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Comparison of leaf angle distribution functions: Effects on extinction coefficient and fraction of sunlit foliage

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Abstract

Leaf angle distribution is a key parameter to characterize canopy structure and plays a crucial role in controlling energy and mass balance in soil-vegetation-atmosphere-transfer system. Several leaf angle distribution functions found in literature have been proposed to account for the non-random distribution of leaf inclination angle with one or two parameters. In this paper, these leaf angle distribution functions (Beta distribution function, ellipsoidal function, rotated-ellipsoidal function, Verhoef's algorithm and de Wit's functions) were compared with field data collected in the First ISLSCP Field Experiment (FIFE) project and two sites within Ku-ring-gai Chase National Park, Sydney, Australia. All functions performed reasonably well. However, the comparison showed that the two-parameter functions including the Beta distribution function and Verhoef's algorithm commonly were more consistent predictors than one-parameter functions. *G*-statistics and χ^2 test applying to the estimates of leaf angle distribution demonstrated that Beta function presented more robustness over other functions, even the ellipsoidal leaf distribution function which has been widely used. Furthermore, the predictions of leaf angle distribution by these functions were used to calculate extinction coefficient and to separate foliage into sunlit and shaded parts. The results suggested that, ellipsoidal function may be suitable to be retrieved with remotely-sensed data and to compute extinction coefficient and fraction of sunlit foliage because this function requires only a single parameter, namely the ratio of the horizontal semi-axis length to the vertical semi-axis length of an ellipsoid. Finally, the comparison of three approaches (Nilson's, Fuchs' and Ross–Goudriaan's algorithms) for computing extinction coefficient indicated that, there was no significant difference between the three approaches.

Keywords: Leaf angle distribution; Extinction coefficients; Beer's law; Sunlit foliage

1. Introduction

One primary parameter to simulate radiation transmission through the canopy is the angular distribution of leaves. Generally, the radiative transfer within a vegetative canopy and the interception of light by a plant canopy can be described by the gap frequency model (Nilson, 1971),

$$P(r_s) = \exp(-K(r_s)L), \tag{1}$$

where $P(r_s)$ represents the probability of beam radiation penetrating a canopy without being captured at an incident direction r_s, L the leaf area index for the canopy, and $K(r_s)$ the so-called extinction coefficient (Monsi and Saeki, 1953). For the leaves randomly distributed in space, $K(r_s)$ is the mean projection of unit leave area on the plane perpendicular to the direction of

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beam r_s and is mainly determined by the angular distribution of the leaves and r_s which is represented by zenith and azimuth angles of beam.

The two-big-leaf (Wang and Leuning, 1998; Dai et al., 2004) and sun/shaded (de Fury and Farquhar, 1997) models has been widely used to integrate foliage photosynthesis, transpiration, conductance and temperature from leaves to whole canopy. Following the study by Wilson (1967) and Isobe (1969), these models divide the canopy into sunlit and shaded fractions through,

$$F_{\text{sun}} = \frac{(1 - \exp(-K(r_s)L))}{K(r_s)L}, \tag{2}$$

$$F_{\text{shade}} = 1 - F_{\text{sun}}, \tag{3}$$

where F_{sun} and F_{shade} are the projected fractions of sunlit and shaded leaves, respectively. Separation into sunlit and shaded foliage is important in scaling canopy processes such as photosynthesis and conductance, due to the fact that the responses of foliage to diffuse and direct solar radiation are different (Gu et al., 2002).

Leaf angle distribution also is a key parameter to represent canopy structure and plays a crucial role in determining energy and mass balance and microclimate of intra- and inter-canopy (Thanisawanyangkura et al., 1997). Leaf angle distribution, which interacts to the micro-climatic environment (Mooney et al., 1977; Hegazy and Amry, 1998) and light competition (Hikosaka and Hirose, 1997), are extremely variable for intra- and inter-species of plant canopy (Hutchison et al., 1986; Jane et al., 2001) and exhibit a highly spatial and temporal variability (Wirth et al., 2001).

Although leaf angle distribution is crucial for mass and energy balance modeling, few approaches have been proposed to estimate leaf angle distribution from remotely-sensed data, unlike the study of leaf area index (Jonckheere et al., 2004; Weiss et al., 2004; Casa and Jones, 2005; Fang and Liang, 2005) and clumping index (Lacaze et al., 2002; Chen et al., 2005). Sensitivity analysis demonstrated that, a spherical leaf angle distribution, which is commonly assumed for a vegetative canopy, may result in significant underestimation of light transmission (Stadt and Lieffers, 2000). Recently, Widlowski et al. (2004) has evaluated the feasibility of retrieving leaf angle distribution with multi-angular remotely-sensed data. An objective of this paper is to find the appropriate candidate function for leaf angle distribution with a view to the algorithm design for retrieving leaf angle distribution.

Efforts simplifying the measurements of leaf angle distribution have resulted in numerous methods including both retrieval with remotely-sensed data (Kucharik et al., 1997) and mathematical description (de Wit, 1965; Goel and Strebel, 1984; Campbell, 1990; Thomas and Winner, 2000; Teh et al., 2000). Despite the fundamental importance of leaf angle distribution functions, few comparisons and validations have been conducted due to the lack of field measurements which traditionally are laborious, time-consuming and require repeated determination as the canopy develops (Daughtry, 1990).

The aims of this paper are to, (1) quantitatively compare the performance of leaf angle distribution functions to describe the empirical leaf angle distributions and find an appropriate function for the retrieval of leaf angle distribution with remotely-sensed data; (2) estimate the effects of leaf angle distribution functions on extinction coefficients and the separation of sunlit and shaded leaves; (3) compare different approaches for computing extinction coefficient.

The relationship between extinction coefficient and leaf angle distribution is introduced in Section 2. Section 3 presents five distribution functions of leaf angle. A brief description of field data and analysis methods is given in Section 4. The comparison results are shown in Section 5. A brief conclusion and summary are provided in Section 6.

2. Relationships between extinction coefficient and leaf angle distribution

Several approaches have been proposed to compute extinction coefficient from leaf angle distribution. Different procedures are taken into account for the effect of leaf angle and direction of beam path.

2.1. Nilson's algorithm

Following the pioneering works by Nilson (1971) and Ross (1981), the extinction coefficient is related to the mean projection of unit leaf area on the plane perpendicular to beam direction by:

$$K(\theta, \phi) = \frac{G(\theta, \phi)}{\cos(\theta)}, \tag{4}$$

where the projection of foliage area, $G(\theta, \phi)$, is represented by leaf angle distribution through,

$$G(\theta, \phi) = \frac{1}{2\pi} \int_0^{2\pi} d\phi_L \int_0^{\pi/2} f(\theta_L, \phi_L) \cos(\vec{r_L r}) \sin\theta_L \, d\theta_L, \tag{5}$$

where $f(\theta_L,\phi_L)$ is the leaf angle distribution and can be written as $f(\theta_L)$ under the assumption of symmetric distribution of leaf azimuth angle. The term $\cos(\vec{r_L r})$ is the directional cosine between the leaf's normal (r_L) and the incident beam (r) and can be expressed as,

$$\cos(\vec{r_L r}) = \cos(\theta)\cos(\theta_L) + \sin(\theta)\sin(\theta_L)\cos(\phi_L - \phi), \tag{6}$$

where θ and ϕ are the zenith and azimuth angles of beam direction, θ_L and ϕ_L the inclination and azimuth angles of vegetation foliage, respectively.

Commonly, leaf azimuth angle is assumed to be random. Then the computation of G can be simplified as (Wilson, 1960),

$$G(\theta) = \int_0^{\pi/2} A(\theta,\theta_L) f(\theta_L) d\theta_L. \tag{7}$$

In above equation, $A(\theta, \theta_L)$ is given by,

$$A(\theta,\theta_L) = \begin{cases} \cos\theta\cos\theta_L, & |\cot\theta\cot\theta_L| > 1 \\ \cos\theta\cos\theta_L[1 + (2/\pi)(\tan\psi - \psi)], & \text{otherwise} \end{cases}, \tag{8}$$

where $\psi = \cos^{-1}(\cot\theta\cot\theta_L)$.

