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IPR 1.0: an efficient method for calculating solar radiation absorbed by individual plants in sparse heterogeneous woody plant communities

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Abstract

Climate change may alter the spatial distribution, composition, structure, and functions of plant communities. Transitional zones between biomes, or ecotones, are particularly sensitive to climate change. Ecotones are usually heterogeneous with sparse trees. The dynamics of ecotones are mainly determined by the growth and competition of individual plants in the communities. Therefore it is necessary to calculate solar radiation absorbed by individual plants for understanding and predicting their responses to climate change. In this study, we developed an individual plant radiation model, IPR (version 1.0), to calculate solar radiation absorbed by individual plants in sparse heterogeneous woody plant communities. The model is developed based on geometrical optical relationships assuming crowns of woody plants are rectangular boxes with uniform leaf area density. The model calculates the fractions of sunlit and shaded leaf classes and the solar radiation absorbed by each class, including direct radiation from the sun, diffuse radiation from the sky, and scattered radiation from the plant community. The solar radiation received on the ground is also calculated. We tested the model by comparing with the analytical solutions of random distributions of plants. The tests show that the model results are very close to the averages of the random distributions. This model is efficient in computation, and is suitable for ecological models to simulate long-term transient responses of plant communities to climate change.

1 Introduction

Climate change is expected to alter the composition (species types and their density), structure (heights, leaf area, crown size, etc.), and spatial distribution (locations and extents) of terrestrial ecosystems (Cramer et al., 2001), which directly affect animals' habitats and human applications of the lands, and have strong feedbacks on the climate system (Parry et al., 2007). Transitional zones between biomes, or ecotones, are particularly sensitive to climate change and could provide early signs of climate change

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impacts (Fankhauser et al., 2001). Transitional zones are usually heterogeneous with sparse trees, such as the tree-line between boreal forest and Arctic tundra (the width of the tree-line usually ranges about 100 km; Timoney et al., 1992). Field observations and remote sensing data (aerial photos and satellite images) have detected increases in greenness (Xu et al., 2013) and changes in density and height of trees and shrubs in the transitional zones between boreal forest and Arctic tundra (Gamache and Payette, 2004; Sturm et al., 2001; Tape et al., 2006). Relative changes in height, crown size, and the density of trees, shrubs and herbs usually occur before major shifts in biomes as projected by some vegetation models (e.g., Gamache and Payette, 2004; Tape et al., 2007; Callaghan et al., 2005). Novel ecosystem types could appear as well since individual species independently adjust to climate forcing (Overpeck et al., 2003; Walker et al., 2006). To understand and predict these transient changes, it is essential to consider light competition among different species in plant communities (the words "light" and "radiation" are used interchangeably in this paper). In sparsely vegetated regions, the solar radiation received on the ground is important as well for soil thermal and hydrological conditions, especially for permafrost conditions in cold regions.

Different methods have been developed to calculate solar radiation absorbed by plants. The major approaches include the one-big-leaf method (considering the whole canopy as one layer; e.g., Sellers et al., 1992), the two-big-leaf method (dividing the canopy into sunlit and shaded leaves; e.g., Norman, 1980; Wang and Leuning, 1998), using Beer's law to estimate radiation distribution in canopies assuming canopies are uniform turbid media (Monsi and Saeki, 1953), and two-stream approximation considering scattering and absorption of down-welling and up-welling light in canopies (Dickinson, 1983). All these approaches assume that the canopy is a uniform layer covering the entire study area. More detailed numerical canopy radiation models have been developed for energy balance and for remote sensing applications (e.g., Cescatti, 1997; Li et al., 1995; Prince, 1987; Myneni et al., 1995; Wang et al., 2007). However, these models are usually time consuming in computation and do not pay much attention to light competition among individual plants and species.

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In the past decade, several models considered the composition of different plant types in a community and their competition for light and other resources (e.g., Foley et al., 1996; Sitch et al., 2003; Zhang et al., 2002). For example, Sitch et al. (2003) considered the light competition among plant functional types based on leaf area index of individual plants and their density, but did not consider the effects of plant heights on light competition. Foley et al. (1996) assumed that trees are always higher than grasses for light competition. Zhang et al. (2002) used a similar approach but considered three strata (upper-story, under-story, and ground-growth). Ryel et al. (1990) simulated light competition in multi-species crop communities based on the foliage composition of the species in each canopy layer. These studies considered the vertical structure of the canopies but assumed that the canopy layers/strata are uniform and cover the entire study area continuously. Several studies developed three-dimensional models to simulated radiation distribution in sparsely distributed trees, mainly for fruit orchards (de Castro and Fetcher, 1998; Oyarzun et al., 2007; West and Welles, 1992; Baldocchi and Collineau, 1994). However, the plant communities considered are usually composed of only one type of trees. Therefore there is no light competition among plant species or types. Song and Band (2004) develop a model to simulate the spatial patterns of solar radiation under discrete forest canopies. The approach could be improved to calculate solar radiation received by individual crowns.

In this study, we developed an individual plant radiation model, IPR (version 1.0), to calculate solar radiation absorbed by individual plants in sparse heterogeneous (i.e., the canopy is discontinuous and composed of different plant types or the same type but with different heights) woody plant communities. Solar radiation under the woody plants was calculated as well. Because the solar radiation intercepted by sunlit leaves is much higher than that of the shaded leaves, an efficient way to up-scale photosynthesis from leaves to canopy is to divide the canopy into sunlit and shaded leaf classes (Norman, 1993). Therefore, we calculated the fractions of sunlit and shaded leaf classes of individual plants and the solar radiation absorbed for each class based on geometric optical relationships.

2 Methodology

2.1 The assumptions of the model

Natural plant communities, especially in northern high latitudes, are usually composed of trees, shrubs, herbs, mosses and lichens. To simplify the calculation, the IPR model was developed based on the following assumptions (The first seven assumptions are for plant communities, and the remaining three are for radiation conditions.): (1) the plant community may include woody plants (trees and shrubs), herbs, and mosses/lichens in a large flat area (the area is so large that the margin effects can be ignored); (2) woody plants are higher than herbs, and herbs are higher than mosses/lichens; (3) woody plants can be categorized into several strata based on their heights and crown sizes, which can be different species or one species but in different ages; (4) the plants of each woody stratum are distributed somewhat regularly (equivalent to the average of random distributions), mixed with plants of other woody strata and are trying to avoid overlapping with one another (Ward et al., 1996); (5) the herb stratum is distributed uniformly, and is treated collectively without considering individual plants; (6) mosses/lichens cover the entire ground or cover part of the ground randomly; (7) the crowns of woody plants are treated as rectangular boxes, and the leaf area density is distributed uniformly within a box; (8) the sky diffuse radiation is from the whole hemisphere and is in isotropic distribution, as used by Goudriaan (1977); (9) scattered radiation generated from reflection and transmission in canopies is in all directions, and the recollision probability remains constant in successive scattering (Panferov et al., 2001; Smolander and Stenberg, 2005); and (10) both the sky diffuse radiation and the scattered radiation are uniformly distributed in a crown.

There are several reasons for treatment of crowns as somewhat regularly distributed but not exactly regular (the assumption 4). First, plants tend to be distributed somewhat regularly because of the competition (Ward et al., 1996); second, although plants of one stratum can be distributed regularly based on geometry assuming equal spacing among nearest plants (e.g., at centers and nodes of hexagons), it is difficult to distribute plants of two or more strata without overlapping among plants of different strata; and third, the fractions of sunlit leaf area can be different between the average of random distribution and exact regular distribution. Crowns of woody plants can be in different shapes depending on the genetic features of the species and the environment. To simplify the calculation, we treated crowns as rectangular boxes. Oyarzun et al. (2007) also treated fruit-tree crowns as prisms in orchards. However, their prism-shaped crowns are always aligned with the rows of the plants in an orchard, while we assumed that a crown looks like a rectangular box (or has the same optical length) in all azimuth directions and there is always a side facing the sun considering that crowns are usually symmetrical. This treatment allows quasi-analytical solutions and greatly simplifies the calculation.

Based on this rectangular box assumption, the leaf area density of a crown can be expressed as

$$\rho = L_0/[D^2(H-h)], \quad (1)$$

where ρ is the leaf area density of the crown (m^2 leaf m^{-3} space), L_0 is the leaf area of the crown (m^2 leaf/plant), or expressed as $L_0 = \mathrm{LAI_p} \cdot D^2$. $\mathrm{LAI_p}$ is the local leaf area index of the individual crown, defined as the ratio between the leaf area and the ground area directly projected under the crown (m^2 leaf m^{-2} land). D is the width of the crown (m), H and h are the heights (m) of the top and bottom of the crown, respectively.

2.2 The algorithms of the model

Solar radiation absorbed by leaves includes direct solar radiation (or solar beam), diffuse radiation from the sky (or simply called diffuse radiation), and scattered radiation which is defined as the radiation generated by reflection and transmission of direct and diffuse radiation intercepted by leaves. Sunlit leaves and sunlit ground receive solar beam, diffuse radiation and scattered radiation, while shaded leaves and shaded ground receive only diffuse radiation and scattered radiation. The radiation on the

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ground is considered as the radiation available for mosses and lichens. The unknown variables need to be calculated are the fractions of sunlit leaf area of woody strata and the herb stratum, the sunlit fraction of the ground, the intensity of the direct beam, diffuse radiation, and scattered radiation absorbed by leaves of the woody strata, the herb stratum, and the ground.

