Simplifying data acquisition in plant canopies- Measurements of leaf angles with a cell phone

Adrián G. Escribano-Rocafort , Agustina B. Ventre-Lespiaucq , Carlos Granado-Yela , Antonio López-Pintor , Juan A. Delgado , Vicente Muñoz , Gabriel A. Dorado and Luis Balaguer

Summary

- 1. Canopies are complex multilayered structures comprising individual plant crowns exposing a multifaceted surface area to sunlight. Foliage arrangement and properties are the main mediators of canopy functions. The leaves act as light traps whose exposure to sunlight varies with time of the day, date and latitude in a trade-off between photosynthetic light harvesting and excessive or photoinhibitory light avoidance. To date, ecological research based upon leaf sampling has been limited by the available technology, with which data acquisition becomes labour intensive and time-consuming, given the overwhelming number of leaves involved.
- 2. In the present study, our goal involved developing a tool capable of measuring a sufficient number of leaves to enable analysis of leaf populations, tree crowns and canopies. We specifically tested whether a cell phone working as a 3D pointer could yield reliable, repeatable and valid leaf angle measurements with a simple gesture. We evaluated the accuracy of this method under controlled conditions, using a 3D digitizer, and we compared performance in the field with the methods commonly used. We presented an equation to estimate the potential proportion of the leaf exposed to direct sunlight (SAL) at any given time and compared the results with those obtained by means of a graphical method.
- 3. We found a strong and highly significant correlation between the graphical methods and the equation presented. The calibration process showed a strong correlation between the results derived from the two methods with a mean relative difference below 10%. The mean relative difference in calculation of instantaneous exposure was below 5%. Our device performed equally well in diverse locations, in which we characterized over 700 leaves in a single day.
- **4.** The new method, involving the use of a cell phone, is much more effective than the traditional methods or digitizers when the goal is to scale up from leaf position to performance of leaf populations, tree crowns or canopies. Our methodology constitutes an affordable and valuable tool within which to frame a wide range of ecological hypotheses and to support canopy modelling approaches.

Introduction

Canopies are complex multilayered structures resulting from the coalescence of individual plant crowns within any community, from forests to grasslands and from terrestrial to freshwater and marine environments (Moffett 2000). Canopies expose a multifaceted surface area of phytoelements, such as leaves and stems, which intercept sunlight, precipitation, wind, particulates and aerosols (Monteith 1973; Gutschick 1999; Huang *et al.* 2007; Asner & Martin 2011). Canopy processes (e.g. primary production, evapotranspiration, gas

exchange, etc.) and concomitant phenomena such as heat absorption, light reflection, temperature regulation or erosion reduction are among the ecosystem functions supporting some of the most important ecosystem services (see for instance Lowman & Schowalter 2012). Canopy performance integrates multiple contributions and synergies across scales, from community overstorey to plant crown and to individual leaves (Barthélèmy & Caraglio 2007). At the crown level, plant performance depends not only on the environmental conditions experienced by the plant but, to a large extent, on the modulation of the plant's environment by tree crown development and architecture (Rubio de Casas *et al.* 2007, 2011). The light environment within crowns is highly

heterogeneous at the spatial and temporal scale. Spatially, tree crown structure mediates the exponential decrease in light intensity (Wang & Jarvis 1990; Uemura et al. 2006). Temporally, light intensity is determined by the interplay between crown anisotropy, the daily and seasonal motion of the sun and the atmospheric conditions (Granado-Yela et al. 2011). Foliage characteristics, arrangement and properties are the main mediators of the biological processes occurring within crowns (Hallé, Oldeman & Tomlinson 1978; Room, Maillette & Hanan 1994; Sterck & Bongers 2001). Indeed, leaves are functional units that link global climate and ecosystem dynamics, participating in food webs, biogeochemical cycles and constituting an important microhabitat in the biosphere (Wright et al. 2004; Pincebourde & Woods 2012). Leaf size and arrangement ultimately reflect functional strategies evolutionarily shaped to optimize light harvesting (Hansen 1917; Walter 1973; Lowman & Schowalter 2012). Overall light interception by leaves depends on abiotic factors (e.g. wind conditions, atmospheric transmissivity) and on biotic factors, such as leaf anatomy and position within the canopy (Campbell & Norman 1989; Terashima & Hikosaka 1995; Vogelmann, Bornman & Yates 1996; Smith et al. 1997; Gu et al. 2003). The leaves of some annuals or ephemerals form sparse canopies that track changes in solar elevation and azimuth throughout the day (Ehleringer & Forseth 1980). In denser canopies, however, solar tracking by the upper leaves reduces the light available to the lower ones, in turn reducing net canopy photosynthesis (Denison, Fedders & Harter 2010). Most species, particularly perennials, are static-leaved plants, that is, they maintain leaf orientation through the leaf life span (minimum variation in leaf angles caused by active or passive movements). These leaves act as fixed light traps whose exposure to sunlight varies with time of the day, date and latitude. In these cases, leaf position represents a tradeoff between photosynthetic light harvesting and excessive or photoinhibitory light avoidance, which acquires its full ecological and evolutionary meaning once contextualized within the geometry and dynamics of a plant's crown (Givnish 1988; Smith et al. 2004).