Basically, the measurements of leaf angle distribution are binned to leaf angle intervals ranging from 0 to $\pi/2$. Thus, the relationship between G and discrete leaf angle observations is,

$$G(\theta) = \sum_{j=1}^{N} h_j(\theta) f_j, \tag{9}$$

where f_j is the leaf area fraction of interval centered at θ_j, N the total number of leaf angle intervals, and $h_j(\theta)$ is computed by,

$$h_j(\theta) = \int_{\theta_{j-1}}^{\theta_j} A(\theta,\theta_L)\, d\theta_L, \tag{10}$$

where $A(\theta, \theta_L)$ is defined by Eq. (8).

2.2. Fuchs' algorithm

Fuchs et al. (1984) proposed a simple formula to compute G values with mean leaf angle,

$$G = \cos(\bar{\theta}_L), \tag{11}$$

where $\bar{\theta}_L$ is the mean leaf inclination angle.

2.3. Ross–Goudriaan's algorithm

A so-called χ_L index defined by Ross (1975) to characterize the departure of the actual leaf angle distribution from a spherical one is expressed as (Goudriaan, 1977),

$$\chi_L = \pm \int_0^{\pi/2} |\sin\theta_L - f_s(\theta_L)| d\theta_L, \tag{12}$$

where $f_s(\theta_L)$ is the spherical leaf angle distribution. Thus $\chi_L = 0$ for spherical leaf angle distribution, +1 for horizontal foliage, -1 for vertical foliage. Goudriaan (1977) provided a fitted nonlinear expression to estimate the average leaf projection in any direction given the value of χ_L,

$$G(\theta) = \phi_1 + \phi_2\cos\theta, \quad \phi_1 = 0.5 - 0.633\chi_L - 0.33\chi_L^2, \; \phi_2 = 0.877(1 - 2\phi_1). \tag{13}$$

2.4. Suits' algorithm

Suits proposed a relationship between G and incident angle as following (Suits, 1972),

$$G(\theta) = e_L\cos\theta + \frac{2}{\pi}(1 - e_L)\sin\theta, \tag{14}$$

where e_L is a parameter to be determined and related to the leaf angle distribution. In this paper, by means of least squares method, e_L was estimated by fitting to G values computed with leaf angle measurement through Nilson's algorithm.

3. Models for leaf angle distribution functions

Leaf angle distribution function is generally defined as the probability density of leaf angle, namely the fraction of leaf area per unit leaf zenith angle or leaf azimuthal angle. To compute the fraction of leaves between leaf inclination angles (from horizontal) θ_1 and θ_2, leaf angle distribution function can be integrated from θ_1 to θ_2.

3.1. de Wit's leaf angle distribution functions

For species with no preferred azimuthal direction, de Wit (1965) proposed six special functions to characterize leaf angle distribution.

The six functions are:

planophile, where horizontal leaves are most frequent, namely,

$$f(\theta_L) = \frac{2}{\pi}(1 - \cos 2\theta_L), \tag{15}$$

where $f(\theta_L)$ is the probability density function, θ_L the leaf inclination angle in radian;

erectophile, where vertical leaves are most frequent,

$$f(\theta_L) = \frac{2}{\pi}(1 + \cos 2\theta_L); \tag{16}$$

plagiophile, where oblique leaves are most frequent,

$$f(\theta_L) = \frac{2}{\pi}(1 - \cos 4\theta_L); \tag{17}$$

extremophile, where oblique leaves are least frequent,

$$f(\theta_L) = \frac{2}{\pi}(1 + \cos 4\theta_L); \tag{18}$$

spherical, where the relative frequency of leaf angle is the same as for surface elements of a sphere,

$$f(\theta_L) = \sin \theta_L; \tag{19}$$

uniform, where proportion of leaf angle is the same at any angle,

$$f(\theta_L) = \frac{2}{\pi}. \tag{20}$$

3.2. Two-parameter Beta distribution

Goel and Strebel (1984) have employed two-parameter Beta distribution to represent leaf angle distribution for a variety of vegetation canopies. If θ_L is the leaf inclination angle in radians and $t = 2\theta_L/\pi$, the probability density of leaf angle distribution is given by,

$$f(t) = \frac{1}{B(\mu, \nu)}(1 - t)^{\mu-1} t^{\nu-1} \tag{21}$$

where ν and μ are two parameters, $B(\mu, \nu)$ the Beta function (Abramowitz and Stegun, 1972) defined as,

$$B(\mu, \nu) = \int_0^1 (1 - x)^{\mu-1} x^{\nu-1}\,dx = \frac{\Gamma(\mu)\Gamma(\nu)}{\Gamma(\mu + \nu)}, \tag{22}$$

where Γ is Gamma function computed with GNU Scientific Library (Galassi et al., 2003) based on the formulae proposed by Abramowitz and Stegun (1972).

Parameters ν and μ are related to mean $\bar{t}$ by,

$$\nu = \bar{t}\left(\frac{\sigma_0^2}{\sigma_t^2} - 1\right), \tag{23}$$

$$\mu = (1 - \bar{t})\left(\frac{\sigma_0^2}{\sigma_t^2} - 1\right), \tag{24}$$

where σ_0^2 and σ_t^2 are the maximum standard deviation and variance of t, respectively, and expressed as,

$$\sigma_0^2 = \bar{t}(1 - \bar{t}), \tag{25}$$

$$\sigma_t^2 = \mathrm{var}(t). \tag{26}$$

The form of Beta distribution presented by Eqs. (21)–(26) is a bit different from the original one proposed by Goel and Strebel (1984) to improve the readability.

3.3. Ellipsoidal distribution function

The ellipsoidal function initially described by Campbell (1990) has been widely used to represent leaf angle density. Based on the assumption that the angular distribution of leaves in a canopy is similar to the distribution of area on the surface of a prolate or oblate ellipsoid, the leaf angle density function was derived as a generalization of the spherical distribution function. This function is expressed by,

$$f(\theta_L) = \frac{2\chi^3 \sin \theta_L}{\Lambda(\cos^2\theta_L + \chi^2 \sin^2\theta_L)^2}, \tag{27}$$

where χ is the ratio of the horizontal semi-axis length to the vertical semi-axis length of an ellipsoid, θ_L leaf inclination angle, and Λ a parameter determined by χ. When $\chi = 1$, the ellipsoidal distribution becomes spherical and $\Lambda = 2$.

For $\chi < 1$,

$$\Lambda = \chi + \frac{\sin^{-1}\epsilon}{\epsilon}, \qquad \epsilon = (1 - \chi^2)^{1/2}, \tag{28}$$

and for $\chi > 1$,

$$\Lambda = \chi + \frac{\ln[(1 + \epsilon)/(1 + \epsilon)]}{2\epsilon\chi}, \qquad \epsilon = (1 - \chi^{-2})^{1/2}. \tag{29}$$

The relationship between χ and mean leaf angle is,

$$\chi = -3 + \left(\frac{\bar{\theta}_L}{9.65}\right)^{-0.6061}, \tag{30}$$

where $\bar{\theta}_L$ is the mean leaf angle and defined as,

$$\bar{\theta}_L = \int_0^{\pi/2} \theta_L f(\theta_L) d\theta_L. \tag{31}$$

For the discrete leaf angle measurements, Eq. (31) is written as,

$$\bar{\theta}_L = \sum_{j=0}^{N} \theta_j f_j, \tag{32}$$

where f_j is the leaf area fraction for a leaf angle interval centered at θ_j.

3.4. Rotated-ellipsoidal distribution function

From ecological perspective, horizontal foliage may represent a functional optimum for canopy plants in many situations and be very common. However, the ellipsoidal function is constrained to show a peak probability density of zero at an inclination of zero, a pattern inconsistent with this ecological theory. To overcome this, Thomas and Winner (2000) described a rotated ellipsoidal distribution function, which geometrically corresponds to an ellipsoid in which small surface elements are rotated normal to the surface. The rotated ellipsoidal distribution function is given as,

$$f(\theta_L) = \frac{2\chi'^3 \cos\theta_L}{\Lambda'(\sin^2\theta_L + \chi'^2 \cos^2\theta_L)^2}, \tag{33}$$

where $\Lambda' = \Lambda$, θ_L leaf inclination angle, and $\chi' = \chi$ of Eqs. (28) and (29).