2.2.1 The fractions of sunlit leaf area of the woody strata

When a solar beam goes through a small column of plant canopy (Fig. 1), the sunlit leaf area can be estimated based on Norman (1982)

$$dL_b = F_1/K[1 - \exp(-K \cdot \rho \cdot l)]dA, \quad (2)$$

where dL_b is the sunlit leaf area of the column (m^2 leaf), dA (in m^2) is the basal area of the column directly facing the beam, and F_1 is the solar beam before entering the column, expressed as the fraction of sunlit area on a surface. l is the length of the column or the path length of light (m), and ρ is the density of the leaf area of the column (m^2 leaf m^{-3} space), which can be calculated by Eq. (1). K is effective light extinction coefficient including the clumping effects

$$K = K_0 \cdot \Omega, \quad (3)$$

where K_0 is the light distinction coefficient when leaves are randomly distributed, and is a constant of 0.5 (Norman, 1982). Ω is the clumping index of the leaves in the crown (Chen and Black, 1992). It equals 1 when leaves are randomly distributed. It is larger than 1 when leaves are distributed side by side, and it is smaller than 1 when leaves are stacked on each other (Chen and Black, 1992). The solar beam after the interception of the canopy can be determined based on the Beer–Lambert law

$$F_2 = F_1 \cdot \exp(-K \cdot \rho \cdot l), \quad (4)$$

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where F_2 is the solar beam after the interception of the canopy, expressed as the fraction of sunlit area on a surface. The solar beam intercepted by the column of canopy would be

$$dF = F_1 - F_2 = F_1[1 - \exp(-K \cdot l \cdot \rho)]dA = K \cdot dLb, \tag{5}$$

where dF is the solar beam intercepted by the column of canopy (in the same unit as F_1 and F_2). The shading effects of this column on subsequent objects can be expressed as

$$f = F_2/F_1 = \exp(-K \cdot \rho \cdot l), \tag{6}$$

where f is the shading effects of the column on subsequent objects (in fractions ranged from 0 to 1. $f = 1$ for no shading, and $f = 0$ for completely shaded).

For a plant at any moment, the total sunlit leaf area of the crown is the integration of dL_b for the entire crown. For rectangular box shaped crowns, we can integrate numerically by dividing the crown into small slices parallel to the solar beam (Fig. 2a). The length of a slice or the light path length (equivalent to l in Eq. 2) can be calculated analytically based on the height of the slice when the beam enters it (Fig. 2). There are two cases: when $(H_i - h_i)/\tan\theta \geq D_i$ (Fig. 2b)

$$l_{z_i} = \begin{cases} 0 & (z_i \leq h_i \quad \text{or} \quad z_i \geq H_i + D_i \cdot \tan\theta) \\ (z_i - h_i)/\sin\theta & (D_i \cdot \tan\theta + h_i \geq z_i > h_i) \\ D_i/\cos\theta & (H_i \geq z_i > D_i \cdot \tan\theta + h_i) \\ D_i/\cos\theta - (z_i - H_i)/\sin\theta & (H_i + D_i \cdot \tan\theta > z_i > H_i) \end{cases}, \tag{7a}$$

and when $(H_i - h_i)/tan\theta < D_i$ (Fig. 2c)

$$l_{z_i} = \begin{cases} 0 & (z_i \leq h_i \quad \text{or} \quad z_i \geq H_i + D_i \cdot \tan\theta) \\ (z_i - h_i)/\sin\theta & (H_i \geq z_i > h_i) \\ (H_i - h_i)/\sin\theta & (h_i + D_i \cdot \tan\theta \geq z_i > H_i) \\ D_i/\cos\theta - (z_i - H_i)/\sin\theta & (H_i + D_i \cdot \tan\theta > z_i > h_i + D_i \cdot \tan\theta) \end{cases}, \tag{7b}$$

where l_{z_i} is the path length of light going through a slice of crown of a plant of stratum i. z_i is the height of the crown slice when the solar beam enters it, and dz_i is a small height difference (or thickness in vertical direction) of the crown slice (m) (Fig. 2a). The cross-section area of the crown slice directly facing the solar beam can be expressed as

$$dA_i = D_i \cdot \cos\theta \cdot dz_i, \quad (8)$$

where dA_i is the area of the crown slice directly facing the solar beam (equivalent to dA in Eq. 2). θ is the elevation angle of the sun. D_i is the width of the crown (m), H_i and h_i are the heights of the top and bottom of the crown, respectively (m) (the subscript i is for a plant of stratum i, or sometimes simply called plant i).

Some of the solar beam may be blocked by its neighbouring plants. For a stratum j, only the plants growing in a stripe of $D_i + D_j$ wide in the direction of the sun can shade plant i (Fig. 3). Their shading effects can be estimated by dividing the land stripe into D_j by $D_i + D_j$ rectangles (except the first rectangle close to plant i, whose width is defined by Eq. 14) to calculate the shading effects of the plants of stratum j in each rectangle (Fig. 3)

$$f_{i,jk} = (1 - p_j) + p_j \cdot f_{0i,jk}, \quad (9)$$

where $f_{i,jk}$ is the average shading effects on a slice of crown of plant i by the plants of stratum j in rectangle k. It is the weighted sum of the solar beam from the gaps (no shading) and the solar beam going through the crowns of plants of stratum j. $f_{0i,jk}$ is the shading effects on a slice of crown of plant i by a crown of plant j in rectangle k. p_j is the probability of solar beam going through crowns of stratum j in the rectangle. It equals to the fraction of the land area covered by the crowns of the plants of the stratum (therefore it did not change with i and k), and can be calculated as

$$p_j = D_j^2 \cdot d_j, \quad (10)$$

where d_j is the density of plants of stratum j (plants m^{-2}). Since the width of the rectangle is D_j, there is only one row of plants of stratum j in a rectangle (i.e., the solar beam goes through no more than one crown of stratum j in a rectangle). Therefore $f_{0i,jk}$ can be calculated based on Eq. (6) for a slice of crown

$$f_{0i,jk} = \exp(-K_j \cdot \rho_j \cdot l_{z_j,k}), \quad (11)$$

where K_j is the effective light extinction coefficient for plant j, $l_{z_j,k}$ is calculated by Eq. (7) but for plants of stratum j in rectangle k corresponding to the height $z_{j,k}$, which depends on distance between the plant i and plants of stratum j in rectangle k (Fig. 3)

$$z_{j,k} = z_i + X_{i,jk} \cdot \tan\theta, \quad (12)$$

where

$$X_{i,jk} = X_{i,j1} + (k-1)D_j, \quad (13)$$

and

$$X_{i,j1} = [0.5(1 - E_{Tj}) + E_{ij}]D_j. \quad (14)$$

Where $X_{i,jk}$ is the distance between the edge of the crown of plant i and the farther edge of the crown of plant j in rectangle k, and $X_{i,j1}$ is the distance when k equals 1 (the first rectangle near plant i, Fig. 3). E_{ij} is the fraction of crown of plant i overlapped vertically with the crown of plant j, and E_{Tj} is the total fraction of the crowns of all the plant strata overlapped with a crown of stratum j on average, calculated as

$$E_{Tj} = \sum_{m=1}^{N} p_m \cdot E_{jm}, \quad (15)$$

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where N is the total number of woody strata of the plant community. E_{jm} is the fraction of crown of plant j overlapped vertically with the crown of plant m, defined as

$$E_{jm} = \begin{cases} 0 & (h_m \geq H_j \quad \text{or} \quad H_m \leq h_j) \\ [\min(H_j, H_m) - h_m]/(H_j - h_j) & (H_j \geq h_m \geq h_j) \\ [H_m - \max(h_j, h_m)]/(H_j - h_j) & (H_j \geq H_m \geq h_j) \end{cases}, \tag{16}$$

where min() and max() are operations to get the minimum and the maximum of the variables in the brackets, respectively. Since E_{jm} is calculated relative to the crown height of plant j, it can be different from E_{mj}. Similar to E_{mj}, E_{ij} is the fraction of crown of plant i overlapped vertically with the crown of plant j. Equation (14) was designed that way so that $X_{i,j1}$ approximately equals D_j (plant j is very close to plant i) when the woody plants are dense ($E_{Tj} \approx 1$); $X_{i,j1}$ is about $1.5D_j$ when the woody plants are sparse ($E_{Tj} \approx 0$); and $X_{i,j1}$ can be less than $0.5D_j$ when stratum j is completely above or below stratum i ($E_{ij} = 0$), especially when the woody plants are dense ($E_{Tj} \approx 1$).

The shading effects on a slice of crown by all the neighbouring plants of stratum j can be expressed as

$$F_{1,ij} = \prod_{k=1}^{M_j} f_{i,jk}, \tag{17}$$

and the shading effects on a slice of crown by all the neighbouring plants of all the strata can be expressed as

$$F_{1,i} = \prod_{j=1}^{N} F_{1,ij} = \prod_{j=1}^{N} \prod_{k=1}^{M_j} f_{i,jk}, \tag{18}$$

where $F_{1,i}$ is the shading effects on a slice of crown i by all the neighbouring plants of all the strata, or the fraction of direction radiation available for entering the slice of

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the crown of plant i after the interception of all its neighbouring plants. M_j is the total number of rectangles considered in calculating the shading effects of stratum j on plant i. It can be estimated by

$$M_j = 1 + (X_{\max} - X_{i,j1} - D_i)/D_j, \tag{19}$$

where $X_{\max}$ is a predefined maximum distance for shading effects (e.g., 100 m) beyond that the shading effects of neighbouring plants are negligible. The total sunlit leaf area of the crown i is the integration of Eq. (2) for all the slices of the crown (using Eq. 8 for $\mathrm{d}A$ and Eq. 18 for F_1 and integrating $\mathrm{d}z_i$ from h_i to $H_i + D_i \cdot \tan\theta$)

$$L_{\mathrm{b}i} = D_i \cdot \cos\theta / K_i \int_{h_i}^{H_i + D_i \cdot \tan\theta} [1 - \exp(-K_i \cdot \rho_i \cdot l_{z_i})] \cdot \prod_{j=1}^{N} \prod_{k=1}^{M_j} f_{i,jk} \cdot \mathrm{d}z_i, \tag{20}$$

where $L_{\mathrm{b}i}$ is the total sunlit leaf area of the plant i (m^2 leaf/plant). K_i is the effective light extinction coefficient of plant i. The fraction of sunlit leaf area would be

$$f_{\mathrm{sunlit},i} = L_{\mathrm{b}i} / L_{0i}, \tag{21}$$

where $f_{\mathrm{sunlit},i}$ is the fraction of sunlit leaf area of a plant of stratum i. L_{0i} (m^2 leaf/plant) is the total leaf area of a plant of stratum i.

The fraction of the sunlit area on a horizontal surface after the interception of all the woody strata, $F_{2\mathrm{w}}$, can be estimated by

$$F_{2\mathrm{w}} = 1 - \sum_{i=1}^{N} L_{\mathrm{b}i} \cdot d_i \cdot K_i / \sin\theta. \tag{22}$$

$F_{2\mathrm{w}}$ would be the solar beam available for the herb stratum under the woody strata, expressed as the fraction of the sunlit area.