Unfortunately, to date, ecological research on canopies and crowns based on leaf sampling has been limited by the available technology. In many studies, data acquisition is labour intensive and time-consuming due to the overwhelming number of leaves present in tree crowns and their limited accessibility (Wang & Jarvis 1990; Parveaud et al. 2008). Field measurements of leaf angles have been customarily performed with clinometers, compasses, protractors, angle finders, rulers, plumb lines and callipers (hereafter, traditional methods; Comstock & Mahall 1985; Ehleringer & Werk 1986; Fleck et al. 2003; Granado-Yela et al. 2011) or with three-dimensional motion trackers or digitizing systems (hereafter, digitizers; Pearcy & Yang 1996; Sinoquet & Rivet 1997; Falster & Westoby 2003; Hanan & Wang 2004). Traditional methods are portable but require at least three sequential measurements (see below) to characterize a single leaf's spatial position, which increases data acquisition time and the accumulated error. Additionally, traditional methods are frequently analogue, a

fact that reduces measurement resolution. These disadvantages have been emphasized in previous studies (Jennings, Brown & Sheil 1999; Jonckheere et al. 2004; Seidel et al. 2011). Digitizers are highly accurate, precise and effective for characterizing leaves in reference to others (Falster & Westoby 2003). Digitizers, however, are difficult to implement under field conditions for a number of reasons. They require a static point of reference, are expensive and, in practical terms, are not portable because of their size and weight. Moreover, they are usually wired, which limits their use in the field. Wiring tends to impose movement constraints - particularly when working within the canopy - and limits the equipment's reach, which consequently restricts the data acquisition range. It also implies the relocation of the reference point within a single crown, increasing the time required for measurements and for subsequent conversion of coordinates. Finally, digitizers most often require an external power supply, which increases expenses and can make its use in remote locations unfeasible. For all these reasons, when traditional methods and digitizers are used to describe forest canopies or tree crowns, they fail to characterize a representative number of leaves within a reasonable time, and consequently, any attempt to scale up from the leaf to higher functional and architectural levels will be considerably hindered, or even thwarted, by this severe drawback.

The aim of the present study involved developing a userfriendly, simple, fast, precise, digital, affordable, portable and highly autonomous tool capable of measuring a sufficient number of leaves to enable analysis of leaf populations, tree crowns and canopies. This tool should be sufficiently small, light and manageable to be used single-handed within the canopy. It should also measure all angles describing a leaf's position simultaneously without requiring an external reference point. We specifically tested whether a cell phone equipped with an ad hoc software application is more effective than both, traditional methods and digitizers. We evaluated the accuracy of this method under controlled conditions using a 3D digitizer and compared performance in the field with traditional methods. We presented an equation to estimate the potential proportion of the leaf exposed to direct sunlight at any given time and compared the results with those obtained by means of a graphical method. Furthermore, we describe our research experience, highlighting the advantages and drawbacks of our method when used in intensive field campaigns at several sites.

Materials and methods

DEVICE IMPLEMENTATION

In order to measure the leaf lamina angles, we developed a specific application software to be implemented on a cell phone operating under Symbian OS (Nokia N86, Nokia Group, Espoo, Finland). This device incorporates a 3-axis accelerometer and a magnetometer that records its spatial position in relation to magnetic north (m) and to gravitational force (g) as XYZ coordinates (Fig. 1). These electromechanical sensors, however, have been common features in most of the commercialized cell phones for the past decade. Fitted with our

software, the device acts as a 3D pointer with top/bottom, left/right and front/back side that enables the measurement of leaf angles with a single gesture (Fig. 1).

LEAF LAMINA CHARACTERIZATION

To describe leaf spatial position, we assume that leaves lie on a plane with adaxial/abaxial sides and a longitudinal axis running along the leaf midrib. Thus, a leaf, as a three-dimensional object, can be parameterized with spherical coordinates (Fig. 2). This system allows us to calculate leaf lamina course angle and leaf inclination angle, which we used to estimate the area of the leaf lamina exposed to the sun in per cent of the total leaf area. Lamina course angle (β) is the angle between north and the horizontal projection of a normal vector to the leaf lamina. Lamina inclination angle (p) is the angle of the maximum slope of the leaf from vertical. These two angles can be determined through a matrix of three vectors, which comprises leaf pitch, roll and midrib azimuth angle (α, γ, ι) . Pitch angle (α) is the angle between the vertical and the midrib of the leaf lamina. Roll angle (γ) is the angle of rotation from horizontal along the longitudinal axis of the leaf (Fig. 2) and combined with α defines the maximum slope of the leaf above horizontal or lamin a inclination angle (ρ). Midrib azimuth angle (ι) is the angle between magnetic north and the projection of the midrib from petiole insertion to the tip of the leaf. Together with α and γ midrib azimuth angle defines lamina course angle (β) (Fig. 2).

Using the above-described angles (α, γ, ι) , the device mathematically determines a trihedron in space according to the following form:

saved as text for further analysis. Data can be downloaded via Bluetooth, a flash memory card (microSD), USB or send via email.

LEAF EXPOSURE TO DIRECT SUNLIGHT

We used leaf angles to estimate the instantaneous silhouette area of the leaf blade (SAL), that is, the area of one side of the leaf blade that would receive direct sunlight, ignoring possible leaf overlaps (Granado-Yela et al. 2011). We calculated SAL through the cosine of the angle of the incidence (cos(θ); Comstock & Mahall 1985; Ehleringer & Comstock 1987) of direct sunlight to a tilted surface, following a modified equation from Pearcy et al. (1989), which accounts for Earth's orbit and axial tilt (Eqn. 3). The equation involves (β) and (ρ) angles, relating to the spatial position of the leaf, and latitude (Φ) , declination (δ) and hour angle (ω) relating to leaf location on Earth and sun relative position. Thus, for a given geographical coordinate (latitude and longitude), the day of the year and a period of time within the day, we can determine $cos(\theta)$ of direct sunlight to the leaf lamina, where SAL = 100 $cos(\theta)$ to obtain the proportion of leaf exposed to direct sunlight. Details of calculations and an example for distinct locations are provided in Appendix S1.

