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Estimation of plant area index of grasslands from measurements of canopy radiation profiles

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Abstract

A method is presented by which a simple physical model of radiative transfer may be used to estimate the vertical distribution of the plant area index (PAI) from measurements of average photosynthetically active radiation at various heights within the canopy and a known phytoelement inclination distribution. Eight semi-natural mountain grasslands, differing in land use, are investigated. Using a set of baseline parameters obtained from the literature, predicted plant area indices compare both qualitatively and quantitatively favourably with those determined from destructive harvesting. Model predictions are shown to be sensitive to the phytoelement dispersion coefficient and phytoelement optical properties. Due to mutually opposing effects on PAI predictions, their parameterisation is found to be critical. Predictions assuming a spherical phytoelement angle distribution are demonstrated to be not significantly different from those based on measured inclination distributions.

Keywords: Canopy structure; Line quantum sensor; Model; Mountain grassland; PPFD

1. Introduction

The amount and spatial distribution of plant matter plays a central role in the biosphere–atmosphere exchange of mass, energy and momentum. Quantifying canopy structure is therefore essential to the understanding of these processes, both from a theoretical, modelling point of view, as well as with regard to the interpretation of respective experimental observations.

Most commonly, the amount of plant matter is quantified in terms of the plant area index (PAI), expressed as square meter of plant area per square meter ground area. Since most canopies comprises non-flat phytoelements, such as stems or fruits, the correct basis for the phytoelement area is the hemi-surface area (Chen and Black, 1992) and not the projected or silhouette area.

Measurements of canopy structure may be divided into two broad categories: direct and indirect techniques. Direct methods rely on determining the area of harvested plant material, plus some up-scaling logic, if not the entire above-ground material is harvested (Monsi and Saeki, 1953). As such, they are usually laborious and time consuming, in particular if the vertical distribution of plant matter is to be determined. Even more so, destructive harvesting is likely to become impractical if the spatial heterogeneity is to be studied (Baldocchi and Collineau, 1994), or if the canopy must not be disturbed, e.g. long-term free air CO_2 enrichment (FACE) experiments.

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Nomenclature

B_l	normalised view factor (−)
B_u	zonal distribution of scattered radiation (−)
F	phytoelement inclination distribution (−)
FACE	free air CO_2 enrichment
G	projection of leaves with inclination λ into inclination β (−)
GAI	green area index ($m^2\,m^{-2}$)
j	subscript indicating canopy layer
n	number of canopy layers
PAI	plant area index ($m^2\,m^{-2}$)
P_i	probability of interception (−)
PPFD	photosynthetic photon flux density ($\mu mol\,m^{-2}\,s^{-1}$)
Q_d	downward flux of diffuse radiation ($W\,m^{-2}$)
Q_{dir}	downward flux of direct beam radiation ($W\,m^{-2}$)
Q_{ls}	downward flux of total (direct beam + diffuse) radiation ($W\,m^{-2}$)
Q_u	upward flux of diffuse radiation ($W\,m^{-2}$)

Greek symbols

α_c	phytoelement absorption coefficient (−)
β	angle of incidence (rad)
β^*	angle of the sun (rad)
β'	angle for scattered radiation (rad)
ΔL	PAI in canopy layer ($m^2\,m^{-2}$)
λ	phytoelement angle (rad)
ρ_c	phytoelement reflection coefficient (−)
ρ_s	soil reflection coefficient (−)
τ_c	phytoelement transmission coefficient (−)
ξ	reflection–transmission distribution function (−)
Ω	phytoelement dispersion coefficient (−)

A wide variety of indirect techniques exists (Norman and Campbell, 1989; Welles, 1990), including likewise laborious and time consuming ones such as the inclined point quadrat method (Warren-Wilson, 1960). Another family of indirect techniques is based on the tight correlation between canopy structure and radiative transfer and employs measurements of radiation attenuation and a suitable model to estimate the amount of phytoelements and/or their orientation (Norman and Campbell, 1989; Welles, 1990; Andrieu and Baret, 1993). Most of these methods rely on the inversion of the gap fraction, which is the fraction of view in any particular direction that is unobstructed by phytoelements. Several commercial instruments, based on either linear or hemispherical sensors, are available to this end (see Welles, 1990; Welles and Cohen, 1996).

With (line) quantum sensors, the attenuation of direct beam radiation within the canopy is used as a measure of gap fraction, restricting this technique to clear sky conditions (Welles, 1990). Since measurements below the canopy include a radiation component arising from penetration of sky diffuse and scattering of direct beam radiation, appropriate corrections must be made. This is usually done by the means of empirical formulations derived from more detailed models (e.g. Levy and Jarvis, 1999) or experiments (e.g. Jarvis and Leverenz, 1983; Pierce and Running, 1988). Alternatively, the amount of diffuse radiation may be measured directly by shading out direct beam radiation from some distance (Walker et al., 1988), which is though difficult in dense canopies, such as mountain grasslands.

