

## A method for estimating light interception by a conifer shoot

SAMPO SMOLANDER<sup>1</sup> and PAULINE STENBERG<sup>2</sup>

<sup>1</sup> Rolf Nevanlinna Institute, P.O. Box 4, FI-00014 University of Helsinki, Finland

<sup>2</sup> Department of Forest Ecology, P.O. Box 27, FI-00014 University of Helsinki, Finland

Received August 18, 2000

**Summary** We present an operational method for estimating the amount of PAR intercepted by a coniferous shoot. Interception of PAR by a shoot is divided into three components: the amount of radiation coming from the sky, the transmission of radiation through the surrounding vegetation, and the shoot's silhouette area facing the direction of the incoming radiation. All three components usually vary with direction. Radiation incident from the sky consists of direct and diffuse radiation. The well-known equation of motion for the sun and Beer's Law for atmospheric transmittance are used to simulate the directional distribution of direct sunlight for any given period of time. The diffuse component is assumed to be uniform. Meteorological field measurements are used to calibrate the absolute amounts of the direct and diffuse components. The gap fraction (proportion of visible sky) in different directions around a shoot is measured by analyzing a hemispherical fish-eye photograph, taken at the location of the shoot, with an image processing program. Similarly, the shoot silhouette area (SSA) is measured by photographing the shoot from many different directions. The measurements of SSA are interpolated by a method called trigonometric interpolation to obtain the directional distribution of SSA over the entire hemisphere. This distribution is then rotated according to the shoot's position in the canopy. Multiplying incoming PAR, canopy gap fraction and SSA in different directions, and summing over all directions, gives an estimate of PAR intercepted by the shoot during the chosen period of time. The method is described step by step, and applied, as an example, to a shoot from a Scots pine (*Pinus sylvestris* L.) stand in central Finland. Differences in radiation interception properties between sun and shade shoots and their relevance to canopy-scale models are discussed.

*Keywords:* gap fraction, light interception, shoot silhouette area, SPAR, STAR, trigonometric interpolation.

### Introduction

Characterization of the photosynthetic radiation regime of coniferous forests has proved problematic because of their heterogeneous canopy architecture caused by the grouping of foliage at different levels of hierarchy (Norman and Jarvis 1975, Oker-Blom 1986, Nilson 1992). Many arguments support consideration of the shoot as the basic element of pho-

tosynthetic light capture in conifers (Stenberg et al. 1995). However, the complex geometrical arrangement of needles on shoots requires a different conceptual and methodological approach to quantitatively characterize the amount of photosynthetically active radiation (PAR) absorbed by the shoot.

We note that the PAR intercepted by leaves or shoots in a canopy cannot be directly measured, e.g., by the traditional method of placing horizontal sensors in some fixed arrangement within the canopy. Improved accuracy has been obtained by increasing the number of sensors and the period of measurement; however, the limitation is not related to spatial and temporal resolution but to lack of correspondence. As formulated by Anderson (1966), radiation measurements are invalid because radiation is measured with artificial surfaces that differ from the photosynthetically active elements with respect to size, structure, arrangement and directional distribution.

We have developed a method for estimating the amount of PAR intercepted by a coniferous shoot during a specified period of time. The directional distribution of incoming radiation is modeled, based on the well-known equation of motion for the sun, Beer's Law for atmospheric transmittance, and semi-empirical relationships for the proportion of direct and diffuse radiation. The absolute amount of incoming radiation during the specified time period is calibrated from meteorological field measurements. No measurements of irradiance within the canopy are required, because conifer needles scatter only a minor part of the photosynthetically active radiation (i.e., absorption is close to unity) (Williams 1991). The fraction of above-canopy PAR entering a shoot can thus be estimated based on the canopy gap fraction in different directions of the upper hemisphere. Similarly, for a given direction of radiation, the PAR intercepted by the shoot is proportional to the shoot's silhouette area in that direction. The directional distribution of gaps in the canopy is provided by hemispherical photographs taken at the shoot's location. The directional distribution of shoot silhouette area (SSA), rotated according to the shoot's original position in the canopy, is obtained by trigonometric interpolation based on photographic measurements of the silhouette area in several specified directions. Multiplying incoming PAR, canopy gap fraction and SSA in different directions, and summing over all directions, gives an estimate of the PAR intercepted by the shoot during the chosen time period.