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2.2.2 Relative diffuse radiation of the woody strata

We assume that diffuse radiation is from the entire hemisphere and is in isotropic distribution, following Goudriaan (1977). Thus, diffuse radiation can be considered as solar beams from all the infinite pieces of the hemisphere, and therefore can be calculated for each piece of hemisphere using the approach of the solar beam as discussed above. The solar beam from a piece of the hemisphere intercepted by a column of canopy can be calculated by Eq. (5). And the solar beam from this piece of the hemisphere intercepted by a crown is the integration for all the crown slices

$$F_i(\beta,\varphi) = \int \mathrm{d}F = K_i \int \mathrm{d}L_{\mathrm{b}i} = K_i \cdot L_{\mathrm{b}i}(\beta), \quad (23)$$

where $F_i(\beta,\phi)$ is the intercepted radiation by crown i illuminated from a piece of the hemisphere with the elevation angle of β and azimuth angle of ϕ. $F_i(\beta,\phi)$ is expressed as the ratio to the radiation above the canopy of the plant community from this piece of hemisphere. $L_{\mathrm{b}i}(\beta)$ is the total sunlit leaf area of the crown i when the elevation angle of the beam is β (Eq. 20 but replacing θ with β). We assume that diffuse radiation is uniformly distributed in the crown. The diffuse radiation intercepted by a unit leaf area on average is the integration of $F_i(\beta,\phi)$ for the entire hemisphere divided by the total crown leaf area. Thus we can get

$$F_{\mathrm{d},i} = 2K_i \int_0^{\pi/2} f_{\mathrm{sunlit},i}(\beta) \cdot \cos\beta \cdot \mathrm{d}\beta, \quad (24)$$

where $F_{\mathrm{d},i}$ is the relative diffuse radiation intercepted by the leaves of stratum i, expressed as the ratio to the diffuse radiation on a horizontal surface above the canopy of the plant community. $f_{\mathrm{sunlit},i}(\beta)$ is the fraction of sunlit leaf area of the crown i when the elevation angle of the beam is β, calculated by Eq. (21). Equation (24) can be calculated numerically using the fraction of sunlit leaf area at different elevation angles of the beam from 0 to $\pi/2$.

2.2.3 The fraction of sunlit leaf area and relative diffuse radiation of the herb stratum

We assume that the herb stratum is distributed uniformly; therefore its fraction of sunlit leaf area can be calculated using the two-big-leaf approach (Norman, 1982)

$$f_{\text{sunlit,h}} = F_{2\text{w}} \cdot \sin\theta / (K_\text{h} \cdot \text{LAI}_\text{h})[1 - \exp(-K_\text{h} \cdot \text{LAI}_\text{h} / \sin\theta)], \quad (25)$$

where $f_{\text{sunlit,h}}$ is the fraction of the sunlit leaf area of the herb stratum, LAI_h is the leaf area index of the herb stratum (m^2 leaf m^{-2} ground), K_h is the effective light extinction coefficient of the herb canopy, and $F_{2\text{w}}$ is the solar beam available after the interception of the woody strata, calculated by Eq. (22).

Similar to Eq. (24), the relative diffuse radiation intercepted by the herb stratum can be calculated as

$$F_{\text{d,h}} = 2K_\text{h} \int_0^{\pi/2} f_{\text{sunlit,h}}(\beta) \cdot \cos\beta \cdot \text{d}\beta, \quad (26)$$

where $F_{\text{d,h}}$ is the relative diffuse radiation intercepted by leaves of the herb stratum, expressed as the ratio to the diffuse radiation on a horizontal surface above the canopy of the plant community.

2.2.4 The fraction of sunlit area and relative diffuse radiation on the ground

Since the herb stratum is assumed a uniform canopy, its effects on the fraction of sunlit area on the ground can be expressed based on Beer's law (Monsi and Saeki, 1953)

$$f_{\text{sunlit,g}} = F_{2\text{w}} \exp(-K_\text{h} \cdot \text{LAI}_\text{h} / \sin\theta), \quad (27)$$

where $f_{\text{sunlit,g}}$ is the fraction of sunlit area on the ground below the herb stratum. The exponential multiplier is the fraction intercepted by the herb stratum.

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Similar to Eq. (24), the relative diffuse radiation on the ground can be estimated by integrating $f_{\mathrm{sunlit,g}}$ for all the elevation and azimuth angles

$$F_{\mathrm{d,g}} = 2 \int_0^{\pi/2} f_{\mathrm{sunlit,g}}(\beta) \cdot \sin\beta \cdot \cos\beta \cdot \mathrm{d}\beta, \quad (28)$$

where $F_{\mathrm{d,g}}$ is the relative diffuse radiation on the ground, expressed as the ratio to the diffuse radiation on a horizontal surface above the canopy of the plant community.

2.2.5 Direct and diffuse radiation intercepted by plants and on the ground

The direct radiation intercepted by sunlit leaves can be expressed as

$$I_{\mathrm{b},i} = I_{\mathrm{b0}} \cdot K_i / \sin\theta, \quad (29)$$

$$I_{\mathrm{b,h}} = I_{\mathrm{b0}} \cdot K_{\mathrm{h}} / \sin\theta, \quad (30)$$

where $I_{\mathrm{b},i}$ and $I_{\mathrm{b,h}}$ are the direct radiation intercepted by sunlit leaves of the woody plant i and the herb stratum, respectively ($\mathrm{W\,m^{-2}}$ leaf), I_{b0} is the direct radiation on a horizontal surface above the canopy of the plant community ($\mathrm{W\,m^{-2}}$ ground). The diffuse radiation intercepted by leaves can be calculated by

$$I_{\mathrm{d},i} = I_{\mathrm{d0}} \cdot F_{\mathrm{d},i}, \quad (31)$$

$$I_{\mathrm{d,h}} = I_{\mathrm{d0}} \cdot F_{\mathrm{d,h}}, \quad (32)$$

where $I_{\mathrm{d},i}$ and $I_{\mathrm{d,h}}$ are diffuse radiation intercepted by leaves of woody plant i and the herb stratum, respectively ($\mathrm{W\,m^{-2}}$ leaf). I_{d0} is the diffuse radiation on a horizontal surface above the canopy of the plant community ($\mathrm{W\,m^{-2}}$ ground).

The direct radiation in the sunlit area on the ground equals I_{b0}, and the diffuse radiation on the ground, $I_{\mathrm{d,g}}$, would be $I_{\mathrm{d0}} \cdot F_{\mathrm{d,g}}$ ($F_{\mathrm{d,g}}$ is calculated by Eq. 28).

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2.2.6 Scattered radiation absorbed by woody strata

The scattered radiation received by a woody plant includes scattered radiation generated by its own crown and the scattered radiation from surrounding plants, the latter part usually is very small so we omitted it in the model. The scatter radiation absorbed by a unit leaf area can be estimated based on Smolander and Stenberg (2005)

$$I_{s1,i} = I_{s0,i} \cdot \alpha_i \cdot r_i / [1 - (1 - \alpha_i) r_i], \tag{33}$$

where $I_{s1,i}$ is the average scattered radiation absorbed by a unit leaf area of plant i ($W\,m^{-2}$ leaf). α_i is the light absorption coefficient of the leaves of plant i (α_i can be defined for different ranges of radiation spectrum, e.g., for the total solar radiation or for the photosynthetically active radiation). $I_{s0,i}$ is the average scattered radiation ($W\,m^{-2}$ leaf, averaged for all the leaves in the crown) generated by reflection and transmission when direct and diffuse radiation are first intercepted by leaves of plant i (zero order scattering), and r_i is the recollision probability of scattered radiation, which is assumed remaining constant in successive scattering (Smolander and Stenberg, 2005). $I_{s0,i}$ and r_i can be estimated by

$$I_{s0,i} = (1 - \alpha_i) \left[I_{b,i} \cdot f_{sunlit,i} + I_{d,i} \right], \tag{34}$$

$$r_i = 1 - \exp(-K_i \cdot \rho_i \cdot l_{ai}), \tag{35}$$

where l_{ai} is the average path length from a light source within the crown to outside of the crown, approximated as the average length from the center of the crown to the six sides of the rectangular box

$$l_{ai} = (H_i - h_i)/6 + D_i/3. \tag{36}$$

2.2.7 Scattered radiation absorbed by the herb strata and the ground

On the top of the herb stratum, the scattered radiation from the above woody plants can be estimated as the difference between the scattered radiation generated by the woody plants and the amount of scattered radiation absorbed by the woody plants

$$I_{s1,h} = 0.5 \sum_{i=1}^{M} (I_{s0,i} - I_{s1,i}) \cdot L_{0i} \cdot d_i, \tag{37}$$

where $I_{s1,h}$ is the average scattered radiation from the woody plants on a horizontal surface above the herb stratum ($W\,m^{-2}$ ground). The factor 0.5 is used because the scattered radiation to the upper hemisphere is assumed lost to the sky. The average scattered radiation generated in the herb canopy can be estimated by

$$I_{s0,h} = (1 - \alpha_h)[I_{b,h} \cdot f_{sunlit,h} + I_{d,h}], \tag{38}$$

where $I_{s0,h}$ is the average scattered radiation generated by reflection and transmission when direct and diffuse radiation are first intercepted by leaves of the herb stratum ($W\,m^{-2}$ leaf), and α_h is the light absorption coefficient of the herb stratum. The average scattered radiation received by herb leaves includes scattered radiation from above woody plants and the scattered radiation generated within the herb canopy. The former can be estimated similar to the estimation for diffuse radiation, while the latter can be estimated similar to Eq. (33)

$$I_{s,h} = \alpha_h \cdot I_{s1,h} \cdot F_{d0,h} + I_{s0,h} \cdot \alpha_h \cdot r_h / [1 - (1 - \alpha_h) r_h], \tag{39}$$

Where $I_{s,h}$ is the average scattered radiation absorbed by leaves of the herb stratum ($W\,m^{-2}$ leaf). $F_{d0,h}$ is the relative diffuse radiation for herb stratum when there is no woody stratum, calculated by Eq. (26) but with $F_{2w} = 1$ for $f_{sunlit,h}$ estimation in Eq. (25). r_h is the recollision probability of scattering radiation in the herb canopy, and can be estimated based on Smolander and Stenberg (2005)

$$r_h = 0.88[1 - \exp(-0.7 \cdot LAI_h^{0.75})]. \tag{40}$$

Similarly, the scattered radiation received on the ground, $I_{s,g}$, can be estimated by

$$I_{s,g} = I_{s1,h} \cdot F_{d0,g} + 0.5 I_{s0,h} \cdot \exp(-0.5 K_h \cdot LAI_h), \tag{41}$$

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where $F_{d0,g}$ is the relative diffuse radiation on the ground when there is no woody stratum, calculated by Eq. (28) but with $F_{2w} = 1$ for $f_{sunlit,g}$ estimation in Eq. (27). The factor 0.5 is used because only half of the scattered radiation reaching the ground (the other half scatters to the sky from the top of the herb stratum).