3.5. Verhoef's algorithm

A linear combination of trigonometric functions used to model the leaf angle distribution (Verhoef, 1997) is presented as,

$$y = a \sin x + \frac{b \sin 2x}{2}, \tag{34}$$

where, a and b are two parameters, x and y are related to the cumulative leaf inclination distribution $F(\theta_L)$, which is defined as the fraction of leaf area where the leaf inclination is less than θ_L, through,

$$\begin{aligned} x &= \frac{\pi}{2}F(\theta_L) + \theta_L, \\ y &= \frac{\pi}{2}F(\theta_L) - \theta_L. \end{aligned} \tag{35}$$

For a given value of θ_L, the corresponding $F(\theta_L)$ can be obtained by means of numerical resolution of Eqs. (34) and (35). Pseudo codes for this resolution are as follows:

$x = 2\theta_L$

Repeat

$y = a \sin x + \frac{b \sin 2x}{2}$

$\Delta x = \frac{y - x + 2\theta_L}{2}$

$x = x + \Delta x$

Until $|\Delta x| < t$

$F(\theta_L) = \frac{2(y + \theta_L)}{\pi}$

where, t is a threshold value and needs to be set at small value, e.g. 10^{-6}.

By using the cumulative leaf inclination distribution function $F(\theta_L)$, the fraction of leaf area in an inclination interval θ_1 to θ_2 can be represented by the difference of $F(\theta_L)$ between θ_1 and θ_2.

Parameters of this algorithm can be determined with field measurements. Suppose that F_i is available from field measurements, $\zeta_i = (\pi/2)F_i + \theta_i$ and $\eta_i = (\pi/2)F_i - \theta_i$, the parameters a and b can be determined by,

$$\begin{aligned} a &= \frac{\beta\gamma - \alpha\delta}{\xi\beta - \alpha^2}, \\ b &= \frac{2(\xi\delta - \alpha\gamma)}{\xi\beta - \alpha^2}, \end{aligned} \tag{36}$$

where, $\xi = \sum_{i=0}^{N} \sin\zeta_i$, $\alpha = \sum_{i=0}^{N} \sin\zeta_i \sin(2\zeta_i)$, $\beta = \sum_{i=0}^{N} \sin^2(2\zeta_i)$, $\gamma = \sum_{i=0}^{N} \eta_i \sin\zeta_i$, $\delta = \sum_{i=0}^{N} \eta_i \sin(2\zeta_i)$, and N the total number of leaf angle intervals.

4. Materials and methods

4.1. Leaf angle data set

Two data sets used to compare leaf angle distribution functions included the measurements from the First International Satellite Land-Surface Climatology Project (ISLSCP) Field Experiment (FIFE) project around the Konza Prairie (Li, 1994) and two sites of Ku-ring-gai Chase National Park, Sydney, Australia (Falster and Westoby, 2003).

The leaf angle data of FIFE were obtained during the 1987 growing season for 12 types of plant canopies which mainly were herbaceous, from the Konza Long-Term Ecological Research (LTER) area. These data were measured with spatial coordinate apparatus (Lang, 1973). The leaf angle measurements were distributed into bins based their angle values. The azimuth and zenith angle bins had intervals of 36 and 9.5°, respectively. The center angle of each bin were reported for both leaf azimuth and zenith. The leaf area and percent leaf area located each leaf angle bin were given in the data set. A detailed description of FIFE project refers to Sellers et al. (1988, 1992).

The second data set use measurements from two sites. One site was high-nutrient and contained an overstorey to 20 m dominated by *Syncarpia glomulifera*, *Eucalyptus umbra*, *Livistona australis* and under-story dominated by woody shrubs, climbers, ferns and cycads. Another site was low-nutrient and fire-prone low open sclerophyll woodland with a species rich understorey of woody shrubs, and emergent *eucalypts* to 15 m. The leaf angle data set of the two sites had a step of 5° in leaf inclination angle and included 38 plant species.

To illustrate the statistical characteristic of field data, the mean, standard deviation and specified type of de Wit's functions for each species are presented in Tables 1 and 2.

The results show that, except for *extremphile*, the other five of de Wit's functions occur. There was no explicit relationship between mean leaf angle and given type.

4.2. Analysis procedures

There were two ways to fit the leaf angle distribution functions. First, these functions were directly fitted to the measurements of leaf angle distribution. Eqs. (23) and (24) were employed for the determination of parameters of Beta function, Eq. (30) for ellipsoidal and rotated-ellipsoidal functions, and Eq. (36) for Verhoef's algorithm. For de Wit's functions, one of six functions was selected by least squared estimator. Then, the estimates of leaf angle distribution by these functions were compared with field data.

Beside the above fitting approaches of the functions, G values calculated with leaf angle measurements can be used to fit leaf angle distribution functions. The variations of G with incident angle were computed with leaf angle measurements using Nilson's algorithm. Then nonlinear least squares (Bates and Watts, 1988) was employed to fit leaf angle distribution functions to G.

Statistic program R v.2.2.0 (Ihaka and Gentleman, 1996) was used to conduct the nonlinear regression, numerically integrate the probability density function of leaf angle distribution and predict leave area fraction for specified leaf angle. The G-test (Sokal and Rohlf, 1994), Pearson's χ^2 test and root mean squares (RMS) error were used to demonstrate the goodness of fit.

By employing Nilson's algorithm and assuming uniform leaf azimuthal distribution, extinction coefficients computed using Nilson's algorithm from fitted leaf angle distribution were compared with those from measurements. Fraction of sunlit foliage also was calculated with estimated extinction coefficients.

Three algorithms for computing extinction coefficient were compared and evaluated after being applied to leaf angle distribution measurements. In total, leaf angle measurements of 50 species (including 12 species of FIFE and 38 species of Australia) were concerned in this study.

Table 1
The statistical characteristic (i.e. mean, standard deviation, classic type of leaf angle distribution) of field measurements of FIFE and mean and standard deviation of Beta and ellipsoidal functions

Species name	Statistical characteristic			Mean and S.D. of estimates			
	Mean	S.D.	Type	Mean of Beta	S.D. of Beta	Mean of Ellipsoidal	S.D. of Ellipsoidal
Andropogon gerardii	62.32	20.84	Erectophile	62.08	20.97	58.93	19.17
Vernonia baldwinii	40.17	16.61	Plagiophile	40.17	16.73	39.82	23.23
Panicum virgatum-facing down	72.72	13.95	Erectophile	72.44	13.83	62.31	16.75
Panicum virgatum-facing up	68.01	16.59	Erectophile	67.84	16.41	60.71	17.61
Cornus drummondii	57.37	21.84	Spherical	57.31	20.35	57.51	21.01
Rhus glabra	55.96	16.26	Spherical	55.96	16.47	56.98	21.59
Andropogon gerardii	61.25	22.05	Erectophile	60.45	26.23	58.61	19.53
Asclepias veridis	54.86	21.18	Spherical	54.83	20.56	55.78	21.88
Solidago missouriensis	39.47	17.59	Plagiophile	39.47	17.87	39.09	23.18
Ceanothus herbaceous	39.98	19.33	Plagiophile	39.98	19.82	39.62	23.22
Symphoricarpos orbiculatus	33.97	18.51	Planophile	33.98	18.61	33.37	22.44
Sorghastrum nutans	72.55	13.88	Erectophile	72.29	13.79	62.25	16.78

Table 2
The statistical characteristic (i.e. mean, standard deviation, classic type of leaf angle distribution) of field measurements of two sites of Australia and mean and standard deviation of Beta and ellipsoidal functions