$$\begin{split} \cos(\theta) &= (\sin(\delta) * \sin(\Phi) + \cos(\delta) * \cos(\Phi) * \cos(\omega)) * \cos(\rho) \\ &- (\sin(\delta) * \cos(\Phi) * \cos(\beta) + \cos(\delta) * \sin(\Phi) * \cos(\omega) \\ &* \cos(\beta) + \cos(\delta) * \sin(\omega) * \sin(\beta)) * \sin(\rho) \end{split}$$

$$\begin{pmatrix} \sin(\alpha)\cos(\iota), & \cos(\alpha)\sin(\gamma)\cos(\iota) - \cos(\gamma)\sin(\iota), & -\cos(\alpha)\cos(\gamma)\cos(\iota) - \sin(\gamma)\sin(\iota) \\ \sin(\alpha)\sin(\iota), & \cos(\alpha)\sin(\gamma)\sin(\iota) + \cos(\gamma)\cos(\iota), & -\cos(\alpha)\cos(\gamma)\sin(\iota) + \sin(\gamma)\cos(\iota) \\ \cos(\alpha), & -\sin(\alpha)\sin(\gamma), & \sin(\alpha)\cos(\gamma) \end{pmatrix}$$

Each column in the matrix is a vector; the first column accounts for the leaf midrib, the first and the second columns define the leaf plane, and the third column is the normal vector to the leaf lamina surface. Thus, (ρ) and (β) can be calculated (Eqn. 1 and Eqn. 2) from pitch angle (α) , roll angle (γ) and midrib azimuth angle (ι) :

$$p = a\sin(\sin(\alpha)\cos(\gamma))$$
 eqn 1

$$\beta = \iota + a \tan(\tan(\gamma)/\cos(\alpha))$$
 eqn 2

MEASURING LEAF ANGLES WITH A CELL PHONE

The cell phone must be set in parallel to the leaf, the leaf lamina orientation matching the frontal side (i.e. the screen in the device faces the same orientation as leaf lamina) and the tip of the leaf placed at the upper part of the cell phone (Fig. 3). Thus, the leaf angles match those read by the cell phone and can be recorded by pressing the selection key once. The instantaneous output of the accelerometer and magnetometer varies rapidly during operation of the software due to the high sensitivity of the sensors. The software application averages the last 100 values for the accelerometer and the last 25 values for the magnetometer in order to show a smooth display variation. The reliability of the measurement is visible by means of a green light displayed on the cell phone screen (when the device is held steady, values become stable in about 4 seconds). A characteristic beep sounds once a valid measurement is

VALIDATION OF SAL EQUATION

In order to evaluate the results obtained from the proposed estimation of leaf exposure (Eqn. 3), we recalculated the instantaneous silhouette area of the leaf blade (SAL_t) from the angles of the leaves included in the study by Granado-Yela *et al.* (2011). These authors measured the lamina angles of 308 leaves of *Olea europaea* L, by means of traditional methods. They calculated the instantaneous silhouette area of the leaf blade (SAL_t) graphically through AutoCAD for 250 leaves. We calculated Pearson's correlation coefficient for both estimates of leaf exposure.

CELL PHONE CALIBRATION

In order to assess the error in the measurement of the leaf angles caused by the inaccuracy of the cell phone sensors, we built a custom-made deck. The deck bears a hinge enabling different positions. The main panel has an inscribed circumference and a stand to hold a digitizer. Specifically, we used a 3D motion tracker (Fastrak. Pholemus, Vermont, USA). The deck was built without any metal parts to avoid electromagnetic interferences (Fig. 4). It was set on a range of elevations from the horizontal to the vertical plane every 5° . At each elevation, we made 36 measurements following the graduated notches in the drawn circumference (one measurement every 10°). Desired angles in the adjustable deck were fixed using the digitizer. Using trigonometric functions, we calculated the expected values for the study angles (α_p, γ_p

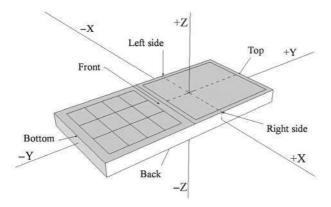


Figure 1. Device's coordinate system and equations which relate the three Euler's angles α : Atan (g_x/g_z) , γ : Atan (g_z/g_y) ι : Asin $(|P_y \times Q|/|P_y| \bullet |Q|)$ and β : Asin $(|P_z \times Q|/|P_z| \bullet |Q|)$ where; P_y and P_z are the axis projection of +Y and +Z axis, respectively, on a normal plane to g $\{P_z = (g \times (+Z)) \times g\}$ and Q is the vector of the geomagnetic field m (from magnetic north) projected on a normal plane to g $\{Q = (g \times m) \times g\}$.

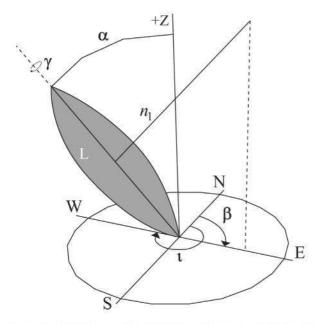


Figure 2. Leaf angles. α : spans from 0 to ± 180 degrees where 0° and $\pm 180^{\circ}$ refer to a vertical leaf and $\pm 90^{\circ}$ to a horizontal leaf. γ : spans from 0 to ± 180 degrees. Negative values account for a right turn from petiole to leaf tip. In the figure, if $\gamma = -90^{\circ}$, the reader should picture a leaf lamina facing North. ι : Projection of leaf midrib vector from petiole insertion to leaf tip into polar coordinates; 0° north, clockwise. β : Projection of n_{ι} vector into polar coordinates; 0° north, clockwise. n_{ι} normal vector to the lamina surface. L: Leaf lamina.

 ι_r , ρ_r), which we compared with the measured ones (see details in Appendix S2). Discrepancies between observed and expected values were assessed in terms of mean relative error. Likewise, we estimated the error of SAL obtained between observed angles (SAL_O) and expected angle values (SAL_E) . Simple correlations were performed between expected and obtained values.