## Methods

### Theoretical background

Let  $q(\omega)$  denote the seasonal amount of radiant energy (from solid angle to unit area;  $\text{J sr}^{-1} \text{m}^{-2}$ ) incident from the direction  $\omega$  of the hemisphere  $\Omega$ . The function  $gf(\omega)$  denotes the gap fraction (proportion of visible sky) of the surrounding vegetation, as seen from the location of a shoot in the direction  $\omega$ . The function  $gf$  has values from 0 to 1. The term  $SSA(\omega)$  denotes the shoot silhouette area on a plane normal to the direction  $\omega$ . A shoot's seasonal light interception ( $SLI_s$ ; intercepted radiation per unit needle area) can be expressed as:

$$SLI_s = \frac{1}{NA} \int_{\Omega} q(\omega) gf(\omega) SSA(\omega) d\omega, \quad (1)$$

where the integral is the total amount of energy intercepted by the shoot. The ratio of the integral to the needle area (NA) of the shoot yields the mean amount of intercepted energy per unit needle area. The ratio of SSA to NA is known as STAR (silhouette to total area ratio), when NA refers to the total (all sides) needle area. The spherically averaged STAR ( $\overline{STAR}$ ) is defined as:

$$\overline{STAR} = \frac{1}{NA} \frac{1}{2\pi} \int_{\Omega} SSA(\omega) d\omega. \quad (2)$$

If NA is expressed on a projected area basis, the corresponding ratios are denoted SPAR and  $\overline{SPAR}$  (Stenberg et al. 1995). Seasonal light interceptance ( $SLI_s$ ; Equation 1) is obtained as an integral of the directional values of STAR (SPAR) weighted by the radiant energy incident from these directions.

For comparison, the intercepted radiation per unit area of a flat horizontal surface (e.g., a flat sensor) at the shoot's location would be:

$$SLI_h = \int_{\Omega} q(\omega) gf(\omega) \sin(a_{\omega}) d\omega, \quad (3)$$

where  $a_{\omega}$  is altitude angle of the direction  $\omega$ . The intercepted radiation per unit cross-sectional area of a spherical surface (e.g., a spherical sensor) would be:

$$SLI_o = \int_{\Omega} q(\omega) gf(\omega) d\omega. \quad (4)$$

This quantity is also known as radiant field strength (Bell and Rose 1981). Note that throughout the paper, radiation is assumed to be incident from the upper hemisphere only.

### Above-canopy radiation regime

In the simulations, the amount of PAR above the atmosphere, or the PAR component of the solar constant, is assumed to be  $S_0 = 600 \text{ W m}^{-2}$  (Weiss and Norman 1985). The instantaneous location of the sun in the sky is given by the solar altitude  $a_s$  and azimuth  $\phi_s$  angles. These can be solved from the formulas:

$$\sin a_s = \cosh \cos \delta \cos \Phi + \sin \delta \sin \Phi \quad (5)$$

and

$$\begin{cases} \sin \phi_s = \frac{\sinh \cos \delta}{\cos a_s} \\ \cos \phi_s = \frac{\cosh \cos \delta \sin \Phi - \sin \delta \cos \Phi}{\cos a_s}, \end{cases} \quad (6)$$

where  $h$  denotes hour angle,  $\delta$  is declination and  $\Phi$  is latitude (Karttunen et al. 1996).

Atmospheric transmittance of direct sunlight from the zenith direction is denoted by  $\tau$  and air mass by  $m$ . Air mass is the relative path length through the atmosphere from solar altitude angle  $a_s$  and is approximated by  $m = \min(1/\sin a_s, 35)$  (List 1984). Assuming clear sky conditions, the instantaneous irradiance of direct sunlight on a surface perpendicular to the radiation is given by Beer's Law as  $S_0 \tau^m$ . Gates (1980) suggests values between 0.6 and 0.7 for  $\tau$ . A value of  $\tau = 0.7$  is used in the example.

