

A rotated ellipsoidal angle density function improves estimation of foliage inclination distributions in forest canopies

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Abstract

The ‘ellipsoidal distribution’, in which angles are assumed to be distributed parallel to the surface of an oblate or prolate ellipsoid, has been widely used to describe the leaf angle distribution (LAD) of plant canopies. This ellipsoidal function is constrained to show a probability density of zero at an inclination angle of zero; however, actual LADs commonly show a peak probability density at zero, a pattern consistent with functional models of plant leaf display. A ‘rotated ellipsoidal distribution’ is described here, which geometrically corresponds to an ellipsoid in which small surface elements are rotated normal to the surface. Empirical LADs from canopy and understory species in an old-growth coniferous forest were used to compare the two models. In every case the rotated ellipsoidal function provided a better description of empirical data than did the non-rotated function, while retaining only a single parameter. The ratio of *G*-statistics for goodness of fit for the two functions ranged from 1.03 to 3.88. The improved fit is due to the fact that the rotated function always shows a probability density greater than zero at inclination angles of zero, can show a mode at zero, and more accurately characterizes the overall shape of empirical distributions. ©2000 Published by Elsevier Science B.V. All rights reserved.

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1. Introduction

One of the primary physical parameters important in modeling radiation transmission through plant canopies is the angular distribution of canopy elements. The transmission of beam radiation through a plant canopy has commonly been described by a ‘Beer-Lambert law’ function:

$$Q_i = Q_0 \exp(-kLAI) \quad (1)$$

where Q_i is the flux density below the canopy, Q_0 the incoming flux density, LAI the leaf area index for the canopy, and k is the extinction coefficient (Monsi and Saeki, 1953). For a spatially random distribution of leaves, k is equal to ratio of the horizontal projection of leaf area to total leaf area. For flat canopy elements such as leaves, k thus depends entirely on the angular distribution of the elements.

Although probability distributions of leaf angles have sometimes been described using discontinuous functions (such as horizontal, vertical, or conical distributions; see Ross, 1981; Campbell and Norman, 1989), real plant canopies always show a continuous range of leaf angles. The most widely-used continuous function for describing such distributions is the ‘ellipsoidal inclination distribution’, initially described

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by Campbell (1986, 1990). This function was derived as a generalization of the spherical or uniform distribution function (Nichiporovich, 1961; DeWit, 1965), and considers leaves as small surface elements distributed on the surface of a prolate or oblate ellipsoid. A 2-parameter beta distribution has also been employed in some studies (Goel and Strebel, 1984; Kucharik et al., 1998). However, the ellipsoidal distribution function has gained wide use due to the fact that it is described by only a single parameter, and is thought to provide a reasonably accurate description of empirical angle distributions for actual plant canopies. The function has been incorporated in inversion methods for measuring LAI and other aspects of canopy structure based on optical measurements (Campbell and Norman, 1989; Norman and Campbell, 1989; Welles and Norman, 1991; Martens et al., 1993), and is also used extensively in physical optical models of radiation transfer in plant canopies (e.g. Nilson and Kuusk, 1989; Kuusk, 1995).

From a functional and evolutionary perspective, one may also ask how leaves should be distributed in plant canopies (e.g. Horn, 1971, Givnish, 1984; Hirose and Werger, 1987). Although leaf angle has received relatively little attention from this perspective (McMillen and McClendon, 1979; Hikosaka and Hirose, 1997; King, 1997), one generalization to emerge is that horizontal leaf display often maximizes light interception and carbon gain of individual plants. The functional significance of horizontal foliage display in understory plants has long been recognized (Horn, 1971, Givnish, 1984); however, recent work suggests that horizontal foliage may also represent a functional optimum for canopy plants in many situations, due to the effects of lateral shading by neighbors (Hikosaka and Hirose, 1997). These considerations lead one to expect that many plants will show leaf angle distributions in which horizontal leaves are ‘common’. In mathematical terms, the $g(\theta)$ function describing the leaf angle distribution should therefore show a positive probability density at zero, and should also be capable of showing a mode at zero. However, the commonly-used ellipsoidal distribution function is constrained such that $g(0)=0$ for all parameter values. This suggests that the ellipsoidal model may systematically underestimate the frequency of leaf angles near the horizontal, and may thus inaccurately describe the overall shape of leaf angle distributions.

The objectives of this paper are (1) to derive a single-parameter ‘rotated ellipsoidal distribution’ function, similar to the ellipsoidal distribution, but with $g(0)>0$ for all parameter values, and capable of showing a mode at zero; and (2) to quantitatively compare the ability of the ellipsoidal model and the rotated ellipsoidal model to describe empirical foliage angle distributions. Empirical data examined describe representative canopy and understory species in an old-growth Douglas-fir — western hemlock forest in Washington state.