FIELD VALIDATION OF THE DEVICE

In order to evaluate whether our device could provide a tool as reliable as the traditional methods used in previous studies, but much

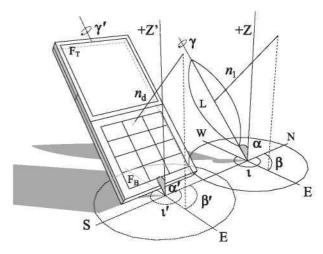


Figure 3. Device set in parallel to a leaf. Device and leaf lamina facing East $(\beta = 90^\circ)$. Angles of interest are the same for the leaf and the device. $\alpha = \alpha'$, $\gamma = \gamma'$, $\iota = \iota'$ and $\beta = \beta'$. n_ι : normal vector to the leaf lamina surface, n_d : normal vector to the device (parallel to each other), F_T : Top part of device's front side, F_B : Bottom part of device's front side, L: Leaf lamina. Insertion angles between leaf and petiole are parallel in this situation in which angle α is the same in leaf and petiole. Setting the device in parallel to a leaf with different insertion angle between petiole and leaf midrib will record α regarding leaf pitch and not petiole pitch.

easier to operate, we measured the leaf angles of 100 leaves using (i) a protractor and a compass, and (ii) our cell phone. Leaves were haphazardly chosen within the crown of ten wild olive trees (Olea europaea L.), c. 1.5 m high and located at the Alfonso XIII Royal Botanical Garden in Madrid (40°26'57"N, 3°43'41"W). Each leaf was measured with our device and then with a protractor (α and γ) and a compass (ι and β), as used elsewhere (Rubio de Casas et al. 2007, 2011; García-Verdugo et al. 2010; Granado-Yela et al. 2011). We analysed the differences between the measurements taken with the cell phone (α_C , γ_C , ι_C , ρ_C and β_C) and with the traditional methods (α_T , γ_T , ι_T , ρ_T and β_T angles) by means of Pearson's correlations. In addition, we assessed the discrepancies in the instantaneous silhouette area of the leaf blade through a Pearson's correlation between those calculated from the angles measured with the cell phone (SALC) and those calculated from data obtained with traditional methods (SAL_T). Mean relative error between methods was quantified for each angle as performed for the calibration process. We adopted the presented method during four field campaigns conducted in Aldea del Fresno (Madrid, Spain), San Luis (Mahón, Spain), Langalanga (Gilgil, Kenya) and Limuru (Nairobi, Kenya), which differed in accessibility and tree size. Effectiveness was described in terms of averaged ratio of measurements per hour, among other important considerations examined in the discussion.

Results

VALIDATION OF SAL EQUATION AND CELL PHONE CALIBRATION

The values of instantaneous silhouette area of the leaf blade (SAL), calculated graphically by Granado-Yela *et al.* (2011) and by means of eqn 3, were strongly correlated (R = 0.98, P < 0.05; Fig. 5). Mean relative error was below 10% for all

angles. Pitch angle (α) showed the biggest differences between measured and expected values with a standard deviation close to 15% (Table 1). Estimations of the response variable between expected values and the angles measured with the cell phone (SAL_E – SAL_O) differed by <2% with a standard deviation below 3% (Table 1).

The expected angles (i.e. angles simulated by spatial geometry) and the angles measured with the cell phone were highly correlated in all cases (R > 0.93, P < 0.05; Fig. 6). Nevertheless, we detected a bias for the measurements of the pitch angle and roll angle due to cross-axis sensitivity. Inclination angle (ρ), however, was not apparently affected by this bias (Fig. 6e). The values of β angle showed greater deviations when the adjustable panel was set near the horizontal plane (no specific orientation), but it remained constant at higher elevations (Fig. 6f).

FIELD VALIDATION OF THE DEVICE

Estimations of the leaf angles measured with the cell phone and by means of traditional methods showed less than 11% of mean relative error for each angle (Table 1). Roll angle experienced the biggest discrepancies and standard deviation between methods. The mean relative error between the SAL calculated from angles measured with traditional methods and with our cell phone was 5.5% with a standard deviation below 7% (Table 1). A strong correlation was found for each angle between methods (R > 0.93; Fig. 7). Correlations between measurements were significant for all angles (P < 0.05, n = 100; Fig. 7). The estimated SAL between traditional methods and our cell phone showed a strong correlation (R = 0.95, P < 0.05, n = 100) (Fig. 7f).

On average, we were able to obtain 146 ± 24 valid measurements per hour and cell phone during the field campaigns, where over 4000 leaves were measured. In practice, a single

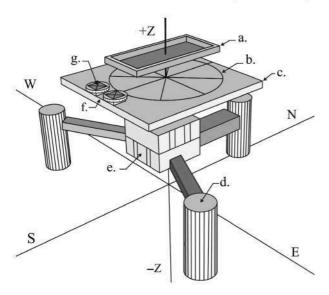


Figure 4. Adjustable deck outline used for calibration. a: cell phone holder (allows turn on Z axis), b: circumference inscribed in panel surface (notched every 10°), c: deck surface, d: supporting legs, e: hinge that allows elevation, f: space for digitizer, g: digitizer holders.

device could perform up to 720 measurements in a single day without running out of battery.

Discussion

Our tests in the laboratory and under field conditions demonstrate that the present method provides accurate and reliable measurements of leaf angles and SAL estimations. The method described constitutes an advance in direct data acquisition based on a widespread, affordable, easy-to-use, portable and wireless methodology that enables leaves to be spatially monitored by any researcher, educator or student. Our method proved to be satisfactory and highly convenient for field designs involving planar leaves/leaflets (leaves and leaflets that can be broken down into planar elements), thus providing many advantages over methods reported in the literature. Nonetheless, the presented method may still require canopy lifters, scaffolds or ladders to reach tree crowns and canopy elements.