2.2.8 Solar radiation absorbed by sunlit and shaded leaves and the ground

The sunlit leaves receive direct radiation from the sun, diffuse radiation from the sky, and scattered radiation, while the shaded leaves receive only diffuse radiation from the sky and scattered radiation. Therefore the total solar radiation absorbed by sunlit and shaded leaves would be

$$I_{sunlit,i} = \alpha_i (I_{b,i} + I_{d,i}) + I_{s1,i}, \quad (42)$$

$$I_{shaded,i} = \alpha_i \cdot I_{d,i} + I_{s1,i}, \quad (43)$$

$$I_{sunlit,h} = \alpha_h (I_{b,h} + I_{d,h}) + I_{s,h}, \quad (44)$$

$$I_{shaded,h} = \alpha_h \cdot I_{d,h} + I_{s,h}, \quad (45)$$

where $I_{sunlit,i}$ and $I_{shaded,i}$ are the total solar radiation ($W\,m^{-2}$ leaf) absorbed by sunlit and shaded leaves of the woody stratum i, respectively, and $I_{sunlit,h}$ and $I_{shaded,h}$ are the total solar radiation ($W\,m^{-2}$ leaf) absorbed by sunlit and shaded leaves of the herb stratum, respectively. For the ground, the total radiation absorbed on sunlit and shaded areas can be expressed as

$$I_{sunlit,g} = \alpha_g (I_{b0} + I_{d,g} + I_{s,g}), \quad (46)$$

$$I_{shaded,g} = \alpha_g (I_{d,g} + I_{s,g}), \quad (47)$$

where $I_{sunlit,g}$ and $I_{shaded,g}$ are the total solar radiation ($W\,m^{-2}$ ground) absorbed by sunlit and shaded areas of the ground, respectively. α_g is the light absorption coefficient of the ground (the albedo of the ground would be $1 - \alpha_g$). The average solar radiation

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absorbed on the ground would be

$$I_{avg,g} = I_{sunlit,g} \cdot f_{sunlit,g} + I_{shaded,g} \cdot (1 - f_{sunlit,g}) = \alpha_g (I_{b0} \cdot f_{sunlit,g} + I_{d,g} + I_{s,g}), \quad (48)$$

where $I_{avg,g}$ is the average solar radiation absorbed on the ground ($W m^{-2}$ ground). Part of the solar radiation received on the ground will be reflected. In this study we did not consider the contribution of this reflected radiation to the leaves.

2.3 Inputs and outputs of the model and calculation procedure

The inputs for the IPR model include plant community features and the radiation conditions above the plant community. The plant community features include the number of woody plant strata (N), the features of each woody stratum (plant density (d_i), heights of the top and the bottom of the crown (H_i, and h_i, respectively), crown width (D_i), leaf area of the crown (L_{0i}), light absorption coefficient (α_i), and the clumping index of the leaves (Ω_i), and the features of the herb stratum (leaf area index (LAI_h), light absorption coefficient (α_h), and the clumping index (Ω_h)). The radiation conditions above the plant canopy include the elevation angle of the sun (θ), and direct and diffuse radiation on a horizontal surface above the plant community at the time (I_{b0} and I_{d0}, respectively). There are two computing parameters: The maximum distance for shading effects (X_{max}) and the integration interval (dz_i). One hundred meters for X_{max} is large enough, and dz_i can be defined as $0.01(H_i - h_i)$.

The outputs of the model include the fractions of the sunlit leaf area for each woody stratum and the herb stratum, and the fraction of sunlit area on the ground, the radiation of the sunlit and shaded leaf classes of each woody stratum and the herb stratum, and the radiation on sunlit and shaded areas on the ground, and the average radiation on the ground. The code and a user's manual of the model can be found in the Supplement.

The IPR model first calculates the fraction of the sunlit leaf area for each elevation angle from 0 to $\pi/2$ with a small step (e.g., $\pi/36$, or 18 steps). The relative diffuse radiation for each stratum and on the ground can be calculated by numerically integrating the above results with the elevation angle. The fraction of sunlit leaf area of each stratum can be interpolated from the above calculation based on the elevation of the sun at the time. Then the solar radiation absorbed by a plant of each stratum and on the ground can be calculated based on the direct and diffuse radiation above the plant community at the times.

2.4 Testing of the model

2.4.1 Comparing with the fraction of sunlit leaf area calculated by the random approach

In IPR, The calculation of solar radiation for herb stratum is based on Norman (1982), which has be tested and used widely. Diffuse radiation is calculated in a similar way as for direct radiation but the beams are from the entire hemisphere. Therefore the core of the IPR model is the calculation of the fraction of sunlit leaf area of individual plants of woody strata. Detailed field measurements are not available for model test. However, we can test the model by numerically tracing light beams to calculate sunlit leaf area assuming plants are randomly distributed but trying to avoid overlapping among one another (abbreviated as the random approach).

The random approach calculates the sunlit leaf area numerically by dividing the crown into small cells (Fig. 4). A light beam going through a cell may go through crowns of its neighboring plants. Based on the locations and crown sizes of the plants, we can geometrically determine whether a neighboring plant could intercept the light beam. If so, its shading effects can be calculated based on Eq. (11) (the height z_i in Eq. 7 can be calculated based on the height of the cell, the distance x and θ, Fig. 4). To avoid overlapping horizontally among crowns, we defined a minimum distance of plants of stratum i and plants of stratum j as $D_i \cdot E_{ij}$. This definition means that a plant will not overlap with plants of the same stratum ($i = j$) or when the crown of stratum i is vertically within the range of the crowns of stratum j, but plants of two strata can distribute

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independently if one stratum is completely over or below another stratum. If the crowns of stratum i partially vertically overlap with crowns of stratum j, plants of stratum i can proportionally overlap horizontally with crowns of stratum j. During the calculation, we first gave a random location for a plant; then we checked its distance to all the existing plants. If the distance was less than the minimum distance to one of the existing plant, we re-generated a pair of random numbers for its location and checked again until the distance requirement was satisfied. The shading effects on a cell of crown from all the neighboring plants are the multiplication of the shading effects of all the plants calculated by Eq. (6). We used X_{max} as 100 m, clumping index Ω as 1, the step-length Δz as $0.01(H_i - h_i)$, and step-length Δy as $0.01D_i$ (Δy was used only for the random approach (Fig. 4), while Δz was used for both the IPR model and the random approach). Tests show that these step-lengths are small enough for the accuracy of the calculation. The calculated fraction of sunlit leaf area under each case of the random distribution of neighbouring plants is different. But their average became very stable after 300 random cases (the variation is less than 0.001 for the fraction of sunlit leaf area). Therefore, we ran 300 random distribution cases for each test and then used their average to compare with the result of the IPR model.

2.4.2 Sensitivity tests

When a plant community has two or more strata and plant density is high, the random approach cannot distribute the plant randomly without overlapping. Thus we cannot test the IPR model by comparing with the results of the random approach. Instead we tested the sensitivity of the model to plant densities to show its consistency under different plant densities.

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3 Results and analyses

3.1 Comparing with the fractions of sunlit leaf area calculated using the random approach

3.1.1 One-stratum plant communities

Figure 5a–d shows comparisons of the fraction of sunlit leaf area (f_{sunlit}) calculated by IPR and the average of the random approach under different plant density, the local leaf area index of the individual crown (LAI_p), and the elevation angle of the sun (θ). f_{sunlit} calculated by the IPR model is very close to the average of the random approach in all the cases. f_{sunlit} increases with the decrease in plant density because of the decrease in shading effects by surrounding plants. For the same reason, the effects of plant density are stronger when θ is low. f_{sunlit} of different plant density converges with increase in θ, and reaches the same value when the light is straight down (in that case, f_{sunlit} only depends on LAI_p). f_{sunlit} decreases with the increase in LAI_p for a given θ (Fig. 5a–c). If we reduce the plant height by half without changing LAI_p, f_{sunlit} decreases significantly (almost equals to doubling LAI_p) when θ is low and the plants are sparse (comparing Fig. 5b and d). This is because higher plants cast larger shadows, especially when θ is low. This effect of height is not significant when plants are dense or when θ is high.

Figure 5e and f shows f_{sunlit} calculated using the two-big-leaf approach (Assuming that the canopy covers the ground uniformly. The leaf area index was calculated as $D^2 \cdot d \cdot \text{LAI}_\text{p}$). The two-big-leaf approach significantly over-estimates f_{sunlit}, especially when plants are sparse or θ is high. Another difference is their variation patterns: f_{sunlit} calculated by the two-big-leaf approach always increases with the increase in θ, but f_{sunlit} calculated by IPR usually increases at the beginning, and then decreases gradually with the increase in θ, especially when plants are not very dense. This is because when θ is very low, increasing θ significantly reduces the shading of neighboring plants, thus f_{sunlit} increases rapidly. But when θ is high, increasing θ results in more light reaching the ground from the gaps among the crowns, thus the leaves intercept less light.

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This difference becomes smaller when the plant community is denser. When plant canopies completely cover the land ($d = 1/D^2$ plants m^{-2}), the IPR model gave almost the same results as the two-big-leaf approach. That means the two-big-leaf approach is not suitable for sparsely vegetated ecosystems while the IPR can be used in all the cases.