The sky is divided into sections by altitude and azimuth angles (see Figure 1). Resolutions of  $5^\circ$  by  $30^\circ$ , or higher, are recommended in the computation. In Figures 1–4, a resolution of  $15^\circ$  by  $45^\circ$  ( $6 \times 8 = 48$  sections) is used. The method is conceptually easy to adjust for uneven divisions in relation to altitude or azimuth angle—for example, so that the solid angles of the sections are equal. The trajectory of the sun is followed throughout the growing season. At every time step (e.g., 1 min), Equations 5 and 6 are used to locate the sun in one of the sections, and the energy input, obtained as  $S_0 \tau^m$  multiplied by the length of the time step, is added to the account of the section. These values are arranged in a matrix  $S$  so that each row corresponds to a class of altitude angles and each column to a class of azimuth angles. For example, at a resolution of  $15^\circ$  by  $45^\circ$ ,  $S_{32}$  would indicate the sky section of  $30\text{--}45^\circ$  by altitude and  $22.5\text{--}67.5^\circ$  by azimuth. The values  $S_{ij}$  give the directional distribution of direct radiation during the growing

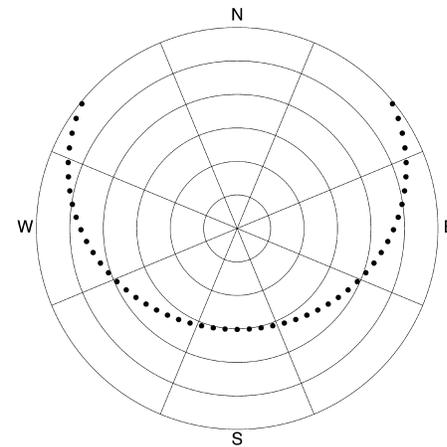


Figure 1. Division of the sky into  $6 \times 8$  ( $15^\circ$  by  $45^\circ$ ) sections and the location of the sun every 20 minutes on August 1, 1998 in Suonenjoki ( $62^\circ 39' \text{ N}$ ,  $27^\circ 05' \text{ E}$ ). In practice, a higher resolution is recommended.

season, assuming that every day was clear. The radiation energy from  $S$  to a unit horizontal surface is given by:

$$E(S) = \sum_i \sum_j S_{ij} \sin_{ij}, \quad (7)$$

where  $\sin_{ij}$  is the sine of the altitude angle of the midpoint of the section  $i, j$ . The summation is carried over all altitude and azimuth angle classes.

We used material from a Scots pine (*Pinus sylvestris* L.) stand at Suonenjoki Research Station (62°39' N) as an example (Stenberg et al. 2001, this issue). The time period considered in the computations of the seasonal estimates (Equations 1, 3 and 4) was August 1998, because this was when the measurements were made. Performing the computation for August 1998 in Suonenjoki gives an irradiance of 188 MJ m<sup>-2</sup> for direct PAR (400–700 nm) to the horizontal plane. Meteorological field measurements give an irradiance of 136 MJ m<sup>-2</sup> of total (300–4000 nm) direct radiation to the horizontal plane in August 1998 (Finnish Meteorological Institute). The proportion of PAR in total radiation is approximately 45% (Larcher 1995), giving a value of 61.2 MJ m<sup>-2</sup> PAR in the meteorological observation. (We note that the proportion of PAR in direct and diffuse radiation depends on many factors—see Ross and Sulev 2000—but for simplicity we used 45% in both cases.) Thus, multiplying every entry in the matrix  $S$  by the factor:

$$k = \frac{61.2 \text{ kJ m}^{-2}}{188 \text{ kJ m}^{-2}} = 0.326, \quad (8)$$

or simply writing  $kS$ , gives a calibrated estimate of the directional distribution of direct PAR radiation above Suonenjoki in August 1998. We note that this estimate is based on the assumption that, on average, the reduction in direct radiation by cloud cover is similar in all directions. If there were only thick clouds, the value for  $k$  would represent the fraction of time when the sun was unobscured by clouds.

The meteorological field measurements give an irradiance of 187 KJ m<sup>-2</sup> for total diffuse radiation to the horizontal plane during August 1998. Again, 45%, or 84.2 KJ m<sup>-2</sup>, is assumed to be PAR. A matrix  $D$  is constructed by:

$$D_{ij} = sa_{ij} \times \frac{84.2 \text{ kJ m}^{-2}}{\pi}, \quad (9)$$

where  $sa_{ij}$  is the solid angle of the section  $i, j$  in steradians. The matrix  $D$  describes a uniform distribution of diffuse PAR radiation. Note that  $D$  represents the sum of all diffuse PAR during the time period considered. Usually, in clear sky conditions, diffuse radiation is higher near the horizon, whereas during overcast conditions it is higher near the zenith (Robinson 1966).