However, the applicability of (line) quantum sensors, as opposed to hemispherical sensors, is not restricted to gap fraction methods, since cumulative plant area indices may be calculated alternatively from average radiation measurements, provided that the model accounts for the fluxes of sky diffuse and scattered direct beam radiation, in addition to direct beam radiation. This is not a trivial task, since multiple scattering of radiation needs to be taken into account (Myneni et al., 1989), which, as a major drawback for on-board processing (Sunscan User Manual, 1996), is computationally time consuming. This limitation is though being steadily removed by advances in computer speed, which makes post-processing of average radiation measurements for the calculation of cumulative plant area indices a viable alternative. Measurements of average radiation are not restricted to particular sky conditions and do not require the diffuse radiation component to be removed from measurements. The application of a model of radiative transfer capable of representing multiple scattering allows a realistic representation of within-canopy light climate, and in addition offers the possibility to adapt some of the parameters, which are usually treated as constants in many (semi-)empirical formulations, according to the own specific needs (e.g. optical properties, phytoelement inclination and dispersion).

Aim of the present paper is to present a method by which a simple physical model of radiative transfer may be used to calculate the vertical PAI distribution from measurements of average photosynthetically active radiation at various heights within the canopy and a known phytoelement inclination distribution. The validity of this method is assessed by comparing simulated cumulative plant area indices against direct measurements made by destructive harvesting. A sensitivity analysis is used to explore the influence of model parameter choice on PAI predictions. Eight semi-natural mountain grasslands, differing in land use, are investigated. These canopies provide an extreme test for the proposed method, consisting of multiple species/components with differing optical properties, phytoelement inclination distributions and spatial arrangements. Moreover they are non-uniform with regard to the vertical phytomass distribution and, particularly close to the soil surface, extremely dense.

2. Material and methods

2.1. Study sites

Field investigations were carried out during the summers of 1994, 1996 and 1999 at the three ECOMONT study areas Monte Bondone (Italy, 46°01′N, 11°02′E, Cescatti et al., 1999), Passeier Valley (Italy, 46°50′N, 11°17′E, Tappeiner et al., 1999) and Stubai Valley (Austria, 47°07′N, 11°18′E; Bitterlich and Cernusca, 1999). Three sites differing in land use were investigated at the Monte Bondone and Passeier Valley study areas and two at Stubai Valley, as shown in Table 1. Two abandoned areas, one pasture and five meadows, mowed between once each second year and three times per year, were investigated (Table 1). In the following the sites will be abbreviated as in Table 1, except if otherwise indicated. Plant area indices of the investigated sites range from 3.7 to 7.0 $m^2\,m^{-2}$, the fraction of photosynthetically active plant matter from 0.45 to 0.93, and canopy heights from 16 to 80 cm (Table 1). Average phytoelement inclinations are around 60°, except for MB/LM (46°) and MB/P (30°). The vertical phytomass distribution of the investigated canopies follows the pyramidal type (see Tappeiner and Cernusca, 1998), decreasing with increasing height above ground, except for PV/IM and SV/IM, where phytoelements are distributed fairly uniformly in the vertical (Fig. 1).

2.2. Experimental methods

Canopy structure was assessed in a destructive fashion by stratified clipping (Monsi and Saeki, 1953) of square plots of 0.3–0.5 m lateral length during the respective peak season (Table 1). Thickness of the harvested layers ranged between 0.01 and 0.1 m, depending on plant area density. The harvested plant material was separated into leaves, stems, reproductive organs, dead plant matter and cryptogams (mainly mosses). Silhouette area was determined by the means of an area meter (LI-3100, Li-Cor, Lincoln, USA). Silhouette areas of non-flat phytoelements were converted to hemi-surface area by multiplying with $\pi/2$, assuming them to be represented by cylinders (Campbell and Norman, 1998). Phytoelement inclinations were measured in the field with a hand inclinometer with a 5° accuracy (Tappeiner and Sapinsky, 1999).