3.1.2 Two-stratum plant communities

For two-stratum plant communities, the fractions of sunlit leaf area calculated by IPR are very close to the averages of the random approach as well for different heights (Fig. 6a–e). When the heights of the two strata are the same, the fractions of the sunlit leaf area for the two strata are the same (Fig. 6a), and are almost the same as the calculated results using one-stratum but double the plant density (the curve is not shown since it is overlapped with other curves in Fig. 6a). When one stratum becomes higher, its f_{sunlit} increases, and f_{sunlit} of the other stratum decreases, because higher stratum shades the lower one (changes from Fig. 6a–e). Figure 6f shows the results of the two-big-leaf approach in two cases: the two strata are in the same height, and one stratum is completely above the other stratum. Again, the two-big-leaf approach over-estimated f_{sunlit} for both strata, and did not show the declining pattern when θ is very high. When one stratum is completely above the other and the canopies of both strata covers the ground completely ($d = 1/D^2$ plants m^{-2}), the IPR model gave almost the same results as the two-big-leaf approach (the results are not shown).

Figure 7 shows comparisons under different combinations of crown heights, plant density, crown width, and leaf area. f_{sunlit} calculated by the IPR model is very close to the average of the random approach in the different cases. Reducing the density of the lower stratum does not affect much the taller stratum. However, reducing the density of the taller stratum increases f_{sunlit} for both strata, especially for the lower stratum when θ is high (Fig. 7a–c), because more light can reach the lower stratum through gaps. Increasing LAI_{p} (no change in crown width) of the taller stratum reduces its f_{sunlit}, especially when θ is high, but that does not affect f_{sunlit} of the lower stratum much,

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because its light mainly comes from the gaps of the taller stratum (Fig. 7b and c). Reducing crown width (no change in LAI_p) can slightly increase f_{sunlit} when θ is low, because the path length of light going through the crown becomes shorter (Fig. 7d). Figure 7d–f shows again that the relative heights of the plants have a significant impact on light competition among plant strata.

3.1.3 Plant communities with three or more strata

The fraction of sunlit leaf area calculated by the IPR model is very similar to the average of the random approach for plant communities with three and four strata as well (Fig. 8). The relative heights are the major factor affecting f_{sunlit} for each stratum (the three strata are overlapped vertically in Fig. 8a and c while they were not overlapped in Fig. 8b). f_{sunlit} of the low stratum also depends on its own crown features and its plant density (comparing stratum 3 in Fig. 8a with 8c).

3.2 Sensitivity analyses

3.2.1 One-stratum plant communities

The fractions of sunlit leaf area and sunlit area on the ground are very sensitive to plant density and local leaf area index of individual plants (Fig. 9). f_{sunlit} decreases with increase in plant density (all curves show declining patterns in Fig. 9a–c), but the decreasing rate becomes smaller when θ is higher (comparing the slopes of the curves with the same colour from Fig. 9a–c), because the shading effects of neighboring plants is less severe when θ is higher (f_{sunlit} is independent of plant density when light is straight down since there is no shading among plants at all in that case. See Fig. 5a–d). The fraction of sunlit area on the ground decreases quickly with increase in plant density. Similar to the changes in f_{sunlit}, the fraction of sunlit area on the ground increases with increase in θ due to decrease of the shading effects (comparing the curves with the same colour from Fig. 9d–f). Increase in LAI_p reduces f_{sunlit}, and also significantly reduces the fraction of sunlit area on the ground (comparing the curves in a panel with different colours). Since the relative diffuse radiation (intercepted by leaves or on the ground, Fig. 9g and h) is an integration of all the elevation angles, its sensitivity to plant density is similar to that of the sunlit fraction (intercepted by leaves or on the ground) when θ is around 45°.

Crown width affects f_{sunlit} mainly when plants are sparse and the elevation angle of the sun is low (LAI_p was kept constant in the tests, Fig. 10). That is because when θ is low, the solar beam goes through a longer path in a crown when the crown is wider. This effect becomes relatively small when plants are dense. The fraction of sunlit area on the ground is more dependent on the fraction of ground covered by crowns (calculated by $D^2 \cdot d$) rather than crown width. The effect of crown heights on the fraction of sunlit area on the ground is very small (assuming no changes in LAI_p, plant density, and crown width. Figures are not shown). However, crown heights are very important for light competition among plant strata, as discussed in the previous section and will be emphasized in the following section as well.

3.2.2 Two-stratum plant communities

Figure 11 shows the sensitivity of the fractions of sunlit area and relative diffuse radiation (on the leaves and on the ground) to plant density for two-stratum plant communities. Increasing the density of the taller stratum has stronger impacts than that of the lower stratum, especially when θ is low (comparing the black curve with the blue curve in each panel in Fig. 11a to f). Even when the total fractions of land covered by the two strata are the constant, increasing the density of the taller stratum (decreasing the density of the lower stratum at the same time) always results in a decrease of f_{sunlit} for both strata (the green curves in Fig. 11a–f). The f_{sunlit} of the lower stratum is more sensitive than that of the taller stratum to changes in plant density of either one or both strata when θ is not very high (comparing the curves of the same colour (excepted the green curves) between Fig. 11a and d, b and e, c and f, respectively). The f_{sunlit} of the lower stratum increases with the increase in θ, because more light can reach the

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lower stratum through the gaps of the taller stratum (comparing the curves of the same colour at the same plant density among Fig. 11d–f).

The fraction of sunlit area on the ground decreases with the increase in the density of either stratum, and is more related with the total plant density of the two strata (Fig. 11g–i). The fraction of sunlit area on the ground is higher when θ is higher, since more light can reach the ground from gaps among plants (comparing the curves of the same colour at the same plant density among Fig. 11g–i). Similar to f_{sunlit}, the relative diffuse radiation intercepted by the lower stratum is more sensitive than that of the taller stratum to plant density of either stratum (comparing the curves of the same colour between Fig. 11j and k). The relative diffuse radiation on the ground depends on the total plant density of the two strata (Fig. 11l).

These sensitivity tests show that the IPR model can calculate the solar radiation intercepted by leaves and the ground consistently from very sparse to continuous plant communities.

4 Discussion and conclusions

Motivated to understand and predict the dynamics of vegetation in northern high latitudes under climate warming, we developed an approach to calculate solar radiation absorbed by individual plants in sparse heterogeneous woody plant communities based on geometrical optical relationships. The core of the calculation is to determine the fraction of sunlit leaf area. We tested the model by comparing with the numerical simulations assuming plants are distributed randomly. The results show that the IPR calculated fractions of sunlit leaf area of the individual plants are very close to the averages under random distributions of the plants, and the results are consistent for different heights, crown width, leaf area, plant density, and under different elevation angles of the sun. The IPR calculated results are consistent with that of the two-big-leaf approach when plants are dense and homogenous.

The IPR is between stand-based canopy models and individual-based radiation models. Comparing to the big-leaf models (e.g., Sellers et al., 1992; Norman, 1980; Wang and Leuning, 1998), the IPR model can be used for discontinuous plant canopies. The plant communities can be composed of several different crown types, and each plant type does not need to be continuous, as required by some the stand-based canopy models (e.g., Foley et al., 1996; Sitch et al., 2003; Zhang et al., 2002; Ryel et al., 1990). Although individual plants are considered as the basic unit of the calculation in the IPR model, we only calculate the solar radiation of one individual plant for each woody stratum in the plant community rather than every individual woody plant. This is similar to the treatment of plant functional types in current vegetation dynamic models (e.g., the models developed by Sitch et al., 2003); therefore IPR could be directly used by these models. IPR focuses on solar radiation accepted by crowns without considering directional reflectance to the sky (as some models for remote sensing purposes, e.g., Li et al., 1995; Myneni et al., 1995), thus greatly simplifies the calculation, and can consider more complex compositions of plant communities and light competition among plants.

Although the fraction of sunlit leaf area can be calculated numerically if we know the locations of all the plants in a community, the calculation is very time consuming. As we did for the model testing, it needs to run about 300 random cases to get the average stabilized since the results are different for different random cases. Furthermore, the average of the random distribution calculated by the IPR is more ecologically meaningful than the individual random cases because the daily average light conditions of a plant is somewhat equivalent to the average of many random cases corresponding to different azimuth directions with the changes of time in a day. That is why the light conditions and the related ecological functions of one plant (e.g., photosynthesis, energy and water fluxes) averaged for a day or longer are similar to other plants of the same stratum although at any moment the light conditions can be very different from plant to plant. The IPR model also calculates the solar radiation under sparse heterogeneous plant communities. The radiation condition on the ground is important for the growth of

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mosses and lichens, and is very important for the whole ecosystems as well by directly affecting soil thermal and hydrological conditions, such as permafrost and active-layer thickness (Zhang et al., 2008). Since the IPR model is efficient in computation, it can be used for long-term, transient, spatial modelling for climate change impact assessment and predictions.

The crowns of woody plants in IPR are represented by rectangular boxes with uniform leaf area densities. Such a treatment allows for a quasi-analytical solution and greatly reduced computation time. However, crowns can be in very different shapes and non-foliage objects (the trunk and branches) also intercept light. Therefore more improvement and modification are needed in future studies.

The current model is developed to calculate the diurnal variations of solar radiation in a day. It can be easily included as a module in ecological models. The inputs of the plant features and radiation conditions above the plant canopy can be passed from the main model. We developed the IPR model using Microsoft Visual C++. The code and an example input dataset and the output result are included as Supplement. A user's manual of the model has been included as well.

Supplementary material related to this article is available online at http://www.geosci-model-dev-discuss.net/6/6927/2013/gmdd-6-6927-2013-supplement.pdf.

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Table 1. Notations.