Finally, the matrix  $T = kS + D$  describes the directional distribution of PAR radiation above Suonenjoki for August 1998. The values of  $T_{ij}$  serve as estimates of the function  $q(\omega)$  (cf. Equations 1, 3 and 4) integrated over the respective sky sections  $i, j$  (see Figure 2).

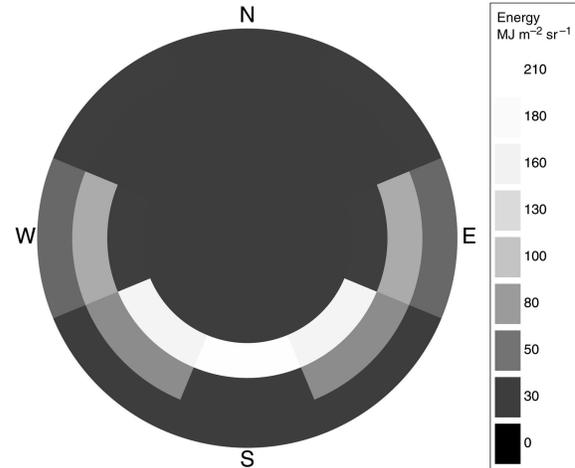


Figure 2. Simulated distribution of above-canopy PAR in Suonenjoki for August 1998. The value assigned to each section is the radiant energy per unit area incident from a unit solid angle of that section.

*Within-canopy radiation regime*

The shading effect of the surrounding vegetation can be analyzed from a hemispherical photograph taken at the location of a shoot. The orientation of the photograph must be known, and the camera should be leveled carefully. By means of hemispherical image analysis software, the photograph is divided into sections  $i, j$  as in Figure 1, and the mean proportion of visible sky within each section is determined as the fraction of white pixels (see Figure 3; for details, see Stenberg et al. 2001, this issue). These values are represented by a matrix  $G$ , where  $G_{ij}$  is the estimate of the function  $gf$  in the corresponding sky section (cf. Equations 1, 3 and 4). Multiplying the incoming energy,  $T_{ij}$ , from the direction  $i, j$ , by  $G_{ij}$  yields an estimate of incoming energy from that particular direction to the location of the shoot (see Figure 4).

The seasonal radiation to a unit horizontal surface at the location of the shoot can be estimated as:

$$SLI_n = \sum_i \sum_j T_{ij} G_{ij} \sin_{ij}. \quad (10)$$

This estimate corresponds to the reading of a flat sensor measuring continuously during August 1998 at the location of the shoot. The estimate of seasonal radiation per unit cross-sectional area of a sphere is:

$$SLI_o = \sum_i \sum_j T_{ij} G_{ij}, \quad (11)$$

which is what a spherical sensor at the shoot's location would detect.

*Light interception by a shoot*

To utilize the directional distribution of incoming energy at a shoot's location to estimate light interception by the shoot, the directional distribution of the shoot silhouette area (SSA) must be known. Before detaching the shoot from the tree for measurements of SSA, the inclination and azimuth of the shoot

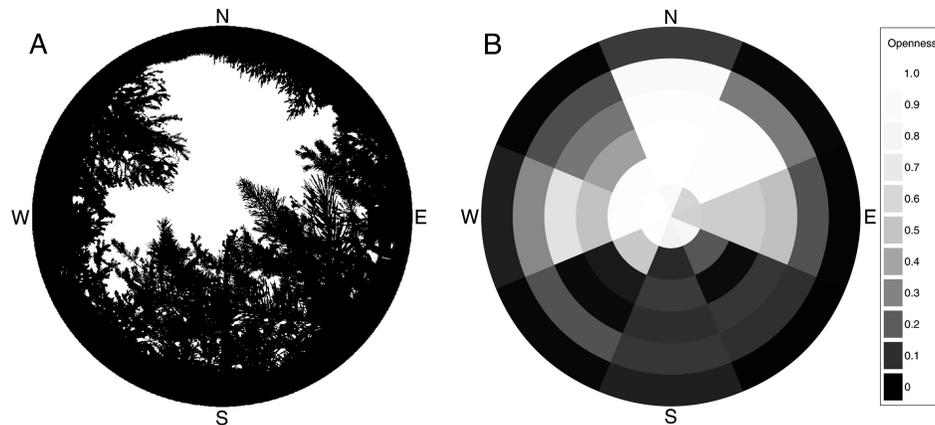


Figure 3. (A) A hemispherical photograph taken at the location of a shoot. Total openness is 0.33. (B) The same photograph after discretizing into sections (see Figure 1) and calculating the mean gap fraction for each section.