Attenuation of photosynthetically active radiation (PPFD) within the canopy was measured prior to destructive harvesting with two sets of line quantum sensors (SunScan, Delta-T-Devices, Cambridge, UK and Ceptometer SF-80, Decagon, Pullman, USA) mounted horizontally at various heights within the canopy, the lowermost sensor always being placed at the soil surface. Incoming total and diffuse PPFD were measured above the canopy with quantum sensors (Li190SA, Li-Cor, Lincoln, USA) calibrated to the line sensors. Data, which were collected from low to high sun angles for at least half a day, were logged at time intervals ranging from 4 to 6 min with the battery-powered data acquisition system MICROMET (Cernusca, 1987). Prior to measurements the line quantum sensors were exposed to uniform light conditions and the deviation between the individual sensors of each instrument (64 and 80 for the SunScan and

Table 1
General characterisation of the investigated sites

	Monte Bondone			Passeier Valley			Stubai Valley	
	Abandoned area (MB/A)	Lightly managed meadow (MB/LM)	Pasture (MB/P)	Abandoned area (PV/A)	Lightly managed meadow (PV/LM)	Intensively managed meadow (PV/IM)	Lightly managed meadow (SV/LM)	Intensively managed meadow (SV/IM)
Altitude (m a.s.l.)	1520	1520	1565	1770	1770	1770	1850	970
Exposure	SE	E	E	SSW	SSW	SSW	SE	–
Inclination (°)	6	3	5	25–40	20–30	15–25	26	0
Land use	Abandoned	Mowed (1×)	Grazed	Abandoned	Mowed (1×)	Mowed (1×)	Mowed[c]	Mowed (2–3×)
Vegetation type	Siversio Nardetum strictae	Geranio Trisetetum	Crepido Cynosyretum	Caricetum Sempervirentis	Hypochoero Nardetum	Festuco Agrostietum	Trisetetum Flavescentis	Pastinaco Arrhenatheretum
Canopy height (m)	0.30	0.30	0.14	0.22	0.16	0.28	0.48	0.80
PAI ($m^2\,m^{-2}$)[a]	4.9	4.4	4.8	5.5	3.7	7.0	5.9	7.0
GAI ($m^2\,m^{-2}$)[a]	2.2	2.2	2.7	2.7	2.8	4.6	4.3	6.5
Av. Inclination (°)	62	46	30	60	59	59	62	60
Date[b]	31 July 1996	31 July 1996	1 August 1996	23 July 1996	23 July 1996	18 July 1996	10 August 1994	10 June 1999

[a] On a hemi-surface area basis.
[b] Date of measurements.
[c] Mowed once each second year.

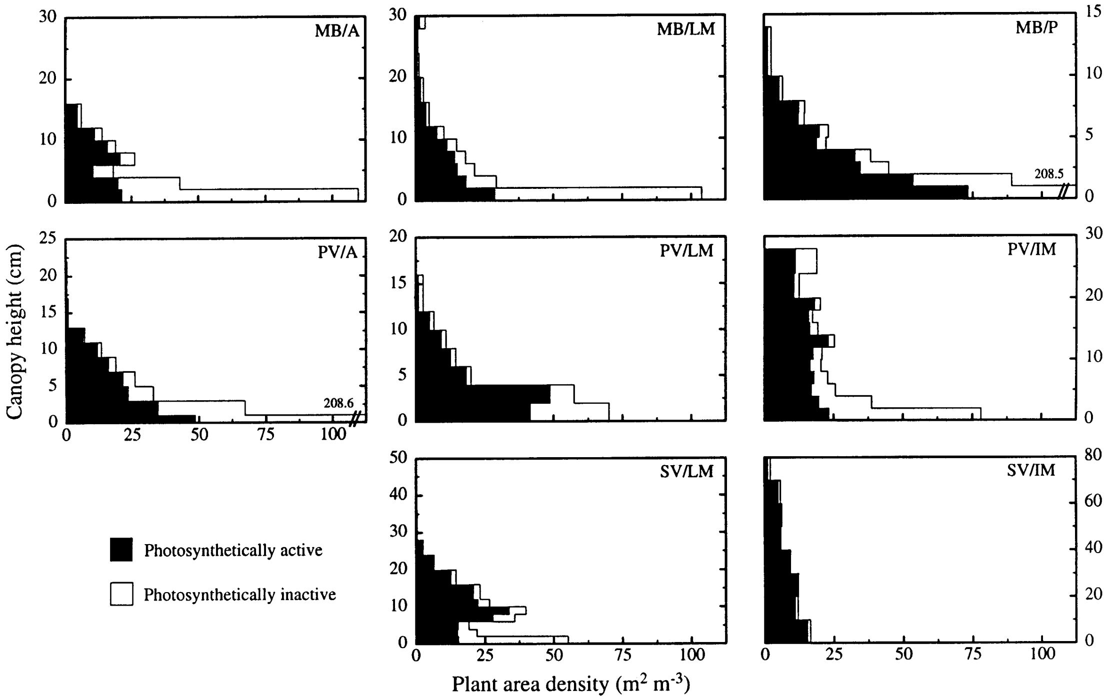

Fig. 1. Vertical distribution of plant area density, separately for photosynthetically active and inactive phytoelements of the investigated canopies. Note the different scales of the height axis.

the Ceptometer, respectively) measured, from which appropriate correction factors were calculated.