Species name	Statistical characteristic			Mean and S.D. of estimates			
	Mean	S.D.	Type	Mean of Beta	S.D. of Beta	Mean of Ellipsoidal	S.D. of Ellipsoidal
Acacia floribunda	57.22	22.40	Spherical	57.18	22.39	57.55	21.10
Acacia myrtifolia	64.03	19.10	Erectophile	63.98	19.08	59.56	18.68
Acacia suaveolens	72.18	17.09	Erectophile	71.92	16.92	62.31	16.91
Angophora hispida	50.61	21.17	Spherical	50.60	21.20	51.17	22.76
Astrotricha floccosa	32.72	14.67	Planophile	32.72	14.74	32.12	22.15
Banksia marginata	51.55	22.48	Spherical	51.54	22.51	52.20	22.61
Banksia oblongifolia	45.95	21.89	Uniform	45.95	21.93	46.08	23.25
Boronia pinnata	44.51	19.62	Plagiophile	44.51	19.67	44.51	23.30
Breynia oblongifolia	33.33	16.46	Planophile	33.33	16.53	32.75	22.27
Conospermum longifolium	71.54	13.67	Erectophile	71.49	13.68	62.08	17.01
Epacris pulchella	44.99	22.00	Uniform	44.99	22.04	45.03	23.29
Eriostemon australasius	62.85	19.94	Erectophile	62.79	19.92	59.20	19.04
Eucalyptus gummifera	55.76	22.14	Spherical	55.73	22.14	56.83	21.66
Eucalyptus haemastoma	64.91	17.59	Erectophile	64.88	17.60	59.84	18.43
Gompholobium latifolium	22.73	16.47	Planophile	22.77	16.48	22.38	19.11
Grevillea buxifolia	47.85	22.03	Uniform	47.84	22.06	48.14	23.11
Grevillea speciosa	58.58	20.30	Spherical	58.56	20.32	57.94	20.55
Hakea dactyloides	60.93	20.07	Erectophile	60.89	20.07	58.62	19.68
Hibbertia bracteata	48.20	22.26	Uniform	48.20	22.30	48.53	23.07
Isopogon anemonifolius	48.29	21.70	Uniform	48.29	21.74	48.63	23.06
Kunzea capitata	55.91	20.51	Spherical	55.90	20.55	57.00	21.62
Lambertia formosa	56.49	15.96	Spherical	56.49	16.02	57.35	21.40
Lasiopetalum ferrugineum	42.92	19.10	Plagiophile	42.92	19.16	42.80	23.31
Leptospermum spp.	67.43	16.62	Erectophile	67.39	16.62	60.66	17.80
Leptospermum trinervium	58.40	19.33	Spherical	58.39	19.36	57.89	20.61
Leucopogon microphyllus	53.20	22.14	Spherical	53.18	22.16	54.02	22.28
Lomatia siliafolia	48.45	20.12	Plagiophile	48.45	20.18	48.81	23.05
Persoonia lanceolata	64.79	17.45	Erectophile	64.76	17.47	59.80	18.47
Persoonia levis	70.90	14.59	Erectophile	70.84	14.58	61.85	17.11
Phyllota phylicoides	48.78	21.20	Plagiophile	48.78	21.25	49.16	23.01
Pomaderris ferruginea	30.49	11.98	Planophile	30.49	12.07	29.88	21.62
Pultenaea daphnoides	36.73	18.20	Plagiophile	36.73	18.26	36.24	22.85
Pultenaea elliptica	45.17	23.88	Uniform	45.17	23.90	45.23	23.28
Pultenaea stipularis	61.89	18.94	Erectophile	61.86	18.95	58.91	19.35
Rapanea variabilis	35.91	18.72	Planophile	35.91	18.78	35.39	22.73
Synoum glandulosum	42.15	16.92	Plagiophile	42.15	16.98	41.97	23.29
Syncarpia glomulifera	37.47	19.57	Plagiophile	37.47	19.62	37.01	22.94
Trema aspera	64.79	17.37	Erectophile	64.77	17.39	59.80	18.47

5. Results

5.1. Leaf angle distribution functions

Leaf area fraction for specified leaf angle interval was estimated with leaf angle distribution functions by integrating the functions over each leaf angle bin. Measurements and estimates of leaf angle distribution were plotted versus central angles of each leaf angle interval for FIFE (Fig. 1). Due to the large number of plant species, the plots of two sites in Australia were not presented here.

Using G-test of Beta functions as a benchmark, the ratio values of G-test of de Wit's functions, ellipsoidal and rotated-ellipsoidal functions to Beta function were computed and shown for the plant species of FIFE sites (Table 3) and two sites in Australia (Table 4). That G-test ratio values of given function was greater than unity meant that the performance of this function was poor when being compared with Beta function. Otherwise, the performance of this function was better than Beta function. Beside G-test, χ^2 test were presented in Tables 3 and 4.

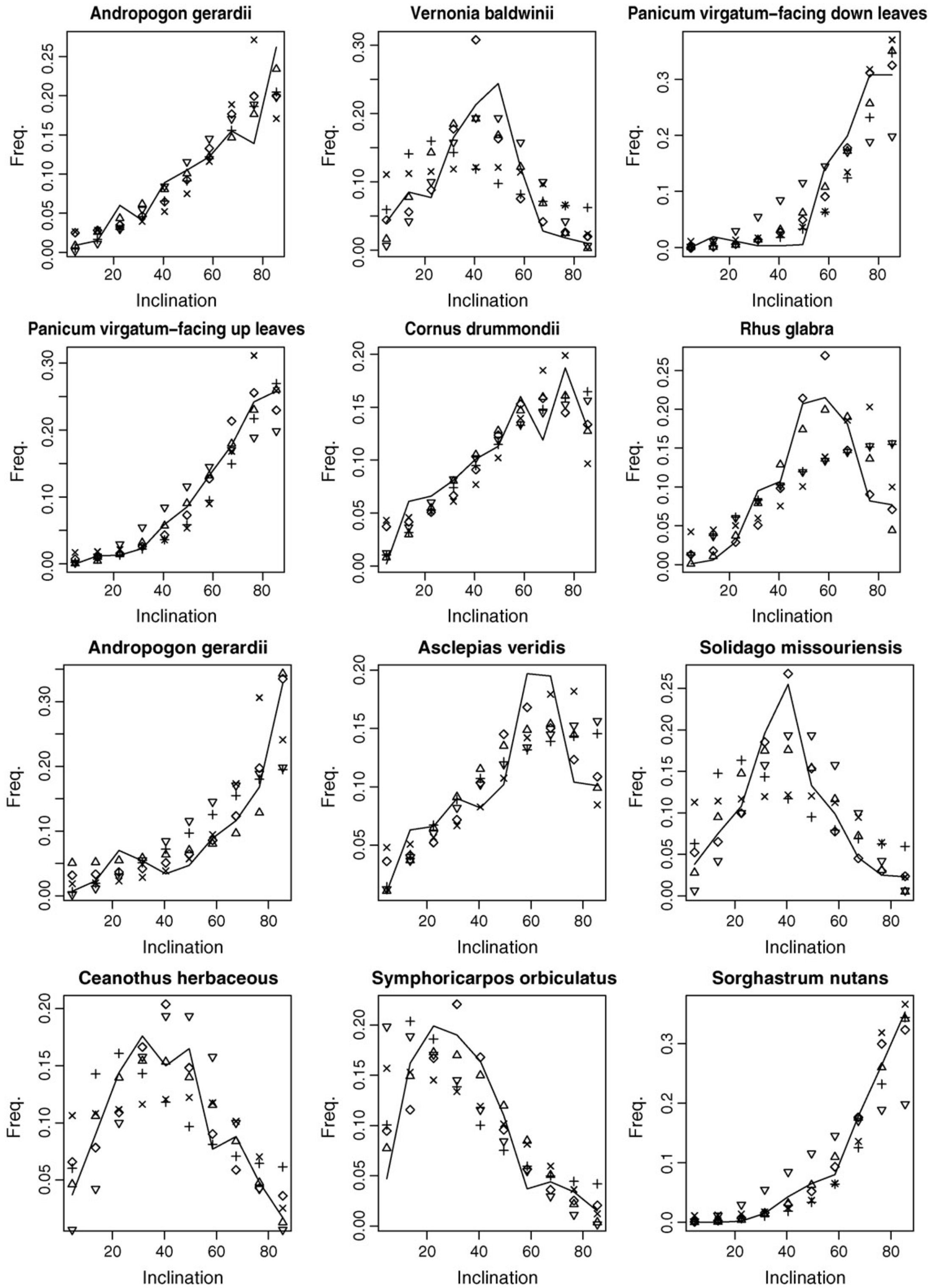

Fig. 1. Plots of measurements of leaf angle distribution measurements (solid line), and estimation with Beta (△), ellipsoidal (+), rotated-ellipsoidal (×), Verhoef's (◇), and de Wit's (▽) functions.