D	Crown width of a plant (m). D_i and D_j are for plants of woody stratum i and j, respectively.
d	Plant density of a stratum (plants m^{-2}). d_i and d_j are for plants of woody stratum i and j, respectively.
$\mathrm{d}A$	The basal area (m^2) of a small column of canopy (perpendicular to the direction of the light beam). $\mathrm{d}A_i$ is the basal area of a crown slice of a plant i.
$\mathrm{d}F$	The light intercepted by a small column of canopy. Its unit is the same as the unit of the beam of light entering the column.
$\mathrm{d}L_\mathrm{b}$	The sunlit leaf area (m^2 leaf) of a small column of canopy or a crown slice.
$\mathrm{d}z_i$	The small height difference or thickness in vertical direction (m) of a crown slice for a plant of stratum i.
E_{jm}	The fraction of the crown of plant j overlapped vertically with crown of plant m, calculated by Eq. (16). Similarly, E_{ij} is the fraction of the crown of plant i overlapped vertically with the crown of plant j.
E_{Tj}	The fraction of the crowns of all the plant strata overlapped with a crown of stratum j on average, calculated by Eq. (15).
$F_{\mathrm{d,g}}$	The relative diffuse radiation received on the ground, expressed as the ratio to the diffuse radiation on a horizontal surface above the plant community.
$F_{\mathrm{d,h}}$	The relative diffuse radiation intercepted by leaves of the herb stratum, expressed as the ratio to the diffuse radiation on a horizontal surface above the plant community.
$F_{\mathrm{d0,h}}$	The relative diffuse radiation intercepted by leaves of the herb stratum when there is no woody strata, calculated by Eq. (26) but with $F_{2\mathrm{w}} = 1$ for $f_{\mathrm{sunlit,h}}$ estimation in Eq. (25).
$F_{\mathrm{d},i}$	The relative diffuse radiation intercepted by the leaves of stratum i, expressed as the ratio to the diffuse radiation on a horizontal surface above the plant community.
$F_{\mathrm{d0,g}}$	The relative diffuse radiation accepted on the ground when there is no woody strata, calculated by Eq. (28) but with $F_{2\mathrm{w}} = 1$ for $f_{\mathrm{sunlit,g}}$ estimation in Eq. (27).

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Table 1. Continued.

$F_i(\beta,\phi)$	The light intercepted by the whole crown of plant i illuminated from a piece of the hemisphere with the elevation angle of β and azimuth angle of ϕ.
F_1	The solar beam before enters a column of canopy, expressed as the fraction of sunlit area on a surface.
F_2	The solar beam after going through a column of canopy, expressed as the fraction of sunlit area on a surface.
F_{2w}	The solar beam available for the herb stratum after the interception of the woody strata, expressed as the fraction of the sunlit area on a horizontal surface.
f	The shading effects of a small column of canopy on subsequent objects (Eq. 6. $f = 1$ for no shading, and $f = 0$ for completely shaded).
$f_{i,jk}$	The average shading effects on a slice of crown of plant i by plants of stratum j in rectangle k.
$f_{\text{sunlit},i}$	The fraction of sunlit leaf area of woody stratum i.
$f_{\text{sunlit,h}}$	The fraction of sunlit leaf area of the herb stratum.
$f_{\text{sunlit,g}}$	The fraction of sunlit area on the ground, which is the fraction of sunlit area available for mosses and lichens as well.
$f_{0i,jk}$	The shading effects on a slice of crown of plant i by a crown of plant j in rectangle k.
H	The height of the top of the crown (m). H_i and H_j are for plants of woody stratum i and j, respectively.
h	The height of the bottom of the crown (m). h_i and h_j are for plants of woody stratum i and plant j, respectively.
$I_{\text{avg,g}}$	The average solar radiation absorbed on the ground (W m^{-2} ground).
$I_{\text{b,h}}$	The direct solar radiation intercepted by sunlit leaves of the herb stratum (W m^{-2} leaf).
$I_{\text{b},i}$	The direct solar radiation intercepted by sunlit leaves of woody stratum i (W m^{-2} leaf).
I_{b0}	The direct solar radiation on a horizontal surface above the plant community (W m^{-2} ground).

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Table 1. Continued.

$I_{d,g}$	The diffuse radiation received on the ground ($W\,m^{-2}$ ground).
$I_{d,h}$	The diffuse radiation intercepted by leaves of the herb stratum ($W\,m^{-2}$ leaf).
$I_{d,i}$	The diffuse radiation intercepted by leaves of woody stratum i ($W\,m^{-2}$ leaf).
I_{d0}	The diffuse radiation on a horizontal surface above the plant community ($W\,m^{-2}$ ground).
$I_{s,g}$	The scattered radiation received on the ground ($W\,m^{-2}$ ground).
$I_{s,h}$	The average scattered radiation absorbed by the leaves of the herb stratum ($W\,m^{-2}$ leaf).
$I_{shaded,g}$	Solar radiation absorbed by shaded area on the ground ($W\,m^{-2}$ ground).
$I_{shaded,h}$	Solar radiation absorbed by shaded leaves of the herb stratum ($W\,m^{-2}$ leaf).
$I_{shaded,i}$	Solar radiation absorbed by shaded leaves of the woody stratum i ($W\,m^{-2}$ leaf).
$I_{sunlit,g}$	Solar radiation absorbed by sunlit area on the ground ($W\,m^{-2}$ ground).
$I_{sunlit,h}$	Solar radiation absorbed by sunlit leaves of the herb stratum ($W\,m^{-2}$ leaf).
$I_{sunlit,i}$	Solar radiation absorbed by sunlit leaves of the woody stratum i ($W\,m^{-2}$ leaf).
$I_{s0,h}$	The average scattered radiation generated by reflection and transmission when direct and diffuse radiation is first intercepted by leaves of the herb stratum ($W\,m^{-2}$ leaf).
$I_{s0,i}$	The average scattered radiation ($W\,m^{-2}$ leaf) generated by reflection and transmission when direct and diffuse radiation is first intercepted by leaves of woody plant i ($W\,m^{-2}$ leaf).
$I_{s1,h}$	The average scattered radiation on the top of the herb stratum generated by the above woody plants ($W\,m^{-2}$ ground).
$I_{s1,i}$	The average scattered radiation absorbed by a unit leaf area of plant i ($W\,m^{-2}$ leaf).
i	Used as a subscript for a plant of a woody stratum.
j	Used as a subscript for a plant of a woody stratum.
K	Effective extinction coefficient for a beam of light. K_i and K_j are for plants of woody stratum i and j, respectively.

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Table 1. Continued.

K_0	The extinction coefficient when leaves are distributed randomly. It equals 0.5.
K_h	The effective extinction coefficient of the herb stratum.
k	The sequence number of a rectangle for calculating the shading effects of neighbouring plants.
L_0	The total leaf area of a crown (m^2 leaf/plant). L_{0i} is for a plant of stratum i.
LAI_p	The local leaf area index of an individual plant, defined as the ratio between the leaf area of the plant and the land area directly below the crown (m^2 leaf m^{-2} ground).
LAI_h	The leaf area index of the herb stratum (m^2 leaf/ground).
L_{bi}	The total sunlit leaf area of the woody plant i (m^2 leaf/plant).
l	The path length (m) of light for a small column of crown.
l_{ai}	The average path length (m) of light from a light source in the crown of plant i to outside of the crown.
l_{z_i}	The path length (m) of the light going through a crown slice of a plant i with z_i as the height of the slice when light enters the crown slice. l_{z_j} is similar to l_{z_i} but for a plant of stratum j.
$l_{z_j,k}$	The path length (m) of light calculated by Eq. (7) but for plants of stratum j in rectangle k corresponding to the height $z_{j,k}$.
M_j	The total number of rectangles considered for calculating the shading effects of plants of stratum j, estimated by Eq. (19).
m	Used as a subscript for a plant of a woody stratum.
N	The total number of woody strata of the plant community.
p_j	The probability of light going through the crowns of stratum j in a rectangle area. It equals to the fraction of the land area covered by the crowns of the plants of the stratum. p_1, p_2 and p_m are for plants of stratum 1, 2, and m, respectively.
r_i	The recollision probability of scattered radiation in the crown of plant i.
r_h	The recollision probability of scattered radiation in the herb canopy.
$X_{i,jk}$	The distance between the edge of the crown of plant i and the farther edge of the crown of plant j in rectangle k (Fig. 4).
$X_{i,j1}$	The distance $X_{i,jk}$ when k equals 1 (the first rectangle near plant i, Fig. 4).

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Table 1. Continued.

X_{max}	A predefined maximum distance (e.g., 100 m) for shading effects calculation. Beyond that distance, the shading effects of plants are negligible.
z_i	The height (m) of a crown slice when light beam enters it for a plant of stratum i.
$z_{j,k}$	The height (m) of a crown slice when light beam enters it for plants of stratum j in rectangle k, calculated by Eq. (12).
α_g	The absorption coefficient of the ground (the albedo of the ground would be $1 - \alpha_g$).
α_h	The absorption coefficient of the herb stratum.
α_i	The absorption coefficient of the woody stratum i.
β	The elevation angle of the light beam from a piece of the hemisphere.
Φ	The azimuth angle for a piece of the hemisphere.
ρ	The density of the leaf area of a crown (m^2 leave m^{-3} space); it can be calculated by Eq. (1). ρ_i and ρ_j are for plants of stratum i and j, respectively.
θ	The elevation angle of the sun (its unit is in radians in equations, but in degrees in figures).
Ω	Clumping index of the leaves. Ω_i is for woody stratum i.
Ω_h	Clumping index of the herb stratum.

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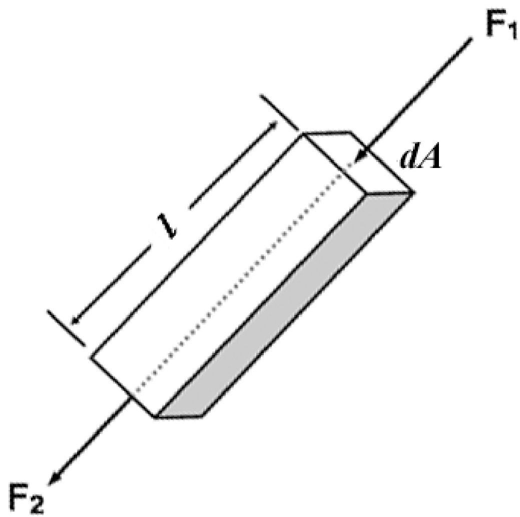

Fig. 1. A general scheme and the related variables for interception of a light beam by a small column of canopy.

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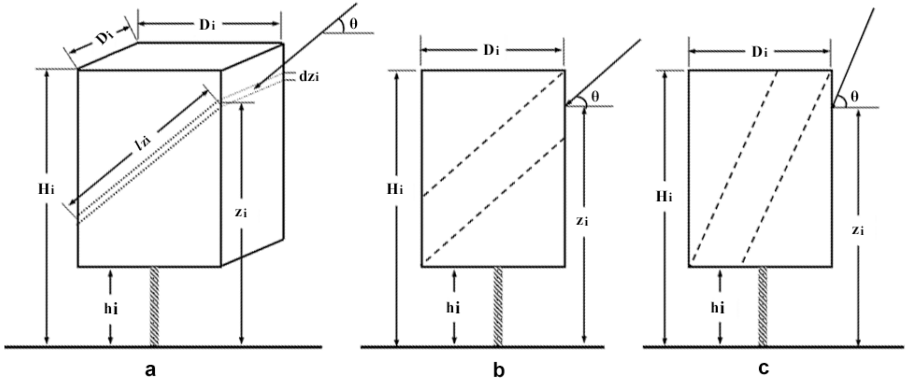

Fig. 2. (a) A three-dimensional show for a light beam going through a slice of crown and the related variables, and **(b** and **c)** two-dimensional shows for the two cases when a light beam going through a crown.