2.3. Model of radiative transfer

The model of radiative transfer treats the canopy as a horizontally homogeneous, plane–parallel turbid medium in which multiple scattering occurs on the elements of turbidity (phytoelements). The canopy is divided into sufficiently small, statistically independent layers, within which self-shading may be considered negligible and phytoelements to be distributed symmetrically with respect to the azimuth. Hemispherical reflection and transmission of radiation, which are allowed to be unequal, are assumed to be lambertian. Nine inclination classes are considered (for symbols and abbreviations refer to the nomenclature).

The probability that a ray of light incident at an angle (from the horizontal) β is intercepted in a layer j (counted from bottom upwards) with a hemi-surface area of ΔL and inclined as described by a inclination distribution F, is given by (Goudriaan, 1977; Ross, 1981; Baldocchi and Collineau, 1994)

$$P_{i(j,\beta)} = \frac{\Delta L_{(j)}\Omega_{(j)}}{\sin\beta}\sum_{\lambda=1}^{9} F_{(j,\lambda)}G_{(j,\beta,\lambda)}. \qquad (1)$$

Where Ω is a phytoelement dispersion factor, being unity for a random distribution, smaller than unity for a clumped and larger than unity for a regular distribution. Ω is assumed only a function of height, neglecting its variation with the angle of incidence (Stenberg, 1996). G is the projection of the phytoelements inclined at an angle λ in a direction with angle β (De Wit, 1965; Ross, 1981; Goudriaan, 1977), and may be calculated as

$$G_{(\beta,\lambda)} = \sin\beta\cos\lambda \quad \text{if } \beta \geq \lambda; \qquad (2)$$

$$G_{(\beta,\lambda)} = \frac{2}{\pi}\left[\sin\beta\cos\lambda\arcsin\left(\frac{\tan\beta}{\tan\lambda}\right) + \sqrt{\sin^2\lambda - \sin^2\beta}\right] \quad \text{if } \beta < \lambda. \qquad (3)$$

The radiation distribution within the canopy is bi-modal. Shaded phytoelements receive diffuse light only, while sunlit ones receive both diffuse and direct radiation, the latter incident at an angle β^*, the elevation of the sun. Solar geometry, determining the position of the sun in the sky, is calculated using the equations given in Campbell and Norman (1998). The attenuation of direct beam radiation (Q_{dir}) is calculated as

$$Q_{\mathrm{dir}(j)} = Q_{\mathrm{dir}(j+1)} - Q_{\mathrm{dir}(j+1)} P_{i(j,\beta^*)}. \tag{4}$$

The flux of diffuse radiation in the canopy consists of diffuse radiation from the atmosphere and of diffused, scattered direct beam radiation. For the treatment of diffuse radiation, the upper and lower hemispheres viewed by the phytoelements are divided into nine sectors of 10° each (due to this discretisation $\sin\beta$ in Eq. (1) needs to be replaced by $(\sin(10\beta) + \sin(10(\beta-1)))/2$ if nine sectors are distinguished; Goudriaan, personal communication). The diffuse downward short-wave fluxes (Q_{d}) within the canopy consist of the non-intercepted diffuse radiation from above (first part on the right hand side of Eq. (5)), the diffuse radiation transmitted from above and reflected from below downwards (second part on the right hand side of Eq. (5)), and the direct, "diffused" radiation transmitted in the downward direction (third part on the right hand side of Eq. (5)) as

$$\begin{aligned} Q_{\mathrm{d}(j,\beta)} = {} & Q_{\mathrm{d}(j+1,\beta)} - P_{i(j,\beta)} Q_{\mathrm{d}(j+1,\beta)} \\ & + B_{\mathrm{l}(j,\beta')} \sum_{\beta=1}^{9} P_{i(j,\beta)} \{ Q_{\mathrm{d}(j+1,\beta)} \\ & \times [\xi_{(j,\beta,\beta')}(\tau_{\mathrm{c}} - \rho_{\mathrm{c}}) + \rho_{\mathrm{c}}] \\ & + Q_{\mathrm{u}(j-1,\beta)} [\xi_{(j,\beta,\beta')}(\rho_{\mathrm{c}} - \tau_{\mathrm{c}}) + \tau_{\mathrm{c}}] \} \\ & + B_{\mathrm{l}(j,\beta')} Q_{\mathrm{dir}(j+1)} P_{i(j,\beta)} \\ & \times [\xi_{(j,\beta,\beta')}(\tau_{\mathrm{c}} - \rho_{\mathrm{c}}) + \rho_{\mathrm{c}}]. \end{aligned} \tag{5}$$

The prime (β') denotes that the angle refers to scattered radiation, ρ_{c} and τ_{c} are wavelength-dependent phytoelement reflection and transmission coefficients, respectively, and ξ is a reflection–transmission distribution function as defined by Goudriaan (1977). The scattered, i.e. reflected and transmitted, radiation is distributed as

$$B_{\mathrm{l}(j,\beta')} = \frac{B_{\mathrm{u}(\beta')} P_{i(j,\beta')}}{\sum_{\beta=1}^{9} B_{\mathrm{u}(\beta)} P_{i(j,\beta)}}, \tag{6}$$

where B_{u} is the zonal distribution of radiation scattered by a lambertian reflector (Goudriaan, 1977).