Table 3
Comparison of leaf angle distribution functions with χ^2 and *G*-ratio using leaf angle data of FIFE

Species name	χ^2					*G*-statistic ratio			
	Beta	Ellipsoidal	Rotated	Verhoef	de Wit	Ellipsoidal	Rotated	Verhoef	de Wit
Andropogon gerardii	0.037	0.052	0.247	0.104	0.067	1.52	6.29	2.71	2.12
Vernonia baldwinii	0.167	0.745	0.578	0.12	0.3	3.60	2.95	0.80	1.61
Panicum virgatum-facing down	0.21	0.4	0.488	0.659	1.68	0.59	0.65	0.76	3.33
Panicum virgatum-facing up	0.009	0.022	0.065	0.019	0.114	1.93	3.26	0.49	9.62
Cornus drummondii	0.058	0.081	0.937	0.671	0.087	1.21	4.83	3.61	1.13
Rhus glabra	0.07	0.547	2.247	0.21	0.537	5.13	9.17	1.58	5.11
Andropogon gerardii	0.339	0.2	0.212	0.118	0.298	1.0	1.13	0.46	1.48
Asclepias veridis	0.072	0.093	0.235	0.126	0.108	1.32	2.18	1.37	1.48
Solidago missouriensis	0.086	0.344	0.383	0.017	0.213	3.36	3.49	0.18	2.29
Ceanothus herbaceous	0.03	0.213	0.214	0.09	0.176	5.52	5.72	2.62	5.98
Symphoricarpos orbiculatus	0.105	0.189	0.362	0.090	0.568	1.81	2.85	0.89	4.09
Sorghastrum nutans	0.017	0.040	0.118	0.032	0.717	2.17	2.37	1.37	24.89

As shown in Table 3, for most species, excluding *Panicum virgatum* with downward facing leaves, the *G*-ratio values of one-parameter functions including ellipsoidal and rotated-ellipsoidal function were greater than or equal to unity. However, the *G*-ratio values of Verhoef's algorithm were less than unity for 6 of 12 species and greater than unity for other 6 species. For all plant species, the *G*-ratio values of de Wit's functions were greater than unity. The ratio values between ellipsoidal function and rotated-ellipsoidal function were nearly equal to each other although *G*-test of rotated ellipsoidal function were a bit less than ellipsoidal function for several species.

Table 4 indicates that the *G*-test ratios for 11 of 38 species were less than unity for the ellipsoidal function. For 8 of 38 species, *G*-test ratio values of ellipsoidal function were near or equal to unity. However, only for four species, *G*-ratio values of rotated-ellipsoidal function were less than unity. For most species, excluding *Angophora hispida* and *Persoonia levis*, the fact that the *G*-statistics values of ellipsoidal function were less than rotated-ellipsoidal function indicated that ellipsoidal function performed better than rotated-ellipsoidal function for these species. *G*-test ratio values of Verhoef's algorithm were less than those of Beta function for 14 species, and greater than those of Beta function for other species. For almost all species, excluding *Pomaderris ferruginea*, *G*-test ratio values of de Wit's functions were greater than unity. χ^2 test gave the similar results with *G* statistic. RMS errors for every distribution function were presented as follows.

The results from Tables 5 and 6 were consistent with Tables 3 and 4. These comparisons demonstrated that two-parameter functions, including Beta function and Verhoef's algorithm, performed better than one-parameter functions including ellipsoidal and rotated-ellipsoidal functions for most species. Although no distinct difference between two-parameter functions was observed for FIFE observations, the estimations of Beta function were closer to the observations at Australian sites than Verhoef's algorithm for about 63% of all species. Among one-parameter functions, ellipsoidal function gave more close results than rotated-ellipsoidal function for most species.

To compare one-parameter and two-parameter functions, the mean and standard deviation of leaf angle computed with ellipsoidal and Beta functions which were the best of the one-parameter and two-parameter functions, respectively, are shown in Tables 1 and 2. Overall, the mean and standard deviation of Beta function were more close to the measurements than ellipsoidal function. For some species including *Conospermum longifolium*, *Acacia suaveolens* and *Leucopogon microphyllus*, although the *G*-ratio or χ^2 test of ellipsoidal function were less than unity or those of Beta function, the mean and standard deviation predicted by Beta function were more accurate than ellipsoidal function. This fact showed that, for these species, mean and standard deviation cannot exactly represent the leaf angle distribution. The reason behind this may lie in the existing of discontinuities or jumping in the curves of leaf angle distribution which were illustrated in Fig. 1.

5.2. Extinction coefficient

Assuming that the azimuthal angle is uniformly distributed and the zenith angles of incident beam are between 0 and 40°, respectively, the extinction coefficients were calculated with the predictions of

Table 4
Comparison of leaf angle distribution functions with χ^2 and G-ratio using leaf angle data of two sites of Australia

Species name	χ^2					G-statistic ratio			
	Beta	Ellip	Rotated	Verhoef	de Wit	Ellip	Rotated	Verhoef	de Wit
Acacia floribunda	0.007	0.014	0.167	0.080	0.011	2.19	21.22	7.50	1.81
Acacia myrtifolia	0.180	0.147	0.242	0.175	0.201	0.86	1.19	0.88	1.10
Acacia suaveolens	0.137	0.057	0.115	0.060	0.619	0.57	0.82	0.21	3.99
Angophora hispida	0.226	0.470	0.194	0.293	0.774	1.63	0.60	0.99	2.36
Astrotricha floccosa	0.256	0.719	0.835	0.081	1.06	1.75	2.18	0.21	3.16
Banksia marginata	0.048	0.033	0.291	0.163	0.104	0.75	4.50	2.27	2.27
Banksia oblongifolia	0.153	0.154	0.337	0.180	0.429	1.07	1.90	1.19	2.29
Boronia pinnata	0.034	0.159	0.372	0.112	0.095	3.74	6.80	2.52	3.34
Breynia oblongifolia	0.030	0.542	0.465	0.072	0.575	10.26	9.35	1.81	10.84
Conospermum longifolium	0.075	0.103	0.147	0.081	0.137	0.89	1.16	0.78	2.35
Epacris pulchella	0.041	0.041	0.075	0.050	0.084	0.75	3.92	1.69	4.70
Eriostemon australasius	0.058	0.054	0.079	0.039	0.055	0.77	1.83	0.80	1.23
Eucalyptus gummifera	0.075	0.075	0.108	0.080	0.076	1.0	1.85	1.21	1.0
Eucalyptus haemastoma	0.073	0.087	0.119	0.071	0.079	0.91	1.18	0.51	1.14
Gompholobium latifolium	0.110	0.097	0.135	0.078	0.137	0.59	0.89	0.49	1.59
Grevillea buxifolia	0.026	0.032	0.068	0.044	0.078	1.31	8.63	3.82	12.76
Grevillea speciosa	0.024	0.039	0.084	0.039	0.036	1.77	10.87	3.34	2.11
Hakea dactyloides	0.035	0.042	00.0	0.047	0.043	1.03	2.78	1.03	1.33
Hibbertia bracteata	0.040	0.041	0.075	0.049	0.080	1.06	4.33	1.97	5.96
Isopogon anemonifolius	0.041	0.043	0.081	0.052	0.088	1.03	5.10	2.35	7.31
Kunzea capitata	0.025	0.039	0.085	0.044	0.041	2.18	15.95	6.46	2.27
Lambertia formosa	0.131	0.178	0.201	0.143	0.177	1.08	1.81	0.68	1.02
Lasiopetalum ferrugineum	0.111	0.138	0.143	0.119	0.123	1.14	1.59	0.98	1.64
Leptospermum spp.	0.047	0.072	0.087	0.047	0.081	1.08	1.18	0.51	2.73
Leptospermum trinervium	0.053	0.067	0.0105	0.065	0.061	1.41	3.29	1.13	1.51
Leucopogon microphyllus	0.024	0.017	0.086	0.039	0.046	0.46	14.64	5.10	3.50
Lomatia siliafolia	0.049	0.082	0.091	0.050	0.080	2.37	3.00	0.78	3.30
Persoonia lanceolata	0.025	0.057	0.106	0.053	0.032	2.86	16.62	4.45	1.98
Persoonia levis	0.069	0.099	0.098	0.053	0.136	1.00	0.45	0.44	3.19
Phyllota phylicoides	0.045	0.048	0.091	0.043	0.091	0.97	4.99	1.45	5.39
Pomaderris ferruginea	0.097	0.220	0.220	0.180	0.215	2.13	1.46	1.84	0.65
Pultenaea daphnoides	0.040	0.097	0.109	0.068	0.128	5.39	7.88	2.95	8.12
Pultenaea elliptica	0.038	0.023	0.074	0.042	0.055	0.37	4.00	1.43	2.42
Pultenaea stipularis	0.018	0.040	0.099	0.052	0.021	3.93	34.11	11.69	1.60
Rapanea variabilis	0.102	0.125	0.139	0.125	0.168	1.10	2.34	1.36	3.59
Synoum glandulosum	0.042	0.130	0.130	0.079	0.054	10.70	12.02	3.23	1.89
Syncarpia glomulifera	0.045	0.081	0.094	0.046	0.126	2.22	3.78	1.06	6.52
Trema aspera	0.068	0.097	0.098	0.048	0.086	1.12	1.58	0.53	1.45

leaf angle distribution functions using Nilson's algorithm. The results show that, for the FIFE sites (Fig. 2) and the Australian sites (Fig. 3), the slope of the regression line increases with the solar zenith angle. As expected, the estimated extinction coefficients with two-parameter functions are very close to those with measurements. The deviation varied for different species depending on leaf angle distribution.