axis and the shoot's rotation angle to the vertical are measured. To define the rotation angle, picture a hypothetical plane dividing the shoot into dorsal and ventral sides, and a vector normal to this plane. The rotation angle is the angle between this vector and a vertical plane through the axis of the shoot. When the tip of the shoot is pointing toward the viewer, the positive opening direction of the rotation angle is clockwise. For the example shoot, azimuth was  $160^\circ$ , inclination was  $45^\circ$  and rotation was  $0^\circ$ .

The SSA of the shoot is measured photographically in different view directions  $(\phi, \gamma)$ . We used a resolution of  $30^\circ$  in the  $\phi$  direction and  $90^\circ$  in the  $\gamma$  direction. The time to take and process the 11 photographs in this example was about 30 min per shoot (for further description of the measurement process see Stenberg et al. 2001, this issue).

The measured values were interpolated by two-dimensional generalization of trigonometric interpolation to give  $SSA(\phi, \gamma)$  for all values of  $\phi$  and  $\gamma$  (Figure 5) (Smolander 1999; see Stoer and Bulirsch 1980, pp 76–84, for trigonometric interpolation, and Press et al. 1992, pp 95–97, for two dimensional interpo-

lation). For the present application, trigonometric interpolation was used, because SSA is a periodic function of the angles. The value of  $\overline{STAR}$  was calculated by Equation 2 based on the interpolated  $SSA(\phi, \gamma)$  values, and  $\Omega = (-\pi/2, \pi/2) \times (-\pi/2, \pi/2)$ ,  $\omega = (\phi, \gamma)$  and  $d\omega = \cos\phi d\phi d\gamma$ .

Shoot silhouette area as seen from direction  $\omega$  of the sky,  $SSA(\omega)$ , is determined from the interpolation function  $SSA(\phi, \gamma)$  (see Figure 5). The recorded information on the shoot's natural orientation in the canopy defines the coordinate transformation required to solve  $\phi = \phi_\omega$  and  $\gamma = \gamma_\omega$  for every  $\omega$ . A matrix of SSA is constructed such that  $SSA_{ij}$  is the shoot silhouette area  $SSA(\phi_\omega, \gamma_\omega)$  as seen from the centerpoint of the sky section  $i, j$ . Now  $SLI_s$  can be estimated as:

$$SLI_s = \frac{1}{NA} \sum_{i,j} T_{ij} G_{ij} SSA_{ij}. \quad (12)$$

## Results

The example shoot intercepted 85.6 kJ of PAR during August 1998. In terms of  $SLI_s$  (Equation 1), this amounted to 3.11 kJ  $cm^{-2}$  per unit projected needle area (measured photographi-

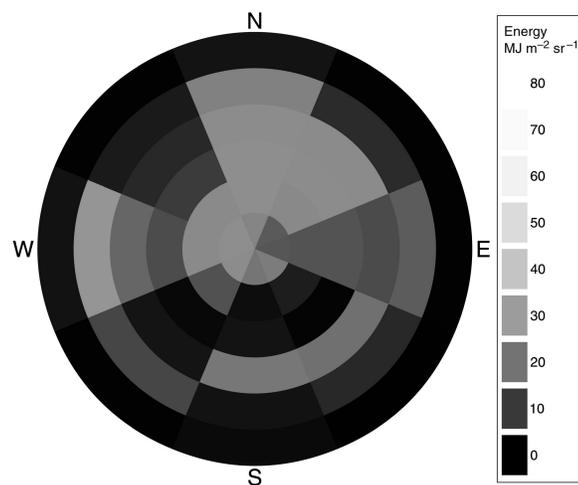


Figure 4. Hemispherical distribution of PAR at the location of a shoot. This image can be thought of as Figure 2 as seen through Figure 3B. Note the different scale.