In analogy to Eq. (5), the diffuse upward short-wave fluxes (Q_{u}) within the canopy consist of the non-intercepted diffuse radiation from below, the diffuse radiation transmitted from below and reflected from above upwards, and the direct, "diffused" radiation reflected in the upward direction as

$$\begin{aligned} Q_{\mathrm{u}(j,\beta)} = {} & Q_{\mathrm{u}(j-1,\beta)} - P_{i(j,\beta)} Q_{\mathrm{u}(j-1,\beta)} \\ & + B_{\mathrm{l}(j,\beta')} \sum_{\beta'=1}^{9} P_{i(j,\beta)} \{ Q_{\mathrm{d}(j+1,\beta)} \\ & \times [\xi_{(j,\beta,\beta')}(\rho_{\mathrm{c}} - \tau_{\mathrm{c}}) + \tau_{\mathrm{c}}] \\ & + Q_{\mathrm{u}(j-1,\beta)} [\xi_{(j,\beta,\beta')}(\tau_{\mathrm{c}} - \rho_{\mathrm{c}}) + \rho_{\mathrm{c}}] \} \\ & + B_{\mathrm{l}(j,\beta')} Q_{\mathrm{dir}(j+1)} P_{i(j,\beta)} \\ & \times [\xi_{(j,\beta,\beta')}(\rho_{\mathrm{c}} - \tau_{\mathrm{c}}) + \tau_{\mathrm{c}}]. \end{aligned} \tag{7}$$

At the soil surface, the lower boundary condition of the model, radiation is reflected lambertian as

$$Q_{\mathrm{u}(0,\beta)} = \rho_{\mathrm{s}} B_{\mathrm{u}(\beta')} \left[Q_{\mathrm{dir}(1)} + \sum_{\beta=1}^{9} Q_{\mathrm{d}(1,\beta)} \right], \tag{8}$$

where ρ_{s} is a wavelength-dependent soil reflection coefficient.

A relaxation method, by which the scattered fluxes are added to the fluxes already there, is applied to solve Eqs. (5), (7) and (8) as described in Goudriaan (1977).

2.4. Calculation of plant area index

An upward-facing (line) quantum sensor mounted horizontally at a certain height within the canopy measures the downward flux of photosynthetically active radiation through a virtual horizontal plane at that respective height, consisting of direct beam, sky diffuse and scattered radiation. In terms of the model this corresponds to

$$Q_{\mathrm{ls}(j)} = \sum_{\beta=1}^{9} Q_{\mathrm{d}(j,\beta)} + Q_{\mathrm{dir}(j)}. \tag{9}$$

For given values of incoming direct beam and diffuse radiation above the canopy (upper boundary condition), the task is now to find for each sensor the $Q_{\mathrm{ls}(j)}$, which most closely matches the reading of sensors.

This is complicated by the interdependence of downward and upward radiation fluxes as formulated in Eqs. (5), (7) and (8), which requires the total PAI and the reflection at the soil surface, the lower boundary condition, to be known. A solution, although iterative, exists, provided that the radiation incident at the soil surface, $Q_{\mathrm{ls}(1)}$, has been measured: Thereby, the total PAI is stepwise increased from a starting value, which is supposed to be below the expected total PAI, until the simulated $Q_{\mathrm{ls}(1)}$ is equal to or greater than the reading of the sensor at the soil surface. For computational efficiency this iterative procedure is first conducted with a coarse step width, e.g. 0.1–0.2 $\mathrm{m}^2\,\mathrm{m}^{-2}$. The so calculated PAI, minus the step width, is then used as the starting point for the iteration with the fine step width, e.g. 0.05–0.01 $\mathrm{m}^2\,\mathrm{m}^{-2}$. The residuals, i.e. the difference between $Q_{\mathrm{ls}(j)}$ and the sensors' reading, may be used to guide the choice for the fine step width. In the present case a step width of 0.01 $\mathrm{m}^2\,\mathrm{m}^{-2}$ was used. Once the final total PAI has been calculated, the array to which the values of $Q_{\mathrm{ls}(j)}$ have been saved, is used as a look-up table to find the cumulative plant area indices which most closely match the readings of the remaining line sensors mounted at various heights within the canopy, if there are any.