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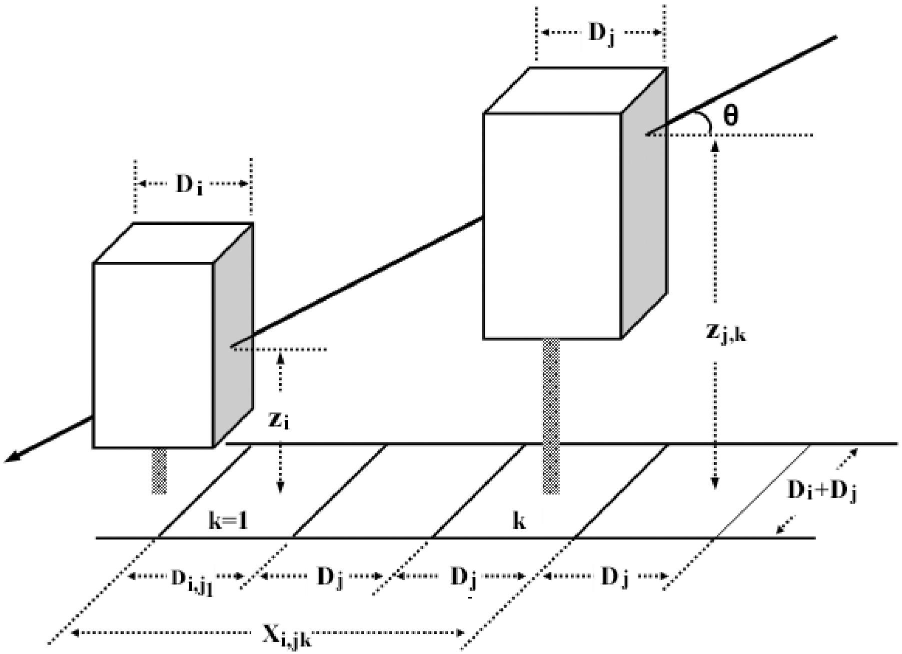

Fig. 3. The scheme to calculate the shading effects of neighbouring plants in the model.

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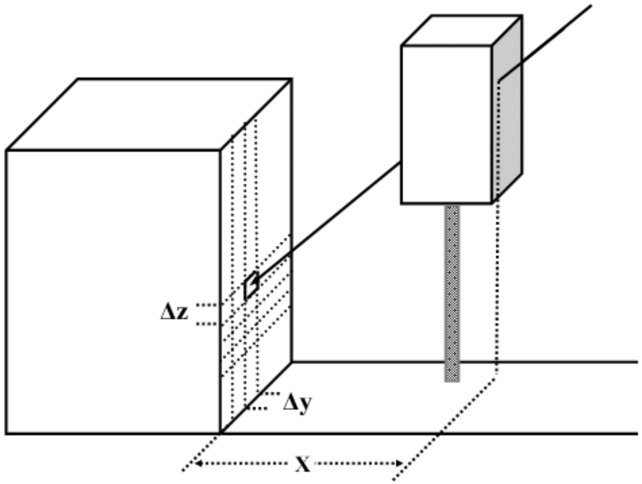

Fig. 4. The scheme of the random approach for numerically calculating sunlit leaf area and the shading effects of the neighbouring plants.

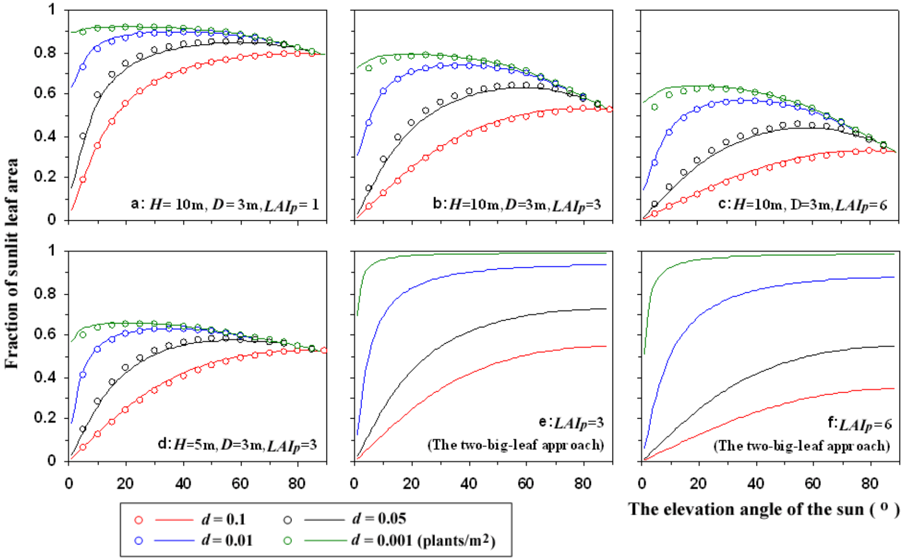

Fig. 5. (a–d) Comparisons of the calculated fractions of sunlit leaf area between the IPR model (curves) and the average of the random approach (circles) for one-stratum plant communities of different heights (H), local leaf area indices (LAI_p), and plant densities (d). The bottom of the crown $h = 0$ m. **(e** and **f)** the fractions of sunlit leaf area were calculated using the two-big-leaf approach (the leaf area index was calculated as $D^2 \cdot d \cdot LAI_p$). Different colours correspond to different plant densities. The circles for $d = 0.1$ plants m^{-2} were calculated assuming plants are distributed regularly because plants cannot be distributed randomly without overlapping in such a dense plant community.

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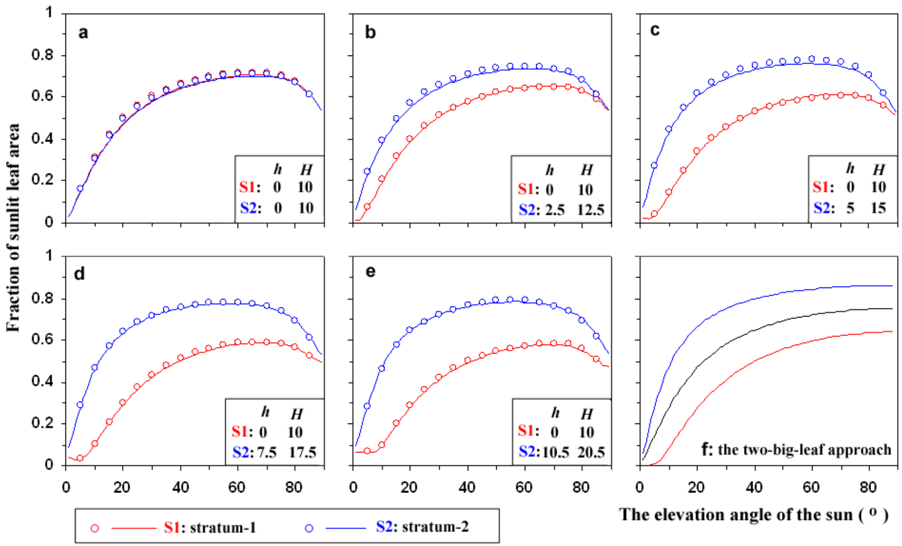

Fig. 6. (a–e) Comparisons of the calculated fractions of sunlit leaf area between the IPR model (curves) and the random approach (circles) for two-stratum plant communities of different heights (Stratum-2 is shifted higher and higher). Red and blue are for stratum-1 (S1) and stratum-2 (S2), respectively. The top and bottom heights of the crowns (h and H) were shown in each panel. Other parameters are the same (crown width D = 1 m, local leaf area index LAI_p = 3, plant density d = 0.2 plants m^{-2}). **(f)** fractions of sunlit leaf area calculated using the two-big-leaf approach assuming the two strata are the same height (the black curve) and the stratum-1 is completely below the stratum-2 (red and blue curves).

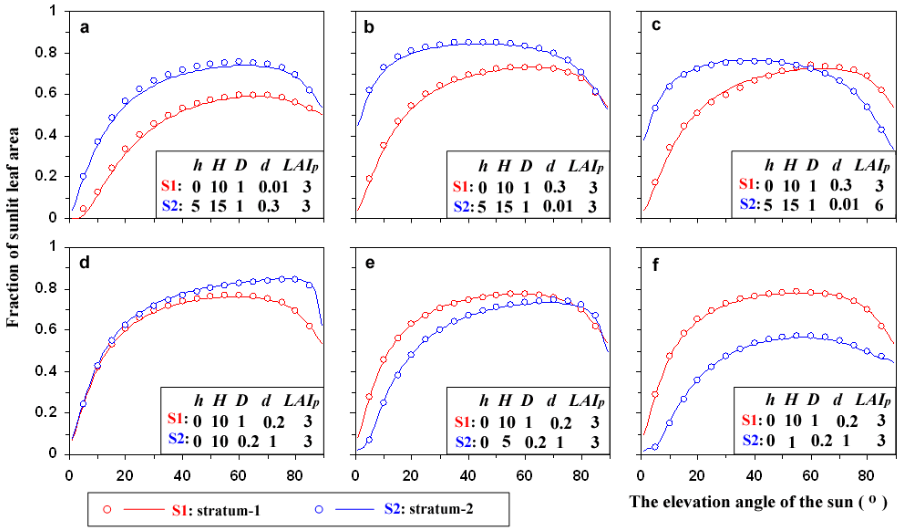

Fig. 7. Comparisons of the calculated fractions of sunlit leaf area between the IPR model (curves) and the random approach (circles) for two-stratum plant communities. Red and blue are for stratum-1 (S1) and stratum-2 (S2), respectively. Their crown parameters are listed in each panel (*H* and *h* are the heights of the top and bottom of the crown, respectively (m), *D* is the width of the crown (m), *d* is the density of plants (plants m^{-2}), and LAI_p is the local leaf area index, m^2 leaf m^{-2} ground).