To compute the extinction coefficient, the parameters of the leaf angle distribution functions were estimated and then leaf angle distributions were calculated based on these functions and parameters. Although extinction coefficients computed with different estimates of leaf angle distributions were very close at nadir, the difference between them increased with the zenith angle of the incident beam. Apparently, the estimations by two-parameter functions were more close to measurements than those by one-parameter functions especially for large incident zenith angle. There was no obvious difference between two two-parameter functions for nadir incident angle. Different approaches were performed to compute extinction coefficients. Although the deviation between these approaches were very small, they increased with large incident zenith angle (the result is not presented).

Leaf angle distribution functions and Suits' algorithm were used to fit the angular variation of G values for incident angles ranging from 0 to $\pi/2$. After getting

Table 5
The root mean squares (RMS) error of each distribution function compared with leaf angle measurements of FIFE

Species name	Root mean squares error				
	Beta	Ellip	Rotated	Verhoef	de Wit
Andropogon gerardii	0.056	0.085	0.175	0.100	0.093
Vernonia baldwinii	0.116	0.223	0.200	0.138	0.117
Panicum virgatum-facing down	0.105	0.144	0.128	0.081	0.221
Panicum virgatum-facing up	0.018	0.064	0.093	0.053	0.097
Cornus drummondii	0.062	0.069	0.096	0.075	0.063
Rhus glabra	0.079	0.170	0.195	0.081	0.171
Andropogon gerardii	0.082	0.161	0.182	0.059	0.180
Asclepias veridis	0.092	0.111	0.109	0.085	0.0116
Solidago missouriensis	0.103	0.189	0.187	0.039	0.134
Ceanothus herbaceous	0.055	0.114	0.122	0.083	0.123
Symphoricarpos orbiculatus	0.071	0.119	0.150	0.085	0.175
Sorghastrum nutans	0.034	0.076	0.082	0.052	0.201

the parameters for each function with least squares, these functions were used to estimate leaf angle distribution and compute G values with Nilson's algorithm. The comparisons of G values for different fitted functions and leaf angle measurements of FIFE are presented in Fig. 4.

Fig. 4 shows large differences between estimated and measured G-value for some species, especially *Cornus drummondii* and *Rhus glabra*. Apparently, for most species the estimates of G values with two-parameter functions were more close to the estimates with measurements than one-parameter functions, especially rotated-ellipsoidal, de Wit's functions and Suits' algorithm. The similar observations were obtained from the results obtained with measurements of Australian sites (which were not presented). The

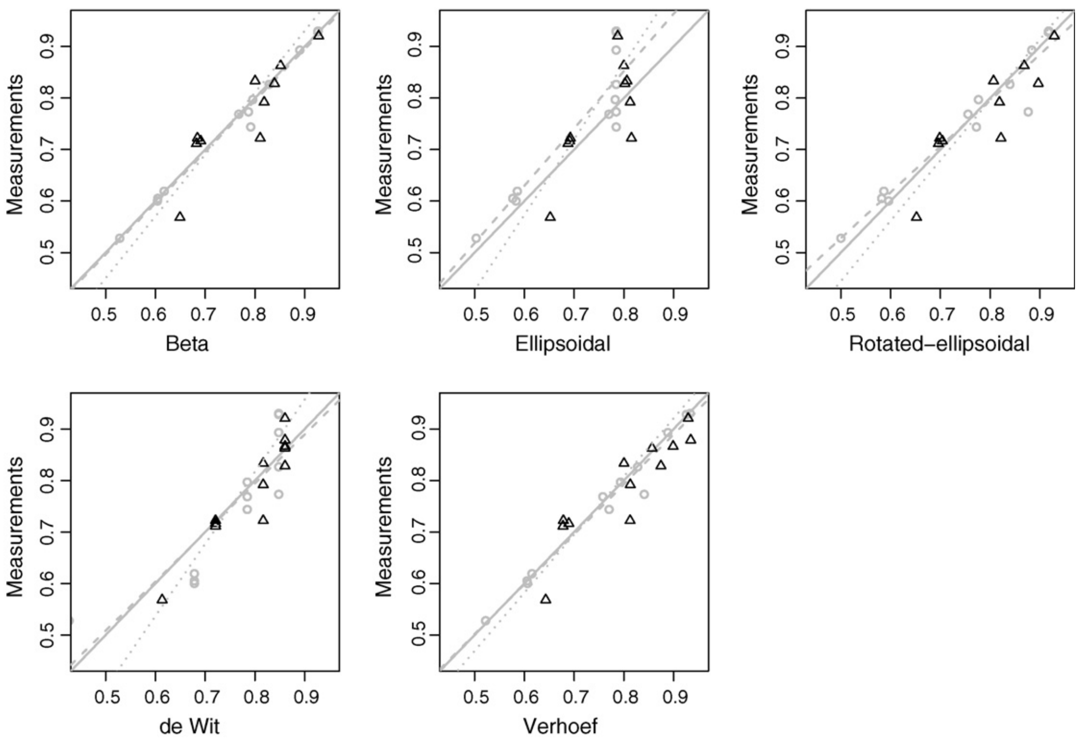

Fig. 2. Plots of extinction coefficient for different species with measurements of FIFE. θ_s was set to 0° (○) and 40° (△). Solid line and dash lines correspond to 1:1 line and regression lines, respectively.

Table 6
The root mean squares (RMS) error of each distribution function compared with leaf angle measurements of two sites of Australia

Species name	Root mean squares error				
	Beta	Ellip	Rotated	Verhoef	de Wit
Acacia floribunda	0.018	0.023	00.0	0.035	0.024
Acacia myrtifolia	0.096	0.099	0.117	0.100	0.098
Acacia suaveolens	0.099	0.070	0.123	0.052	0.181
Angophora hispida	0.093	0.10	0.103	0.103	0.127
Astrotricha floccosa	0.130	0.226	0.221	0.068	0.227
Banksia marginata	0.051	0.047	0.092	0.059	0.076
Banksia oblongifolia	0.075	0.083	0.094	0.081	0.106
Boronia pinnata	0.041	0.077	0.097	0.060	0.066
Breynia oblongifolia	0.039	0.130	0.129	0.055	0.146
Conospermum longifolium	0.075	0.103	0.147	0.081	0.137
Epacris pulchella	0.041	0.041	0.075	0.050	0.084
Eriostemon australasius	0.058	0.054	0.079	0.039	0.055
Eucalyptus gummifera	0.075	0.076	0.108	0.08	0.076
Eucalyptus haemastoma	0.073	0.087	0.119	0.071	0.079
Gompholobium latifolium	0.110	0.097	0.135	0.078	0.137
Grevillea buxifolia	0.026	0.032	0.068	0.044	0.078
Grevillea speciosa	0.024	0.039	0.084	0.039	0.036
Hakea dactyloides	0.035	0.042	00.0	0.047	0.043
Hibbertia bracteata	0.040	0.041	0.075	0.049	0.080
Isopogon anemonifolius	0.041	0.043	0.081	0.052	0.088
Kunzea capitata	0.025	0.039	0.085	0.044	0.041
Lambertia formosa	0.131	0.178	0.201	0.142	0.177
Lasiopetalum ferrugineum	0.111	0.138	0.143	0.119	0.123
Leptospermum spp.	0.047	0.072	0.087	0.047	0.081
Leptospermum trinervium	0.053	0.067	0.105	0.065	0.061
Leucopogon microphyllus	0.024	0.017	0.086	0.039	0.046
Lomatia siliafolia	0.049	0.082	0.091	0.050	0.080
Persoonia lanceolata	0.025	0.057	0.106	0.053	0.032
Persoonia levis	0.069	0.099	0.098	0.053	0.136
Phyllota phylicoides	0.045	0.048	0.091	0.043	0.091
Pomaderris ferruginea	0.097	0.220	0.220	0.180	0.216
Pultenaea daphnoides	0.040	0.097	0.109	0.068	0.128
Pultenaea elliptica	0.038	0.023	0.075	0.042	0.055
Pultenaea stipularis	0.018	0.041	0.099	0.051	0.021
Rapanea variabilis	0.102	0.124	0.139	0.125	0.168
Synoum glandulosum	0.042	0.130	0.130	0.079	0.054
Syncarpia glomulifera	0.045	0.081	0.094	0.046	0.0126
Trema yaspera	0.068	0.097	0.098	0.048	0.086

parameter of Suits' model, e_L, ranged from 0 to 1 and was related to leaf angle distribution. To quantitatively determine this relationship, the variation of e_L with the mean leaf angle was fitted with linear model. A linear expression obtained from this regression was,

$$e_L = -1.266\frac{2\bar{\theta}_L}{\pi} + 1.193, \tag{37}$$

where, $\bar{\theta}_L$ was the mean leaf angle in radian. A correlation efficient of 0.97 was found for above equation with the measurements of leaf angle distribution.