The procedure described above has been implemented into a Visual Basic programme, an executable of which may be obtained from the corresponding author. The programme runs on any IBM-compatible computer under Windows 95/98/2000/NT and can read in arbitrary measurements of short-wave radiation attenuation within the canopy. A convenient user interface allows to adjust all model parameters according to the own needs (see next section). If appropriate optical properties are specified, also measurements in short-wave wave bands other than PPFD may be processed.

2.5. Parameterisation

The model of radiative transfer contains four adjustable parameters: (1) the phytoelement dispersion factor (Ω); (2) the phytoelement reflection (ρ_{c}); (3) transmission coefficients (τ_{c}) and (4) the soil reflection coefficient (ρ_{s}). Neither of these parameters has been determined specifically for the investigated canopies, thus values either had to be assumed or borrowed from various literature sources: ρ_{c} and τ_{c} were taken from Asner et al. (1998) as 0.12 and 0.06; ρ_{s} has been assigned a value of 0.15 (Asner and Wessman, 1997); phytoelements were assumed to be distributed at random ($\Omega = 1$). Given potential uncertainties associated with these baseline values, a sensitivity analysis will be carried out in the following section in order to assess how our parameter choice affects PAI predictions.

3. Results and discussion

The correspondence between the plant area indices predicted by the model and those determined from destructive harvesting is shown in Fig. 2. Predictions, albeit a few exceptions which will be discussed below, agree to within 20% of direct measurements, which, according to comparisons of indirect versus direct methods by Andrieu and Baret (1993) and Welles and Cohen (1996), may be assumed to be an acceptable result. Qualitative correspondence, too, is good, as indicated by the slope and *y*-intercept of a linear regression analysis, which are unity and close

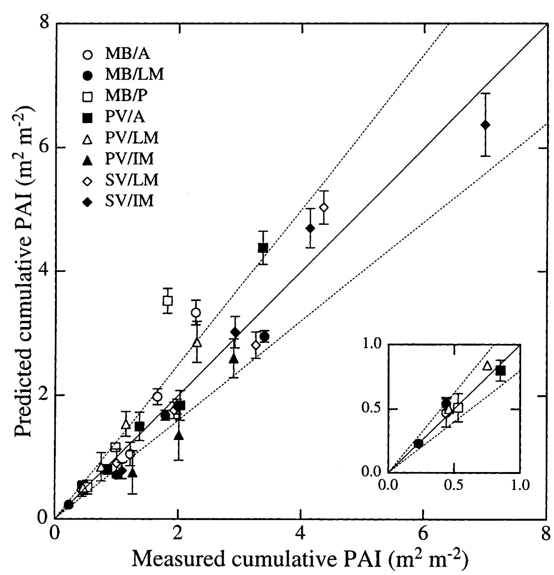

Fig. 2. Comparison of measured and predicted cumulative plant area indices of the investigated canopies. Predictions used the baseline parameter values as described in the text. Study sites have been abbreviated as in Table 1. The solid line indicates 1:1 correspondence, the dashed lines the 20% confidence intervals. Data points smaller than 1 $\mathrm{m}^2\,\mathrm{m}^{-2}$ are shown additionally in the inset.

Table 2
Statistics for comparison between measured and simulated plant area index (PAI)[a]

	Slope	y-intercept	EV	MD
Base line parameterisation	1.00 ± 0.07	0.07 ± 0.16	97	0.07
$\alpha_c = 0.45$ (litter)	1.51 ± 0.11	0.09 ± 0.26	97	1.09
$\Omega = 0.8$ (clumped)	1.53 ± 0.11	0.06 ± 0.25	97	1.08
$\Omega = 1.2$ (regular)	0.82 ± 0.06	0.02 ± 0.14	97	−0.32
Spherical orientation	1.04 ± 0.07	0.07 ± 0.18	96	0.15

[a] Model performance is evaluated by the slope and the y-intercept of a linear regression (mean ± S.E. error), the explained variance (EV) and the mean difference (MD) between measurements and calculations. Units are percent (explained variance) and $m^2\,m^{-2}$. For further information refer to the text.

to zero, respectively (Table 2). Besides the overall satisfying performance of the model, there are though some data points (Fig. 2), which are clearly beyond the 20% limit. Causes for these deviations may be both of experimental nature, as well as related to the model and its parameterisation.

On the experimental side it is important to note, that small deviations in height between the vertical position of the line quantum sensors and the boundaries of the harvested canopy layers, e.g. due to an uneven ground surface, may lead to fairly large discrepancies between direct and indirect PAI estimates in dense canopies. At MB/P or PV/A, where the plant area density exceeds $208\,m^2\,m^{-3}$ in the lowermost canopy layer (Fig. 1), a bias of 1 cm may cause a difference in PAI of up to $2\,m^2\,m^{-2}$. Arguments along this line were raised also by Faurie et al. (1996) and Wohlfahrt et al. (2000). Since average radiation is used to predict PAI in the present approach, averaging of radiation by single sensors of the line quantum sensors due to penumbra or small sunfleck size is less of a problem as compared to approaches based on gap fraction estimates (Norman and Campbell, 1989; Welles, 1990; Welles and Cohen, 1996) and thus not likely to contribute to the observed deviations.