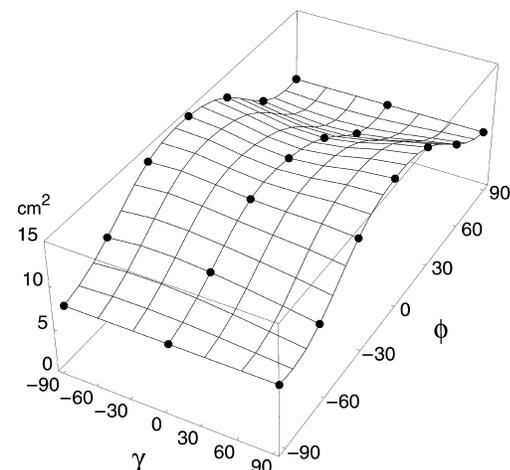


Figure 5. Directional distribution of SSA for the sample shoot. The solid circles denote measured values.

cally to be  $27.5 \text{ cm}^2$ ) or  $0.991 \text{ kJ cm}^{-2}$  per unit (all-sided) needle area (estimated as  $\pi$  times the projected area). By comparison, the energy of PAR received on a horizontal plane ( $\text{SLI}_h$ ) at the shoot's location during the same period was  $4.48 \text{ kJ cm}^{-2}$ , and  $\text{SLI}_O$  was  $7.02 \text{ kJ cm}^{-2}$ . The numbers correspond to the readings that would have been given by a flat and a spherical sensor, respectively, placed at the location of the shoot. Values of  $\text{SLI}_h$ , or preferably  $\text{SLI}_O$ , which is unbiased insofar as it does not discriminate among directions, are appropriate measures of available PAR, and can be used to characterize the light environment at the location of the shoot. However, they are insufficient for estimating PAR intercepted by the shoot, because interception is a function of both the radiation field surrounding the shoot (the receiving object), and the structure and orientation of the shoot (object) itself.

We give an example to illustrate this point. Consider a collection (layer) of randomly distributed and spherically oriented needles situated at the same location (i.e., depth in the canopy) as our experimental shoot. These commonly used model assumptions imply that PAR interception per unit total needle area equals that of a spherical surface at the given location. Thus, in our example, the intercepted PAR per unit total needle area of the layer is estimated as  $\text{SLI}_O$  divided by 4, i.e.,  $7.02 \text{ kJ cm}^{-2}/4 = 1.76 \text{ kJ cm}^{-2}$ . (Notice that the factor 1/4, which is the ratio of cross-sectional to total area of a sphere, enters because the reading of a spherical sensor is per unit cross-sectional area.) The value obtained ( $1.76 \text{ kJ cm}^{-2}$ ) is considerably higher than the calculated PAR interception per total needle area of our shoot ( $0.991 \text{ kJ cm}^{-2}$ ). The relative difference between the estimates  $(1.76 - 0.991)/1.76 = 44\%$  indicates the degree to which the mutual shading of needles on the shoot decreased PAR interception during the time period considered.

The spherically averaged ratio of shoot silhouette area (intercepting area) to total needle area (STAR, Equation 2) of the shoot was 0.141. We note that  $\text{SLI}_O$  multiplied by STAR ( $7.02 \text{ kJ cm}^{-2} \times 0.141 = 0.990 \text{ kJ cm}^{-2}$ ) almost exactly matched the calculated  $\text{SLI}_s$  of the shoot, reflecting that the directional variation in SSA (Figure 5) was not extreme. This simplified method of estimating PAR interception by a shoot may be used as a first approximation, but is theoretically correct only when SSA does not vary with direction, or in the (unrealistic) case when the shoot receives the same amount of PAR from all directions of the upper hemisphere ( $q \times \text{gf}$  constant in Equation 1). In a study on *Abies amabilis* Dougl. ex J. Forbes (Stenberg et al. 1998), the simplified method was found to yield a conservative estimate, i.e., it underestimated  $\text{SLI}_s$  by 15% on average, probably because shoots tend to be oriented so as to increase their PAR interception. This is possible in a nonisotropic radiation field. Comparison between the calculated, true  $\text{SLI}_s$  and the value estimated by the simplified method gives a measure of the gain in PAR interception as a result of a favorable shoot angle.