2. A rotated ellipsoidal distribution function

Following Campbell (1990), the angle density function for leaves with surfaces displayed parallel to an ellipsoid shape is:

$$g(\theta) = \frac{2\chi^3 \sin \theta}{\Lambda (\cos^2 \theta + \chi^2 \sin^2 \theta)^2} \quad (2)$$

where θ is the angle from the horizontal, $g(\theta)$ the probability distribution of θ , and χ is the ratio of the horizontal semiaxis length to the vertical semiaxis length of an ellipsoid. For $\chi < 1$,

$$\Lambda = \chi + \frac{(\sin^{-1} \varepsilon)}{\varepsilon}, \quad \varepsilon = (1 - \chi^2)^{1/2} \quad (2a)$$

and for $\chi > 1$,

$$\Lambda = \chi + \frac{\ln [(1 + \varepsilon)/(1 - \varepsilon)]}{2\varepsilon\chi}, \quad \varepsilon = (1 - \chi^{-2})^{1/2} \quad (2b)$$

To find the angle density function for leaves with surfaces displayed normal to the surface of the ellipsoid, $(\theta - \pi/2)$ is substituted for θ in Eq. (2). This yields the ‘rotated ellipsoidal distribution’:

$$g'(\theta) = \frac{2\chi'^3 \cos \theta}{\Lambda' (\sin^2 \theta + \chi'^2 \cos^2 \theta)^2} \quad (3)$$

where $\Lambda' = \Lambda$ and $\chi' = \chi$ in Eqs. (2a) and (2b), above.

For any value of χ' , the rotated ellipsoidal distribution is simply the mirror image of the ellipsoid distribution over the interval 0 to $\pi/2$. Thus, for $\theta = 0$, $g(\theta)$ is zero for the ellipsoidal distribution, but $g'(\theta) = 2/\Lambda'\chi'$ for the rotated ellipsoidal distribution.

In addition, for values of $\chi' < 1$, a leaf angle of zero is the global maximum for $g'(\theta)$. Eq. (3) thus satisfies the goal of obtaining a single-parameter model in which horizontal leaves have a finite probability density, and where horizontal leaves may also represent the distribution mode. For the rotated ellipsoidal distribution values of $\chi' < 1$ correspond to low leaf angles (a planophile leaf display), while values of $\chi' > 1$ correspond to high leaf angles (an erectophile leaf display).

3. Sampling methods

Observations on foliage angle distributions were collected for nine species at the Wind River Canopy Crane site, located within the Thornton T. Munger Research Natural Area of the Gifford Pinchot National Forest (45°49'N 121°58'W), in southern Washington state. Taxa examined included three dominant coniferous canopy trees (*Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Thuja plicata*), two sub-canopy trees (*Taxus brevifolia* and *Abies amabilis*), three understory shrubs (*Gaultheria shallon*, *Berberis nervosa*, and *Acer circinatum*), and one understory herb species (*Achlys triphylla*). Botanical nomenclature follows Hitchcock and Cronquist (1973).

Branchlets are commonly treated as functional foliage units in coniferous trees (Stenberg et al., 1995), and branchlet angle and morphological measurements were also required for estimation of LAI at the study site (S.C. Thomas and W.E. Winner, manuscript in preparation). Therefore, angle measurements were made on branchlet (internode) angles rather than leaves for all coniferous species. For tree species, the crane's gondola was placed at representative locations in the upper and lower canopy layers of 2–3 representative trees, and branchlets were randomly selected for measurement from among foliage units accessible at a given location. In the case of *T. heterophylla*, additional data based on exhaustive measurements made on three harvested branches were also used. For understory shrubs and herbs, foliage units were selected by enumerating ramets within a given area, and randomly selecting leaves within a given ramet. Five leaves/ramet were measured (except where individual ramets possessed fewer than 5 leaves, in which case all leaves were measured). In all cases measurements

of angular deviations from horizontal were made to the nearest 1° using a clinometer (Suunto MC-1D, Espoo, Finland).

Eqs. (2) and (3) were fit to data using numerical approximations to estimate χ and χ' . For Eq. (2), the arithmetic mean angle (a) was calculated and used to estimate χ using the formula: $\chi = -3 + (a/9.65)^{-0.6061}$ (derived from Eq. (16) in Campbell, 1990). For Eq. (3), the same procedure was used, but angles were first transformed as $\theta' = (\pi/2 - \theta)$ to estimate χ' . Empirical data were binned into 10° classes for comparison to predicted values; the latter were generated by numerical integration of Eqs. (2) and (3), using the program Mathematica v. 2.2 (Wolfram Research). Statistical analyses employed G -tests for goodness of fit (Sokal and Rohlf, 1981).