CALIBRATION AND VALIDATION

The coefficients of correlation between the measurements taken with the cell phone and the expected values simulated by spatial geometry during the calibration process were strong and statistically significant for all angles and estimated SAL. Most values for all angles tested and SAL were tightly clustered around the expected ones, denoting great accuracy and precision (Fig. 6; Table 1). We found a strong linear relationship for all angles, although during the calibration process we detected a bias resulting from low cross-axis sensitivity in pitch and roll angles (Fig. 6a-c). The cross-axis sensitivity is the measure of how much output is seen on one axis when acceleration is imposed on a different axis. It is a product of the 3-axis accelerometer architecture and is a key factor to be implemented and tested by manufacturers (Amarasinghe et al. 2006; Kal et al. 2006; Sankar, Das & Lahiri 2009). The sensor is most sensitive to changes in tilt when the axis involved is perpendicular to the acceleration and is least sensitive when it is parallel. Despite this fact, the effect was negligible in relation to our goals due to the combination of pitch and roll angles in the maximum slope angle (p: Eqn. 1), which minimizes the

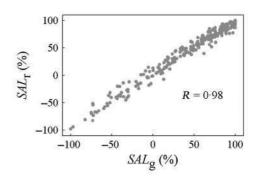


Figure 5. Correlation of recalculated SAL with eqn 3 (SALr) and that obtained by graphical methods (SAL_g) in Granado-Yela *et al.* (2011). n = 250. Negative values indicate underside exposure

Table 1. Mean relative error and SD (%) for each angle and leaf exposure. The error was calculated as the difference between the expected values (digitizer, traditional methods) and the cell phone measurements (observed) for each angle.

	Cell phone vs. DT		Cell phone vs. TM	
	Error (%)	SD (%)	Error (%)	SD (%)
Pitch (a)	8-5	149	8-5	6-1
Roll (y)	1.6	1.0	10.7	10.0
Midrib A. (t)	3.0	0.7	3-4	2.8
L. Course (β)	4-3	5-3	3-8	2.5
Max. Slope (ρ)	4.0	2.0	7.3	6.2
SAL _E -SAL _O	1.5	2.5	_	_
$SAL_{\mathbb{T}}SAL_{\mathbb{C}}$	_	_	5.5	6.8

DT: digitizer, TM: traditional methods. $SAL_{\rm E}$: estimations of SAL from expected angle values during calibration. $SAL_{\rm O}$: estimations of SAL from angles measured by the device during calibration. $SAL_{\rm T}$: estimations of SAL from angles measured by traditional methods during field validation. $SAL_{\rm C}$: estimations of SAL from angles measured with our device during field validation. Cell phone vs. DT n=684 except L. Course, n=648. Cell phone vs. TM n=100.

aforementioned cross-axis sensitivity. Estimations of maximum slope angle were strongly correlated with all tested methods, with small differences with regard to known values (Fig. 6e and 7d; Table 1). Measurements of lamina course angle and midrib azimuth angle were indeterminate in certain positions (e.g. when pointing at zenith), but the trigonometric

relationship between them enables these angles to be calculated with low error as occurs with maximum slope angle. All these findings supported the reliability of the measurements taken by the cell phone, with low mean relative error in the estimation of the desired leaf angles.

The coefficients of correlation between the field measurements taken with the cell phone and traditional methods, and SAL estimated from them, were strong and statistically significant (Fig. 7). The differences between methods of angle measurement remained low in the validation process and for SAL estimations (Table 1). Likewise, the coefficients of correlation of SAL calculated between graphical methods and the equation presented were strong (Eqn. 3; Fig. 5). These findings support our method as a reliable tool for assessing the spatial position of leaves and for calculating potential SAL over time under field conditions.

FUNCTIONAL CONSIDERATIONS: OPPORTUNITIES AND LIMITATIONS

The method presented for estimating SAL does not account for leaf overlapping within canopy layers. Despite this limitation, we found it highly relevant to measure leaf angles and to estimate SAL in the whole canopy regardless of whether the leaves could be directly or indirectly exposed to wind, particulates, irradiation or other effects. At the individual level, recent reports point towards spatial and temporal specialization

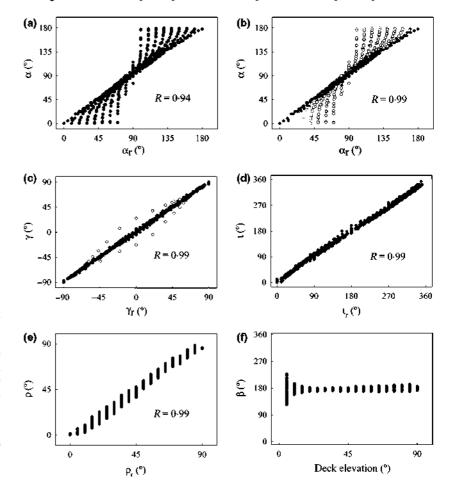


Figure 6. Calibration of the sensors. Correlation coefficients for the accelerometer [pitch angle $(\alpha, a-b)$ and roll angle (γ, c)], magnetometer [midrib azimuth-angle (i), d], lamina inclination angle (p; e), and lamina course-angle $(\beta; f)$. Unbiased (black) and biased (deviation from ideal correlation; white) values are shown for the pitch (a and b, respectively) and roll angle (c). Deviations from ideal correlation in 'a' and 'c' are minimized when accounting for the maximum slope angle (e). Lamina course-angle (f) was measured every 5° from 5° to vertical (90°) . In Fig. 6a-e, n=684; in Fig. 6f, n=648.