As far as model parameterisation is concerned, it needs to be critically assessed in how much the choice of the parameter values affects predicted PAI, in particular if, as in the present case, parameters have been obtained from the literature. For this purpose, we conducted a sensitivity analysis, varying the parameters within reasonable limits, the results of which are shown in Fig. 3 and Table 2. Adjustable parameters are the soil reflection coefficient (ρ_s), the phytoelement optical properties (ρ_c and τ_c) and the dispersion factor (Ω).

The reflectance of a soil is related in a complex fashion to its water content and physical/chemical properties (Baumgardner et al., 1985; Jacquemoud et al., 1992). Since the downward flux of radiation within the canopy, as opposed to the fraction of absorbed radiation (Asner and Wessman, 1997) and canopy reflectance (Goudriaan, 1977), is relatively insensitive to alterations of ρ_s (data not shown), no sensitivity tests were conducted with ρ_s.

Phytoelement optical properties exert a strong influence on the downward flux of radiation, since they determine the fraction of absorbed, transmitted and reflected radiation. The chosen baseline values for ρ_c and τ_c (0.12 and 0.06) result in an absorption coefficient (α_c) of 0.82 ($=1 - (\rho_c + \tau_c)$), which is considered typical for green leaves (e.g. Campbell and Norman, 1998). The investigated canopies, though, are composed by up to 50% by photosynthetically inactive, non-green plant material (Table 1), mainly dead plant parts, but also reproductive organs (in the upper canopy layers), and, in the case of abandoned areas, supporting structures of dwarf shrubs (Wohlfahrt et al., 2001), which may be supposed to be characterised by different optical properties. Optical properties of dead plant matter has been rarely studied, among those few studies Asner et al. (1998) reported an average α_c of 0.45 for grass litter from three savannah ecosystems in Texas. Using this value instead of the baseline value of 0.82 increases predicted plant area indices considerably (Fig. 3/A), since enhanced transmission ($\tau_c = 0.13$) and reflection ($\rho_c = 0.42$) allows more radiation to penetrate. Predictions improve for a few data points which are underestimated by the baseline simulations (Fig. 3/A), but, in contrast to what might be expected, not for MB/A, MB/EM, MB/P or PV/A, which feature the highest fractions of

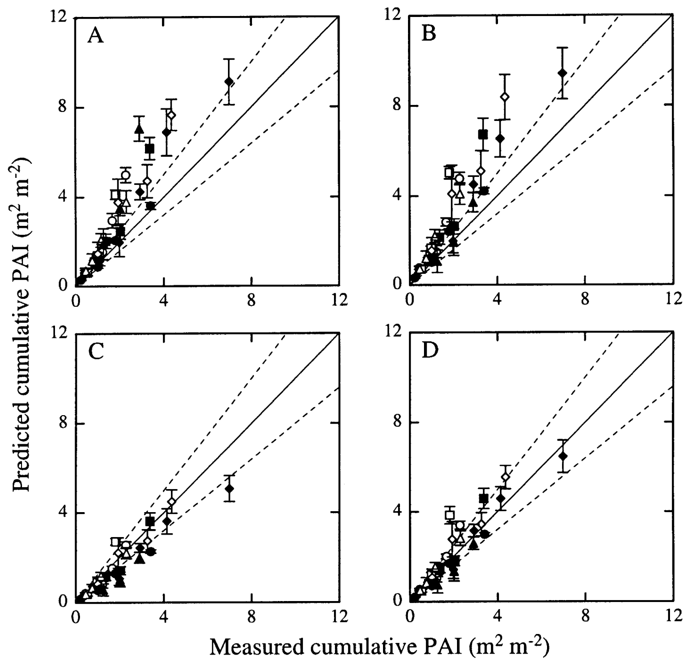

Fig. 3. As Fig. 2, but model simulation have been performed assuming: (A) a phytoelement absorption coefficient of 0.45; (B) phytoelements to be clumped; (C) regularly dispersed; and a spherical phytoelement inclination distribution (D). Symbols and lines are as in Fig. 2.

non-green plant area (Table 1). Whether this is due to the fact that the optical properties from Asner et al. (1998) are not appropriate for the investigated species, or reflects some other problem related to model parameterisation (see below), remains to be determined. On average predictions with $\alpha_c = 0.45$ overestimate measurements by 50% (Table 2), decreasing α_c causes the reverse (data not shown).