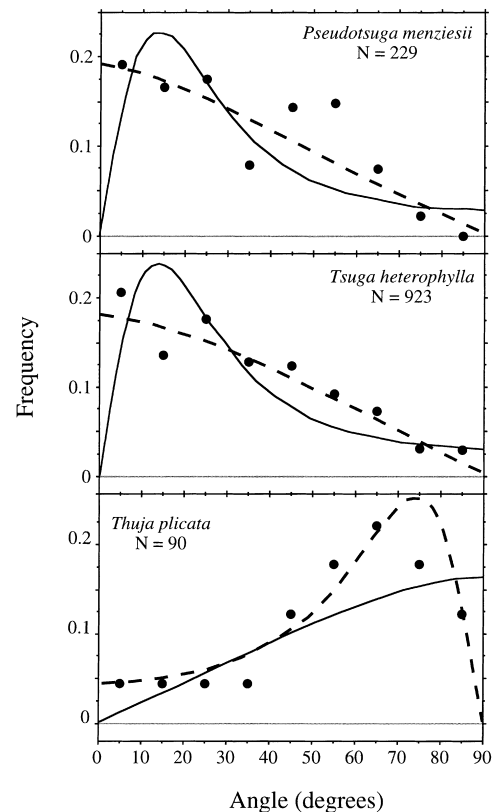


Fig. 1. Leaf angle density functions for three canopy tree species sampled in an old-growth Douglas-fir — western Hemlock forest. The solid line corresponds to the fitted ellipsoidal angle density function, and the dotted line to the rotated ellipsoidal angle density function.

Both functions examined have one parameter; the quantitative values of G -statistics were therefore used to compare goodness of fit between models.

4. Results and discussion

Foliage angle distributions for canopy trees (Fig. 1) as well as sub-canopy trees, herbs, and shrubs (Fig. 2), showed relatively poor agreement with the ellipsoidal distribution model. Goodness of fit tests indicated that distributions deviated significantly from expected values for seven of the nine species examined ($P < 0.01$), including all species with sample sizes greater than 100 (Table 1). For species with relatively plagiophile leaf displays ($\chi' < 1$), the ellipsoidal distribution predicted a pronounced local maximum at leaf angles of 5–20°; however, there was no indication that such a peak was actually present for any species. The

ellipsoidal distribution also tended to systematically underestimate the frequency of foliage angles near 50–70° in canopy tree species, and near 20–40° in several understory species.

Empirical foliage inclination distributions were better approximated by the rotated ellipsoidal model (Figs. 1 and 2). Observed angle distributions appeared to approach a finite value at small inclination angles in all cases, as assumed by the model. Although, statistically significant deviations from the model were detected in six of nine species (Table 1), these deviations showed no obvious systematic pattern across species. Using G -statistic values as an index, the rotated ellipsoidal model resulted in an improved fit to data compared to the ellipsoidal model in every case. The ratio of G -statistics for the two models ranged from 1.03 to 3.88 (Table 1).

The rotated ellipsoidal model, while allowing for peak probability densities at leaf angles of zero,