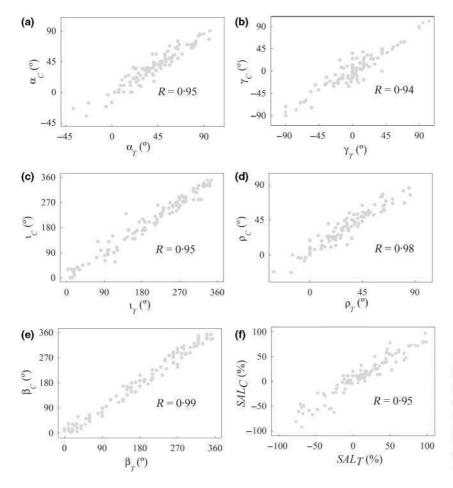


Figure 7. Relationship between traditional methods (α_T , γ_T , ι_T , ρ_T and β_T) and the cell phone (α_C , γ_C , ι_C , ρ_C and β_C) with the coefficient of correlation (R) given for each scatter plot. a: pitch angle, b: roll angle, c: midrib azimuth-angle, d: maximum slope, e: lamina course-angle, f: estimations of SAL between methods (SAL_T - SAL_C , negative values account for underside exposure), n = 100.

through photosynthetic harvesting of complementary light resources (direct and diffuse radiation) and/or segregated time windows in woody plants, which can be explored with our method (Rubio de Casas et al. 2007; Granado-Yela et al. 2011). Indeed, optimization of leaf photosynthetic efficiency through modulation of leaf inclination angle, lamina orientation and lamina exposure will certainly help to scale photosynthesis from leaves to individual crowns and canopies, as suggested by Posada, Lechowicz & Kitajim (2009). The spatial position of leaves and their potential exposure to direct sunlight are relevant to many functional processes operating at the individual level (Givnish 1987; Smith et al. 1997; Falster & Westoby 2003; Pearcy, Muraoka & Valladares 2005; Granado-Yela et al. 2011). The mean relative error in SAL calculations was always below 10%, reaching maximum absolute values at full leaf exposure to the sun. As SAL decreases, sunlight absorption is not expected to decrease in proportion to the reduction in the projected leaf surface, but rather at higher rates due to the expected increase in light reflection and the smearing of the incident photon flux over a larger leaf area.

FIELD EXPERIENCE

The field performance of our device during the research campaigns was remarkable. Its portability was crucial to our research, enabling tree crowns to be sampled and logistic requirements to be fulfilled in remote locations. We wish to stress the ease of travelling, particularly on regular commercial flights, with such an affordable and commonplace device. In the field, the presented device was effortless to carry and to operate several metres above the ground. We found highly advantageous to take measurements with a single hand under these circumstances.

USE RECOMMENDATIONS

In order to improve field estimations, we recommend avoidance of wind and magnetic interferences (e.g. metallic structures adjacent to the individuals selected, grounded conductive structures, power lines, etc.) during measurements. Magnetic declination at each location should be considered to correct for true north. For use in humid environments, we recommend that the device be placed in a resealable, transparent, plastic bag, which can protect the electronic components without interfering with measurements. There is a need to minimize interactions between crown and canopy elements and structural supplementary tools (e.g. ladders, lift platforms, etc.) or between the above-mentioned elements and the researchers themselves. We also highly recommend survey measurements during the day for leaves presenting sun-tracking behaviour. It should be highlighted that the present methodology can involve several devices working together. Efficient field campaigns can therefore be performed by a small work force in relation to time of sampling and coverage of measurements. Finally, the application included in the presented methodology was kept simple regarding software development in order to facilitate portability for the more common mobile operating systems, such as Android, iOS (the Symbian version is available upon request and a free Android version can be downloaded from Google Play website, *Ahmes*). Ultimately, users should estimate the state of preservation of the sensors and their resolution in order to successfully achieve specific aims. We strongly recommend determining whether the device's resolution is suitable for the desired design. This can be achieved by following a calibration process similar to that described herein.

Conclusions

We successfully avoided common constraints in canopy characterization by combining sensitivity, portability and speed of measurements in an affordable and relatively commonplace device. The tests performed support our method as a remarkable tool excelling in field campaigns. Our results demonstrate that the equation implemented in our methodology constitutes a firm estimation of potential instantaneous leaf exposure. The method presented involves direct field measurements providing valuable data in a wide range of ecological scopes (e.g. geometrical approaches, plant modelling, etc.) and functional hypotheses.

We believe that our method is highly relevant in a wide range of scientific approaches. We briefly outline the potential applications in which our methodology could provide insight due to its versatility, even when some of its features are not necessarily involved, such as pollutant deposition/evaporation on planar surfaces, leaf microclimate (proxy for leaf-dwelling organisms), radial location through triangulation (namely, objects of interest within crowns: nests, epiphytes, plagues), slope characterization, termite mound irradiation patterns, spider web spatial arrangement, and many others. To conclude, we would like to emphasize that the methodology presented can play an important role in ecophysiological and educational projects due its affordability to many institutions, researchers and students world-wide.

Acknowledgments

We wish to thank MD Jiménez. A Vázquez, J Serrano, K Carrillo for their valuable assistance during the experimental design. Thanks to F Martínez and to Wasabi App Factory for their expertise and help with the programming and to M Escudero for graphing assistance. We also gratefully acknowledge two anonymous referees for their constructive comments. Special thanks to Mr Cormac de Brun for revision of the English. The presented methodology is a Spanish Patent Pending P201200481. This research was funded by the Spanish Ministry of Science and Education (project CGL2009-10392), through a FPI grant to A.G.E. (BES-2010-032767). We are also indebted to the Madrid Regional Govt. (project REMEDINAL-2, S2009/AMB-1783).