Fig. 4 indicates that, the performance of Suits' algorithm is poor compared with other algorithms for most species, especially for *Cornus drummondii* and *Rhus glabra* which are supposed to be spherical distribution.

5.3. Separation of sunlit and shaded foliage

Assuming leaf area index be 4.0 and solar zenith angle be 0 and 40°, respectively, the estimates of leaf angle distribution with different functions were used to compute the fraction of sunlit foliage for the measurements of FIFE (Fig. 5) and Australian sites (Fig. 6).

Similarly, for the separation of sunlit and shaded foliage, two-parameter leaf angle distribution functions performed better than one-parameter functions especially for large incident zenith angle. Beta function may

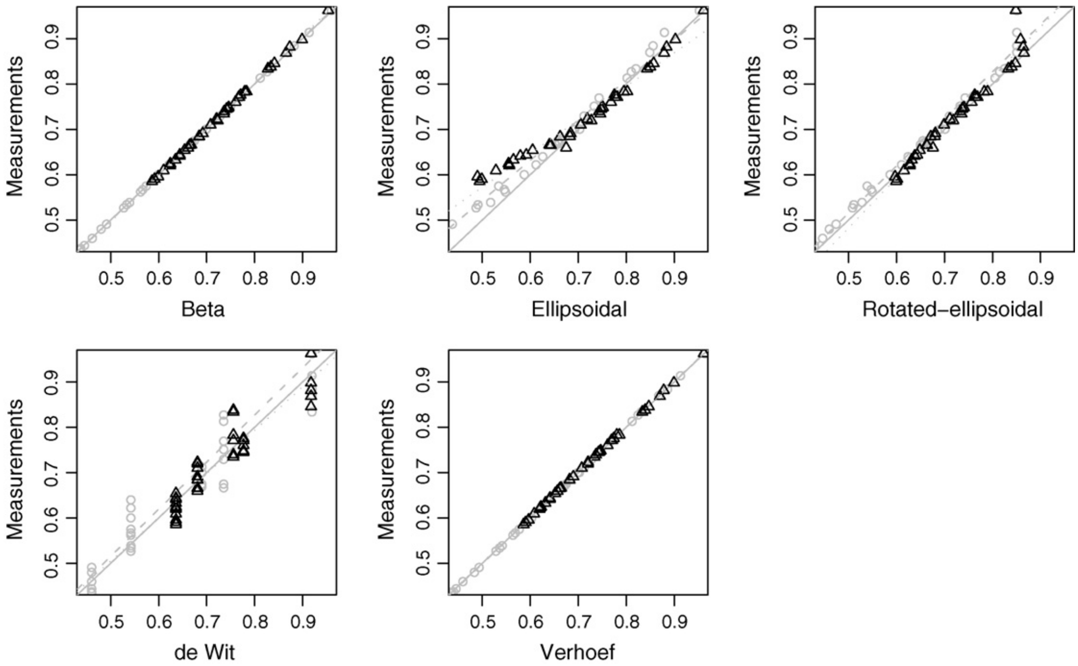

Fig. 3. Plots of extinction coefficient for different species with measurements of two sites in Australia. θ_s was set to 0° (○) and 40° (△). Solid line and dash lines correspond to 1:1 line and regression lines, respectively.

be the best one among all functions to split vegetation foliage. However, for nadir incident direction, the difference between different functions was very small and may be neglected.

6. Summary and conclusion

Leaf angle distribution is one of the key parameters to simulate radiative transfer and energy and mass balance of vegetative canopies. Five leaf angle distributions functions have been proposed to account for the non-random distribution of leaf inclination angle. One or two parameters of these functions were to be estimated with leaf angle measurements. In this paper, these five leaf angle distribution functions were evaluated with two data sets including FIFE and two sites in Australia.

The performance of two-parameter functions is better than one-parameter function for nearly all plant species because only one-parameter, which often is estimated with mean leaf angle, is not enough to describe some leaf angle distributions, which may contain a dual-mode structure or a varied cluster of leaf area fraction with leaf angle. The involvement of standard deviation in Beta function may be a large improvement on the representation of probability density distribution of leaf angle. The fact that *G*-test values of Verhoef's algorithm was greater than those of Beta function for most species demonstrated that, Beta function may be the more appropriate function to simulate leaf angle distribution. On the contrary, for several species, although Beta function can predict much closer mean and standard deviation of leaf angle to measurements than one-parameter function, *G*-ratio or χ^2 test showed a better performance of one-parameter function than Beta function. This may be due to the discontinuities and interrupts of distribution of leaf angle as shown in Fig. 1. For one-parameter functions, a rotation of ellipsoidal function may not improve much its performance for most plant species, which is different from the study conducted by Thomas and Winner (2000) although their conclusion was made based on plant physiological theory.

Nilson's algorithm was applied to leaf angle estimates to compute extinction coefficients. The results showed that, leaf angle functions had a relatively small effect on the estimates of extinction coefficients when the incident beam was in nadir. The deviations from true values increased with the zenith angle of incident beam. An error of about 0.2 on extinction coefficient with ellipsoidal function may be found when the incident zenith angle of beam is 40°.

Although the relatively poor performance of rotated-ellipsoidal function, the estimates of extinction coefficients with rotated-ellipsoidal function was deviated less from those with measurements than