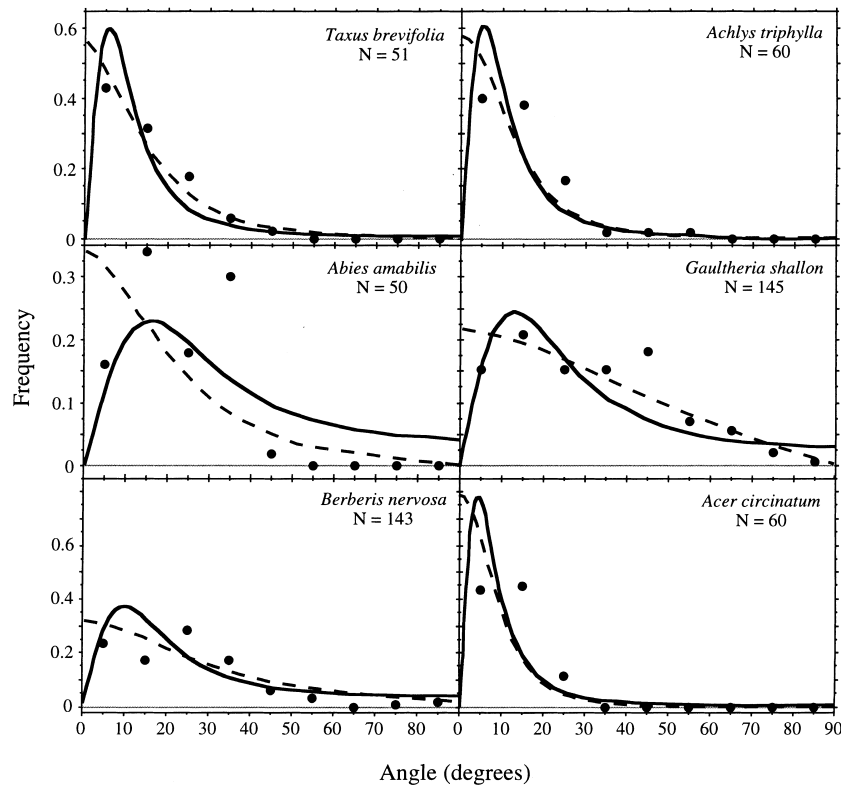


Fig. 2. Leaf angle density functions for sub-canopy and understory species sampled in an old-growth Douglas-fir — western Hemlock forest. The solid line corresponds to the fitted ellipsoidal angle density function, and the dotted line to the rotated ellipsoidal angle density function.

Table 1

Comparison between empirical fits of foliage angle distributions to the ellipsoidal model Eq. (2) vs. the rotated ellipsoidal model Eq. (3) for nine canopy and understory species measured in old-growth forest at the Wind River Canopy Crane site in western Washington state. Measurements on needle-leaved species (denoted *) are for branchlet angles; in other cases measurements are for leaves or scales

Species	N	Mean angle	Ellipsoidal model			Rotated ellipsoidal model			Ratio of $G_E : G_{RE}$
			χ	G_E	P	χ'	G_{RE}	P	
Canopy trees									
<i>P. menziesii</i> *	229	32°	2.63	58.8	<0.0001	0.92	22.6	0.0020	2.60
<i>T. plicata</i>	90	58°	0.94	12.6	0.1266	2.57	5.4	0.7140	2.33
<i>T. heterophylla</i> *	923	33°	2.53	117.9	<0.0001	0.96	30.4	0.0002	3.88
Understory trees									
<i>A. amabilis</i> *	50	21°	4.20	33.0	<0.0001	0.54	27.8	<0.0001	1.19
<i>T. brevifolia</i> *	51	14°	6.20	6.5	0.1643	0.33	4.9	0.2999	1.33
Understory shrubs									
<i>A. circinatum</i>	60	11°	7.80	24.2	<0.0001	0.25	23.6	<0.0001	1.03
<i>B. nervosa</i>	143	24°	3.61	66.8	<0.0001	0.64	19.0	0.0019	3.51
<i>G. shallon</i>	144	31°	2.78	23.9	0.0023	0.86	9.8	0.2777	2.44
Understory herbs									
<i>A. triphylla</i>	60	14°	6.18	11.0	0.0009	0.34	9.7	0.0018	1.14

also assumes a probability density of zero for vertical leaves. The data presented suggest that this is a reasonable assumption for forest species. As expected, understory species consistently showed relatively planophile leaf displays ($\chi' < 1.0$), and also displayed probabilities of vertical foliage that approached zero. The dominant canopy species at the study site, *P. menziesii* and *T. heterophylla*, showed foliage angle distributions that approximated a rotated circular distribution (with $\chi' \cong 1.0$). *T. plicata*, which possesses an erectophile foliage display ($\chi' = 2.57$), also showed a marked drop in probability density for angle values approaching 90° (Fig. 1).

An examination of previous empirical studies of leaf angle distributions suggests that the results presented here have wide generality. Leaf angle distributions have been reported for a coppice stand of *Castanea sativa* in Britain (Ford and Newbould, 1971, Fig. 8), and for a mixed deciduous forest in Tennessee, USA (Hutchison et al., 1986, Fig. 3). Both data sets exhibit peak probability density of leaf angles is zero for sub-canopy foliage layers, both studies show finite probability densities for horizontal foliage for all canopy layers, and both studies also show $g(\theta)$ functions that approach zero for foliage angles near 90°. Some crop species, such as sunflower (Lemour, 1973; Campbell, 1986) also show deviations from the ellipsoidal model

similar to those described here, with the fitted function exhibiting a ‘false peak’ near 10–20°.

In conclusion, the rotated ellipsoidal model presented appears to be a better approximation to empirical foliage inclination distributions in forest canopies than is the widely-used ellipsoidal model. The improved fit is also accomplished without addition of parameters or loss of model flexibility. However, it should be emphasized that any statistical model describing the spatial distribution of plant parts will necessarily be an approximation of the situation in nature. Also, the model presented here, while justified on functional grounds, is not based on any formal model of either physiological or selective processes. Rather, we have sought to provide a tractable statistical description that captures some important qualitative generalizations derived from functional analyses. It is to be hoped that a more accurate representation of $g(\theta)$ functions in forest canopies will lead to improved models of canopy light transmission, and increased accuracy in inversion-based estimates of canopy structure.

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