Abbreviations

- m Geomagnetic field
- g Gravitational force
- φ Latitude
- δ Declination
- ω Hour angle

- α Pitch angle
- γ Roll angle
- 1 Midrib azimuth angle
- β Lamina course angle
- ρ Inclination angle
- θ Angle of incidence
- α_r Pitch angle calculated in calibration
- γ_r Roll angle calculated in calibration
- ι_r Midrib azimuth angle calculated in calibration
- β_r Lamina course angle calculated in calibration
- ρ_r Inclination angle calculated in calibration
- SAL_O Silhouette area of the leaf blade 'observed during calibration'
- SAL_E Silhouette area of the leaf blade 'expected during calibration'
- α_T Pitch angle measured by means of traditional methods during validation
- γ_T Roll angle measured by means of traditional methods during validation
- Midn'b azimuth angle measured means of traditional methods during validation
- β_T Lamina course angle measured by means of traditional methods during validation
- ρ_T Inclination angle measured by means of traditional methods during validation
- α_C Pitch angle measured with the cell phone during validation
- γ_C Roll angle measured with the cell phone during validation
- i_C Midrib azimuth angle measured with the cell phone during validation
- β_C Lamina course angle measured with the cell phone during validation
- ρ_C Inclination angle measured with the cell phone during validation
- SAL_T Silhouette area of the leaf blade 'traditional methods field validation'
- SAL_C Silhouette area of the leaf blade 'cell phone field validation'
- SAL₂ Silhouette area of the leaf blade 'graphical methods'
- SAL_r Silhouette area of the leaf blade 'recalculated'

References

- Amarasinghe, R., Dao, D.V., Toriyama, T. & Sugiyama, S. (2006) Simulation, fabrication and characterization of a three-axis piezoresistive accelerometer. Smart Materials and Structures, 15, 1691–1699.
- Asner, G.P. & Martin, R.E. (2011) Canopy phylogenetic, chemical and spectral assembly in a lowland Amazon forest. New Phytologist, 189, 999–1012.
- Barthélémy, D. & Caraglio, Y. (2007) Plant architecture: a dynamic. multilevel and comprehensive approach to plant form, structure and ontogeny. *Annals of Botany*, 99, 375–407.
- Campbell, G.S. & Norman, J.M. (1989) The description and measurement of plant canopy structure. *Plant Canopies: Their Growth, Form and Function* (eds G. Russell, B. Marshall & P.G. Jarvis), pp. 1–19. Cambridge University Press, Cambridge.
- Comstock, J.P. & Mahall, B.E. (1985) Drought and changes in leaf orientation for two California chaparral shrubs: Ceanothus megacarpus and Ceanothus crassifolius. Oecologia, 65, 531–535.
- Denison, R.F., Fedders, J. & Harter, B. (2010) Individual fitness versus whole-crop photosynthesis: solar tracking tradeoffs in alfalfa. Evolutionary Applications, 3, 466-472.

- Ehleringer, J.R. & Comstock, J.P. (1987) Leaf absorptance and leaf angle: mechanisms for stress avoidance. *Plant Response to Stress* (ed J.D. Tenhunen), pp. 55–76. Springer, Berlin.
- Ehleringer, J.R. & Forseth, I.N. (1980) Solar tracking by plants. Science, 210, 1094–1098
- Ehleringer, J.R. & Werk, K.S. (1986) Modifications of solar-radiation absorption patterns and implications for carbon gain at the leaf level. On the Economy of Plant Form and Function (ed. G. & T. J), pp. 57–82. Cambridge University press, London.
- Falster, D.S. & Westoby, M. (2003) Leaf size and angle vary widely across species: what consequences for light interception? *New Phytologist.* 158, 509–525.
- Fleck, S., Niinemets, U., Cescatti, A. & Tenhunen, J.D. (2003) Three-dimensional lamina architecture alters light harvesting efficiency in Fagus: a leaf-scale analysis. *Tree Physiology*, 23, 577-589.
- García-Verdugo, C., Forrest, A.D., Balaguer, L., Fay, M.F. & Vargas, P. (2010) Parallel evolution of insular *Olea europaea* subspecies based on geographical structuring of plastid DNA variation and phenotypic similarity in leaf traits. *Botanical Journal of the Linnean Society*, 162, 54–63.
- Givnish, T.J. (1987) Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. New Phytologist. 106, 131–160.
- Givnish, T.J. (1988) Adaptation to Sun and Shade a Whole-Plant Perspective. Australian Journal of Plant Physiology, 15, 63–92.
- Granado-Yela, C., García-Verdugo, C., Carrillo, K., Rubio de Casas, R., Kleczkowski, L.A. & Balaguer, L. (2011) Temporal matching among diurnal photosynthetic patterns within the crown of the evergreen sclerophyll *Olea eu*ropaea L. Plant Cell and Environment, 34(5), 800–810.
- Gu. L., Baldocchi, D.D., Wofsy, S.C., Munger, J.W., Michalsky, J.J., Urbanski, S.P. & Boden, T.A. (2003) Response of a deciduous forest to the Mount Pinatubo eruption: enhanced photosynthesis. *Science*, 299, 2035–2038.
- Gutschick, V.P. (1999) Biotic and abiotic consequences of differences in leaf structure. New Physologist, 143, 3–18.
- Hallé, F., Oldeman, R.A.A. & Tomlinson, P.B. (1978) Tropical Trees and Forests. An Architectural Analysis. Springer Verlag, Berlin.
- Hanan, J. & Wang, Y.P. (2004) Floradig: a configurable program for capturing plant architecture. Proceedings of the 4th International Workshop on Functional-Structural Plant Models (eds C. Godin, J. Hanan, W. Kurth, A. Lacointe, A. Takenaka, P. Prusinkiewicz, T.M. DeJong, C. Beveridge & B. Andrieu), pp. 407–411. UMR AMAP, Montpellier, France.
- Hansen, H.C. (1917) Leaf-structure as related to environment. American Journal of Botany, 4, 553–560.
- Huang, C., Marsh, S.E., McClaran, M. & Archer, S. (2007) Postfire stand structure in a semiarid savanna: cross-scale challenges estimating biomass. *Ecological Applications*, 17, 1899–1910.
- Jennings, S.B., Brown, N.D. & Sheil, D. (1999) Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. *Forestry*, 72, 59–73.
- Jonckheere, I., Fleck, S., Nackaerts, K., Muys, B., Coppin, P., Weiss, M. & Baret, F. (2004) Review of methods for in situ leaf area index determination: part I. Theories, sensors and hemispherical photography. Agricultural and Forest Meteorology, 121, 19-35.
- Kal, S., Das, S., Maurya, D.K., Biswas, K., Ravi Sankar, A. & Lahiri, S.K. (2006) CMOS compatible bulk micromachined silicon piezoresistive accelerometer with low off-axis sensitivity. *Microelectronics Journal*, 37, 22–30.
- Lowman, M.D. & Schowalter, T.D. (2012) Plant science in forest canopies the first 30 years of advances and challenges (1980–2010). New Phytologist. 194, 12–27.
- Moffett, M.W. (2000) What's up? A critical look at the basic terms of canopy biology. Biotropica, 32, 569–596.
- Monteith, J.L. (1973) Principles of Environmental Physics. American Elsevier Publications, New York.
- Parveaud, C.E., Chopard, J., Dauzat, J., Courbaud, B. & Auclair, D. (2008) Modelling foliage characteristics in 3D tree crowns: influence on light interception and leaf irradiance. *Trees*, 22, 37–104.
- Pearcy, R.W., Muraoka, H. & Valladares, F. (2005) Crown architecture in sun and shade environments, assessing function and trade-offs with a three-dimensional simulation model. *New Phytologist*, 166, 791–800.
- Pearcy, R.W. & Yang, W.M. (1996) A three-dimensional crown architecture model for assessment of light capture and carbon gain by understory plants. *Oecologia*, 108, 1-12.

