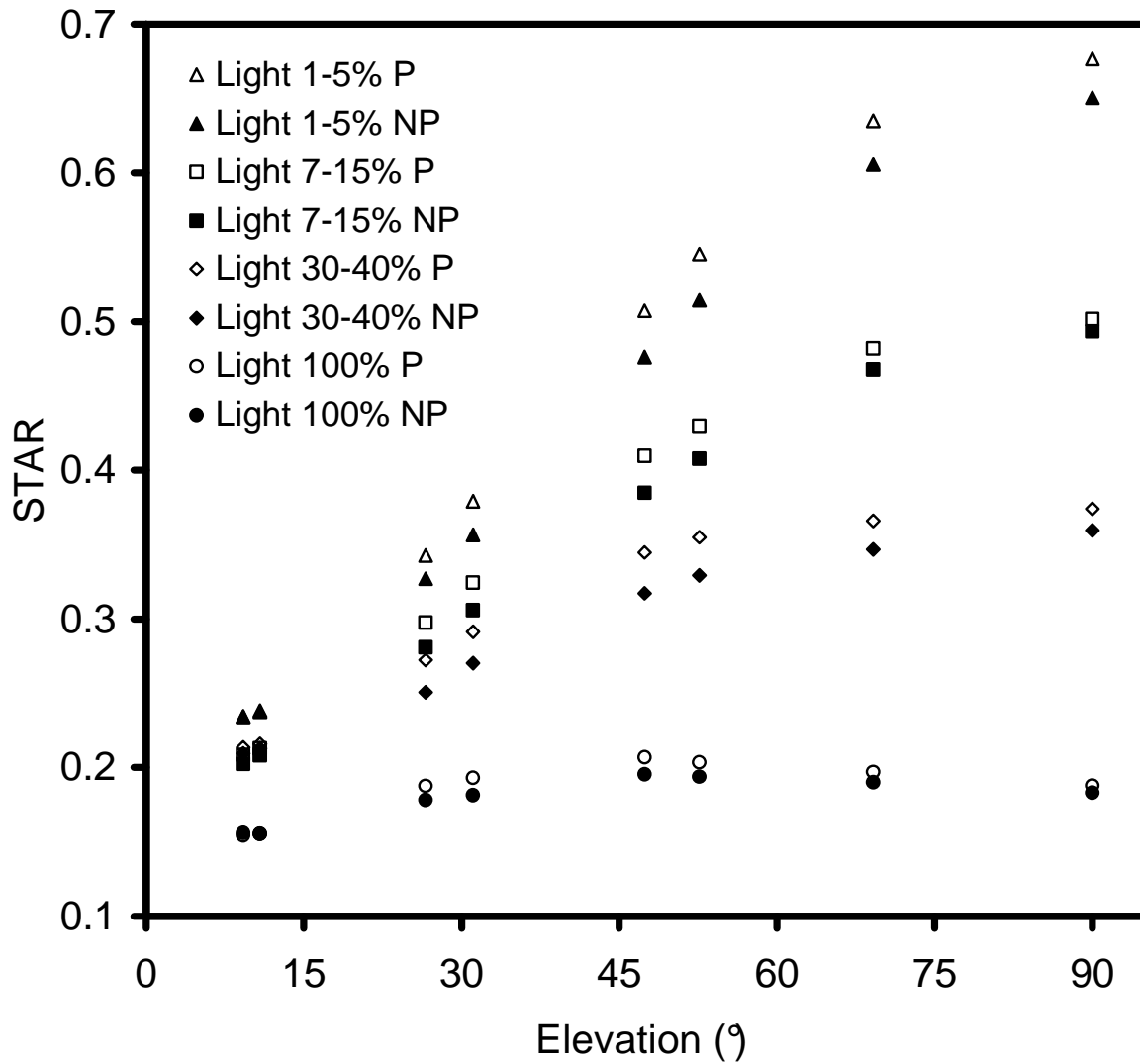
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574 **Fig. 9.** Comparison between silhouette to total leaf area ratio integrated on the whole sky
575 ($STAR_{SKY}$) of *Fagus Sylvatica* trees under different light availabilities in central France
576 calculated on mock-ups with planar and non-planar leaves.

577



578

579 **Fig. 10.** Directional silhouette to total leaf area ration (STAR) as a function of elevation angle
580 of *Fagus Sylvatica* trees under different light availabilities in central France calculated on
581 mock-ups with planar (P) and non-planar (NP) leaves.