The baseline simulations assume phytoelements to be distributed at random. Previous studies on the spatial structure of mountain grasslands have shown that this is a reasonable assumption for pastures, but less so for dwarf shrub communities and meadows (Tappeiner and Cernusca, 1989, 1998). For the latter, phytoelements have been found to be clumped in the upper and regular in the lower canopy layers (Tappeiner and Cernusca, 1998). Wohlfahrt et al. (2000), in contrast, found that radiative transfer may be predicted reasonably assuming a random dispersion across a range of differently managed mountain grassland ecosystems. The effect of non-random phytoelement dispersions on predicted PAI was assessed by assigning Ω in Eq. (1) a value of 0.8 and 1.2, simulating a clumped and a regular distribution, respectively. If phytoelements are clumped more radiation penetrates as would be predicted by the amount of plant area, resulting in an underestimation of the true PAI (Fassnacht et al., 1994; Chen et al., 1997). If phytoelements are regularly distributed the reverse is the case. Since overall correspondence between measured and predicted plant area indices is good assuming a random phytoelement distribution, results are biased towards higher and lower values if a clumped (Fig. 3/B) and a regular (Fig. 3/C) dispersion, respectively, is assumed. The bias is smaller for the regular distribution (Table 2), due to high values of cumulative PAI, i.e. data points deep in the canopy, which are overestimated by a random distribution, now being predicted correctly, confirming the above mentioned results by Tappeiner and Cernusca (1998). In contrast to their findings, though, clumping does not improve results in the upper canopy layers.

The present model requires the phytoelement inclination distribution to be provided as an input parameter, which is a drawback in comparison to methods based on gap fraction measurements, which, provided that measurements are made at multiple angles, allow prediction of both the phytoelement inclination distribution and the PAI (e.g. Perry et al., 1988; Norman and Campbell, 1989). Manual determination of phytoelement angles is simple, but time consuming (but see Deckmyn et al., 2000), since a large sample size is usually required, in particular in multi-species canopies (Tappeiner and Cernusca, 1998). It is thus instructive to explore the sensitivity of the model to variations of the phytoelement inclination distribution in order to estimate how well pre-defined phytoelement inclination distributions, as opposed to the actually measured ones, would perform for predicting PAI. Probably the most popular among the predefined inclination distributions is the spherical one, because it considerably simplifies the computation of radiative transfer, $G(\beta,\lambda)$ from Eq. (1) being equal to 0.5 independent of the angle of incidence (De Wit, 1965). Using a spherical phytoelement inclination distribution, predictions (Fig. 3/D) are almost as good as with the actual distribution (Fig. 2), the directly determined plant area indices being on average slightly overestimated (Table 2). This is not really surprising, given the fact that the actual average inclination angles of most canopies vary between 59 and 62° (Table 1), which is close to the average inclination of approximately 57° for the spherical distribution (De Wit, 1965). Two exceptions are MB/LM and MB/P, whose average phytoelement inclination is 46 and 30°, respectively (Table 1). Since the relatively steeper angles of the spherical distribution allow more light to penetrate (except at low angles of incidence), PAI estimates increase for both of these sites. Quantitatively the effects are though minor, except for the notoriously overestimated data point of MB/P (Fig. 2), which becomes even more biased (Fig. 3/D).

4. Concluding remarks

A method is presented by which a simple physical model of radiative transfer is used to estimate the vertical distribution of the plant area index (PAI) from measurements of average photosynthetically active radiation at various heights within the canopy and a known phytoelement inclination distribution. In contrast to gap fraction techniques based on quantum sensors, the proposed method is independent of sky conditions and does not require the diffuse radiation component to be removed from measurements. Using a set of baseline parameters obtained from the literature, predicted plant area indices compare qualitatively favourably with those determined from destructive harvesting. Quantitative correspondence is within ±20%, a range generally considered acceptable for indirect methods. Deviations between predicted and measured plant area indices are attributed to discrepancies with regard to height between the vertical positions of the quantum sensors and the boundaries of the harvested canopy layers, particularly in the lower, often extremely dense canopy layers. A sensitivity analysis shows predictions to be sensitive to the choice of the values for the phytoelement dispersion coefficient and the optical properties: clumping of phytoelements and decreasing the phytoelement absorption coefficient increases predicted plant area indices, the reverse is the case for phytoelements being regularly distributed and increasing the phytoelement absorption coefficient. Due to these mutually opposing effects on PAI predictions, their parameterisation is critical, since similar results may be obtained with contrasting numerical values. Preferably either the phytoelement dispersion coefficient or the optical properties should be directly determined. As a major reduction of experimental effort, predictions assuming a spherical phytoelement angle distribution are found to be not significantly different from those based on measured inclination distributions.

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