- Pearcy, R.W., Ehleringer, J.R., Mooney Harold, A. & Rundel, P.W. (1989) Plant Physiological Ecology, Field Methods and Instrumentation. Chapman & Hall, London, GB, 457.
- Pincebourde, S. & Woods, H.A. (2012) Climate uncertainty on leaf surfaces: the biophysics of leaf microclimates and their consequences for leaf-dwelling organisms. *Functional Ecology*, 26, 844–853.
- Posada, J.M., Lechowicz, M.J. & Kitajim, K. (2009) Optimal photosynthetic use of light by tropical tree crowns achieved by adjustment of individual leaf angles and nitrogen content. *Annals of Botany*, **103**, 795–805.
- Room, P.M., Maillette, L. & Hanan, J.S. (1994) Modular and metamer dynamics and virtual plants. Advances in Ecological Research, 25, 105–157.
- Rubio de Casas, R., Vargas, P., Perez-Corona, E., Manrique, E., Quintana, J.R., García-Verdugo, C. & Balaguer, L. (2007) Field patterns of leaf plasticity in adults of the long-lived evergreen Quercus coccifera. *Annals of Botany*. 100, 325-334.
- Rubio de Casas, R., Vargas, P., Pérez-Corona, E., Manrique, E., García-Verdugo, C. & Balaguer, L. (2011) Sun and shade leaves of Olea europaea respond differently to plant size, light availability and genetic variation. Functional Ecology, 25(4), 802–812.
- Sankar, A.R., Das, S. & Lahiri, S.K. (2009) Cross-axis sensitivity reduction of a silicon MEMS piezoresistive accelerometer. *Microsystem Technologies*, 15, 511-518.
- Seidel, D., Fleck, S., Leuschner, C. & Hammett, T. (2011) Review of ground-based methods to measure the distribution of biomass in forest canopies. *Annals of Forest Science*, 68, 225-244.
- Sinoquet, H. & Rivet, P. (1997) Measurement and visualization of the architecture of an adult tree based on a three-dimensional digitising device. *Trees*, 11, 265-270
- Smith, W.K., Vogelmann, T.C., DeLucia, E.H., Bell, D.T. & Shepherd, K.A. (1997) Leaf Form and Photosynthesis. BioScience, 47, 785–793.
- Smith, S.D., Naumberg, E., Niinemets, Ü. & Germino, M. (2004) Leaf to landscape. *Photosynthetic Adaptation Chloroplast to Landscape* (eds W.K. Smith, T.C. Vogelmann & C. Critchley), pp. 262–296. Springer, New York.
- Spencer, J.W. (1971) Fourier series representation of the position of the sun. Search 2, 172.
- Sterck, F.J. & Bongers, F. (2001) Crown development in tropical rain forest trees: patterns with tree height and light availability. *Journal of Ecology*, 89, 1-13.
- Terashima, I. & Hikosaka, K. (1995) Comparative ecophysiology of leaf and canopy photosynthesis. Plant Cell and Environment, 18, 1111–1128.
- Uemura, A., Harayama, H., Koike, N. & Ishida, A. (2006) Coordination of crown structure, leaf plasticity and carbon gain within the crowns of three winter-deciduous mature trees. *Tree Physiology*, 26, 633–641.
- Vogelmann, T.C., Bornman, J.F. & Yates, D.J. (1996) Focusing of light by leaf epidermal cells. *Physiologia Plantarum*, 98, 43–56.
- Walter, H. (1973) Vegetation of the Earth in Relation to Climate and the Ecophysiological Conditions. Springer-Verlag, New York, NY.
- Wang, Y.P. & Jarvis, P.G. (1990) Influence of crown structural properties on PAR absorption, photosynthesis, and transpiration in Sitka spruce: application of a model (MAESTRO). Tree Physiology, 7, 297–316.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, P. et al. (2004) The world-wide leaf economics spectrum. Nature, 428, 821–827.

Received 17 August 2013; accepted 6 November 2013 Handling Editor: Robert Freckleton

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Details of SAL.

Appendix S2. Calibration details.

Appendix S3. Further development.