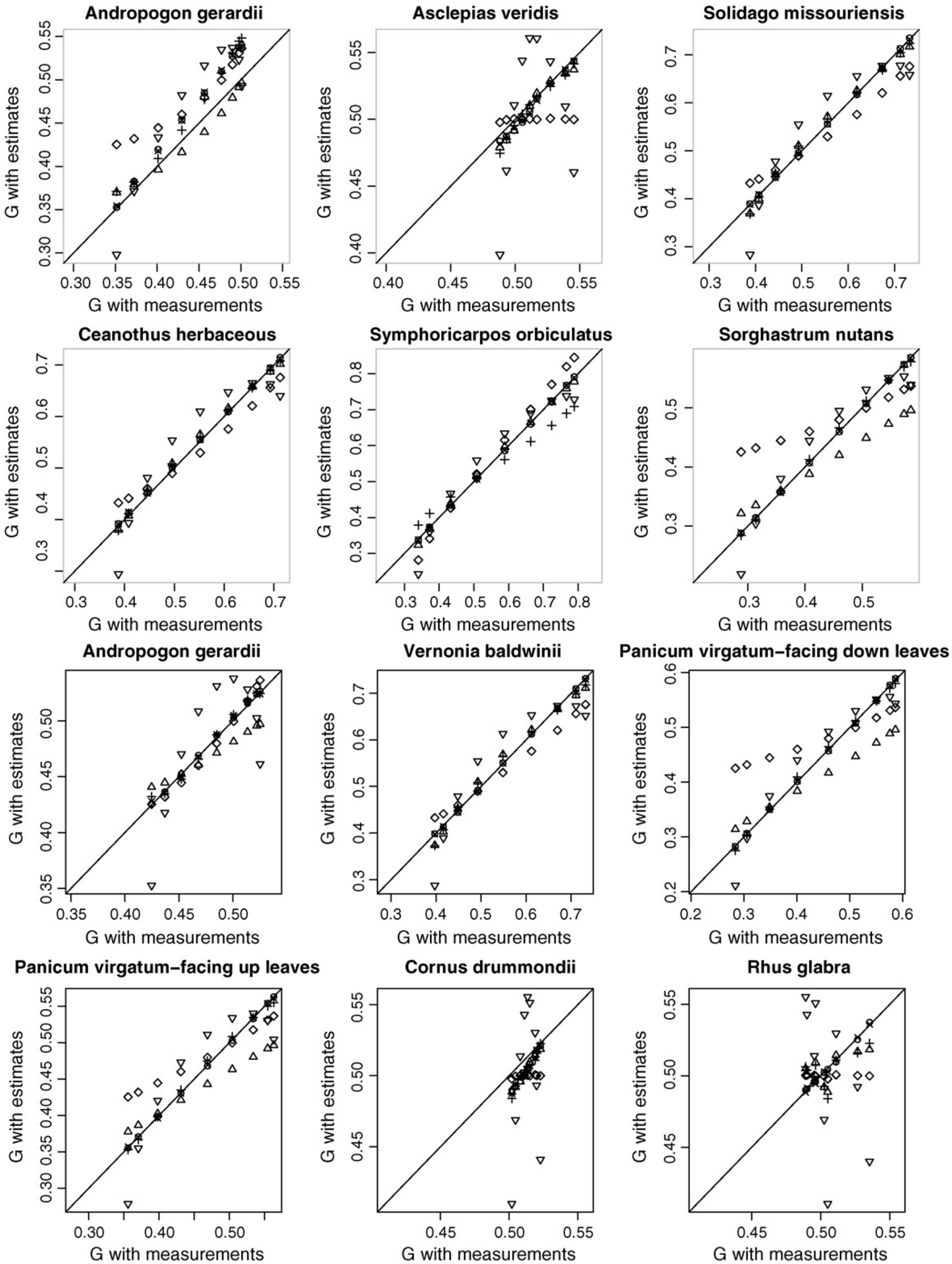

Fig. 4. Plots of extinction coefficients computed by measurements of FIFE vs. leaf angle distribution functions, which are fitted to extinction coefficients, including Beta (○), ellipsoidal (△), rotated-ellipsoidal (+), Verhoef's (×), de Wit's (◇), and Suits' (▽) functions. Solid line corresponds to 1:1 line.

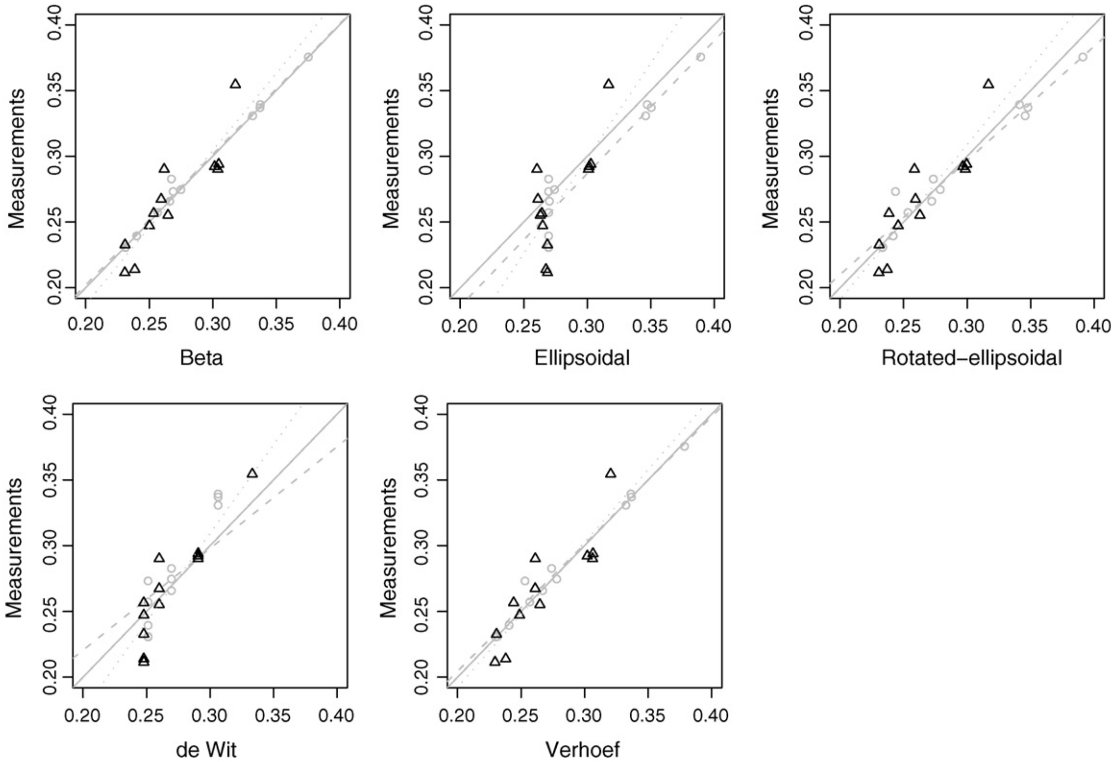

Fig. 5. Plots of fraction of sunlit foliage for different species with measurements of FIFE. θ_s was set to 0° (◯) and 40° (△). Solid line and dash lines correspond to 1:1 line and regression lines, respectively.

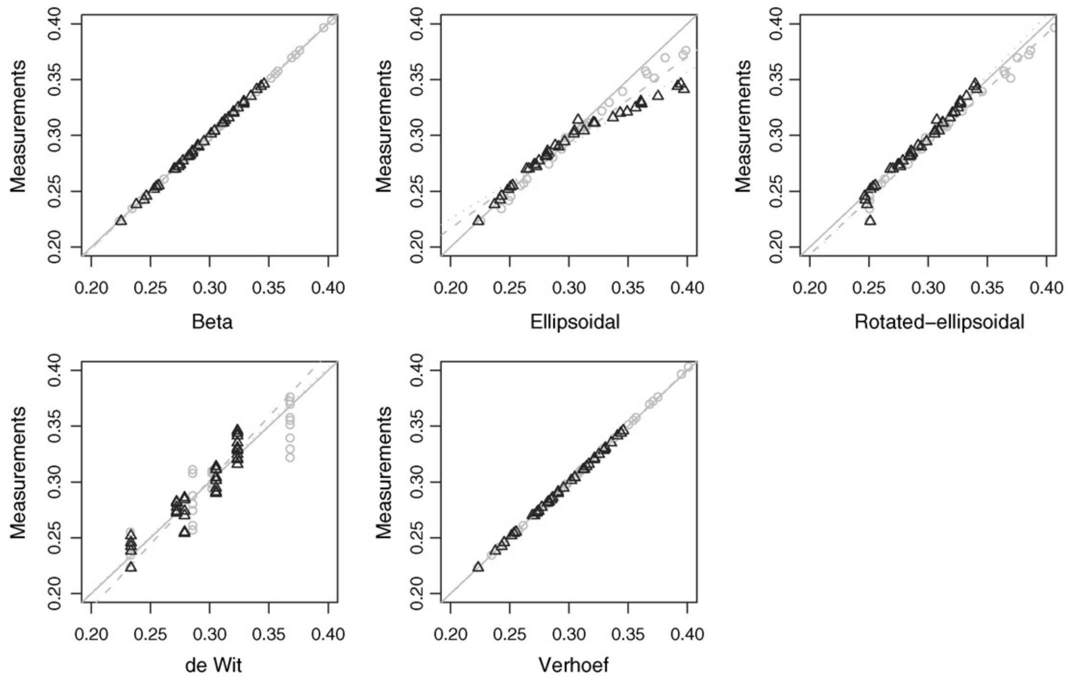

Fig. 6. Plots of fraction of sunlit foliage for different species with measurements of two sites in Australia. θ_s was set to 0° (◯) and 40° (△). Solid line and dash lines correspond to 1:1 line and regression lines, respectively.

ellipsoidal function. The fact may be explained by that, G-test is used to evaluate the probability density distribution and gives a larger weight value to the leaf inclination angle of larger leaf area fraction. However, extinction coefficients are computed based on the projection of foliage geometry and give larger weight value to the foliage which are perpendicular to the direction of incident beam and commonly do not coincide with those of large leaf area fraction. Different approaches gave close estimates of extinction coefficients for nadir incident beam. However, deviations between them increased with the zenith angle of incident beam. Fuchs' algorithm may not be appropriate for large zenith angle of incident beam due to the large deviation from other two algorithms. In fact, Fuch's and Ross–Goudriaan's algorithms were derived and simplified based on different assumptions of leaf angle distribution and these simplifications may not be needed any more now due to the improvements of computing capability. Similar with the pattern of extinction coefficients, the predictions of sunlit foliage fraction with leaf angle distribution functions were close to those from in situ measurements when the incident beam is in nadir. The deviations increased with incident angle. As being expected, ellipsoidal function also gave closer estimates than those of rotated-ellipsoidal function.

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