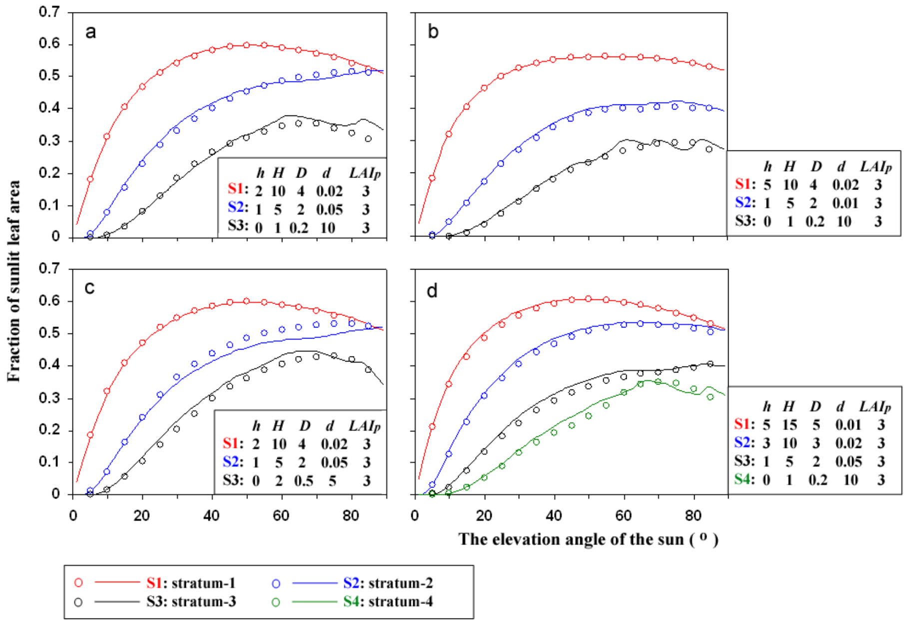

Fig. 8. Comparisons of the calculated fractions of sunlit leaf area between the IPR model (curves) and the random approach (circles) for **(a–c)** three-stratum plant communities and for **(d)** four-stratum plant communities. Different colours are for different strata. The crown parameters are listed within or beside each panel (*H* and *h* are the heights of the top and bottom of the crown, respectively (m), *D* is the width of the crown (m), *d* is the density of plants (plants m^{-2}), and LAI_p is the local leaf area index (m^2 leaf m^{-2} ground)).

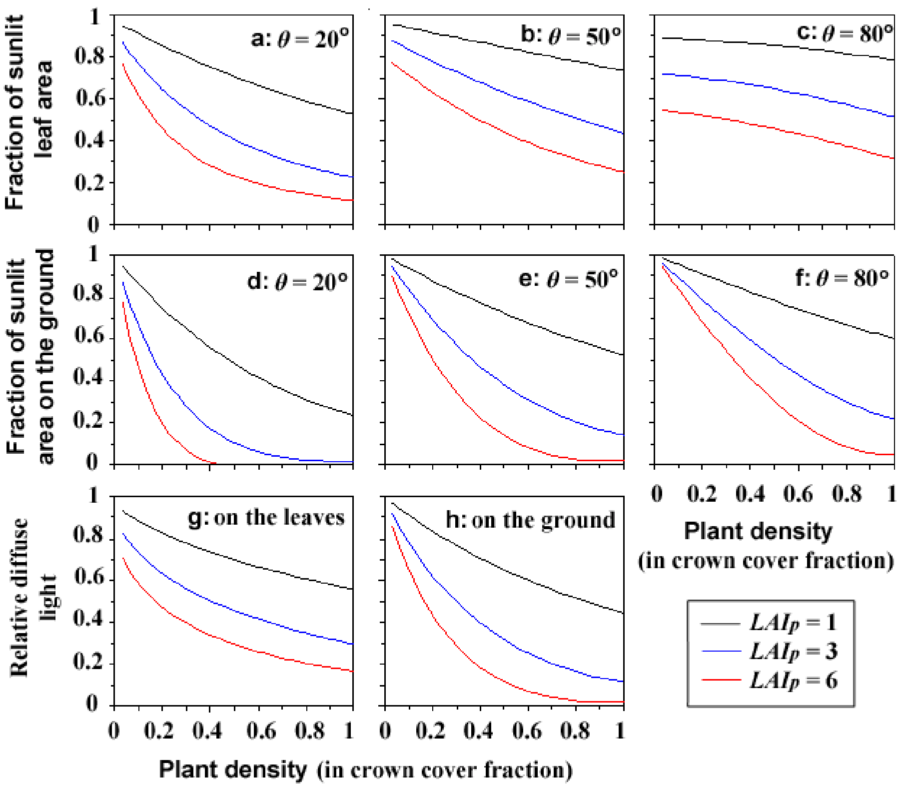

Fig. 9. The sensitivity of the fractions of sunlit area on the leaves and on the ground to plant density and the local leaf area index of the plant. Plant density is expressed as the fraction of land covered by crowns, calculated by D^2d (D is the width of the crown and d is the number of plants per square meter). The relative diffuse light is the ratio to the diffuse light on a horizontal surface above the canopy. The plant communities are composed of only one stratum ($h = 0$ m, $H = 10$ m, $D = 1$ m).

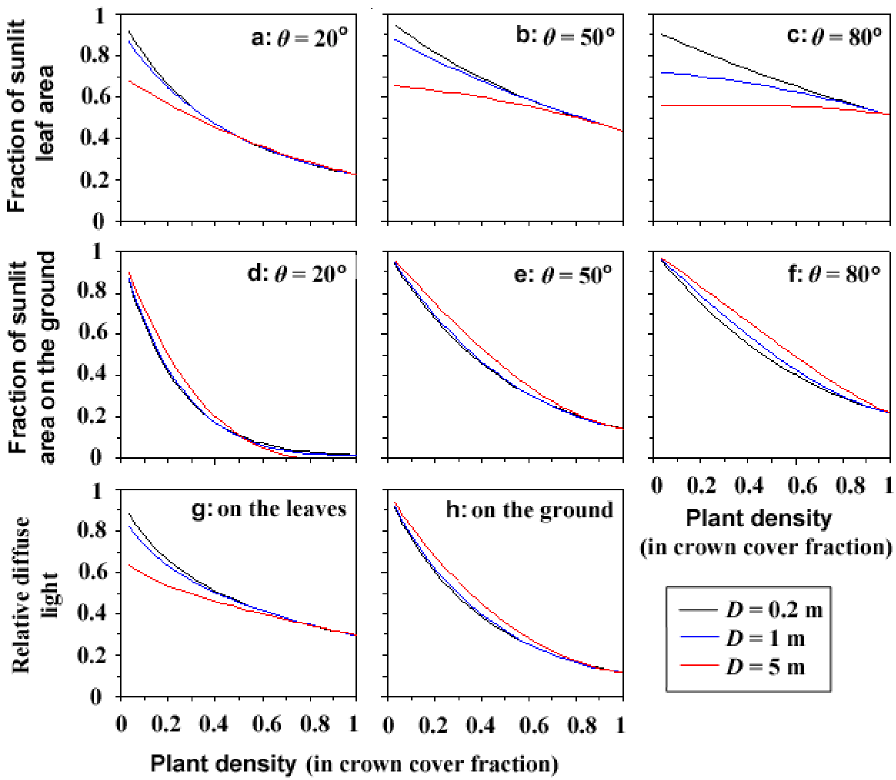

Fig. 10. The sensitivity of the fractions of sunlit area (on the leaves and on the ground) and relative diffuse radiation to plant density and crown width. Plant density is expressed as the fraction of land covered by crowns, calculated by $D^2 d$ (D is the width of the crown and d is the number of plants per square meter). The relative diffuse light is the ratio to the diffuse light on a horizontal surface above the canopy. The plant communities are composed of only one stratum ($h = 0$ m, $H = 10$ m, $\mathrm{LAI_p} = 3$).

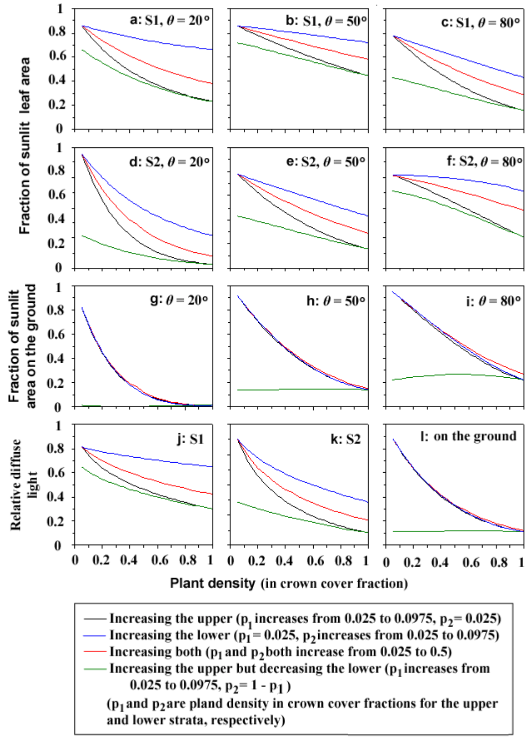

Fig. 11. The sensitivity of the fractions of sunlit area (on the leaves and on the ground) and relative diffuse radiation to plant density for two-stratum plant communities (stratum-1 (S1): $h_1 = 2\,\text{m}$, $H_1 = 10\,\text{m}$, $D_1 = 1\,\text{m}$, $\text{LAI}_{p1} = 3$; stratum-2 (S2): $h_2 = 0\,\text{m}$, $H_2 = 5\,\text{m}$, $D_2 = 1\,\text{m}$, $\text{LAI}_{p2} = 3$). Plant density is expressed as total fraction of land covered by the crowns of both strata, calculated by $D_1^2 d_1 + D_2^2 d_2$ (where D_1 and D_2 is the widths of the crowns of the two strata, respectively. d_1 and d_2 are the numbers of plants per square meter for the two strata, respectively). The relative diffuse light is the ratio to the diffuse light on a horizontal surface above the canopy.

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