## Discussion

Assessment of photosynthetic productivity and resource-use

efficiency in plant canopies requires accurate estimates of the distribution of intercepted PAR by the foliage elements. Technical difficulties in measuring this distribution arise because of the large temporal and spatial variations in irradiance that occur within a canopy. Moreover, and more importantly, measurements are of transmitted rather than intercepted PAR. Because coniferous shoots in general are not structurally similar throughout the canopy (e.g., sun shoots and shade shoots), the efficiency with which they intercept the available (transmitted) PAR varies. As a result, the amount of PAR intercepted by shoots along the light gradient in the canopy is not directly proportional to the available PAR at the same locations. This realization has led to a deeper understanding of the role of structural adjustment as a mechanism for enhanced photosynthetic performance of shade foliage (shade acclimation) in conifers (Stenberg 1996, Sprugel et al. 1996). For example, in recent studies on *Picea abies* (L.) Karst and *Abies amabilis* (Stenberg et al. 1998, 1999; see also Sprugel et al. 1996) it was found that the increase in STAR (SPAR) with shading allowed shade shoots to intercept about twice as much PAR per unit needle area as sun shoots would intercept in similar radiation conditions.

Based on model terminology, the observed pattern means that the extinction coefficient increases as transmitted PAR decreases. This pattern is not captured by the classical canopy radiation models, which are built on the assumption of statistically independent leaf locations, described by a probability density function (e.g., the Poisson distribution) (Ross 1970, Mann et al. 1977, Norman 1980). In these models, the extinction coefficient is equivalent to the mean projection of unit leaf area, and varies only with leaf orientation and direction of radiation. Statistical dependency (nonrandomness) in leaf dispersion, e.g., deviations toward clumped or regular distributions, is a classical issue in radiation models (cf. Nilson 1971). For example, in many models, leaves are clumped into tree crowns, which may be regularly spaced, and the classical random theory is applied to individual crowns (e.g., Norman and Welles 1983). However, the clumping of needles on shoots cannot be treated by this approach because a statistical probability density function is not relevant for describing the spatial distribution of needles within the small region occupied by a shoot. The whole concept of leaf area density starts to collapse when smaller and smaller regions are considered (see an analog in Mandelbrot 1983, p. 8). This creates the well known problem in radiative transfer theory of how to handle small-scale structures (e.g., Knyazikhin et al. 1998).

In our model approach, we define the shoot as the basic unit, and describe crown structure in terms of shoot structure, and the angular and spatial distribution of shoots (Stenberg et al. 1993). The extinction coefficient then corresponds to mean STAR, averaged with respect to the directional distribution of PAR at the considered location. In addition to the effect of needle angles, it includes a factor ( $< 1$ ) accounting for self-shading of shoots. Similar approaches have been used by, e.g., Smith et al. (1993), Cescatti (1998), and Nilson (1999). However, because of a lack of data, the extinction coefficient has

commonly been assumed to be constant throughout the canopy (spatially invariant). We emphasize that a vital part of shoot-level models is that they allow inclusion of the dynamic interaction among shoot structure, within-canopy PAR regime, and leaf area development. To this end, information is needed on how differences in shoot structure modify the gradients of PAR within the canopy and, conversely, how the availability of light influences shoot structure.

The methodology described in this paper forms part of our long-term goal to develop a proper characterization of the PAR regime within coniferous canopies. The method offers an operational means to estimate the PAR intercepted by shoots during any specified time period. Calculation of intercepted PAR is not by itself sufficient for predicting canopy photosynthesis without consideration of other environmental variables. For example, a detailed analysis of shoot photosynthesis requires estimates of the temporal distributions of irradiance on the needle area of the shoots (Stenberg et al. 2001, this issue). However, the method provides the necessary data for shoot-level models, which we believe are best suited to capture the effect of small-scale structure on the spatial distribution of PAR. Moreover, the method can be used to derive quantitative relationships among available PAR, shoot structure, and intercepted PAR, thus providing a tool for including structural acclimation as an active feedback mechanism in long-term simulations.

At present, accuracy in the measurement of canopy gap fractions (transmission) and shoot silhouette area (SSA) is ensured by high-resolution digital cameras. Also, the estimates of SSA in unmeasured directions, obtained by trigonometric interpolation, are believed to be accurate. Uncertainty remains regarding a realistic description of the above-canopy radiation field. The simulated directional distribution of above-canopy radiation was based on two assumptions: first, that cloud cover reduces direct radiation similarly in all directions; and second, that the directional distribution of incoming diffuse radiation is uniform. We believe that these assumptions are good for longer (month-scale) time periods, when the random effects of clouds average out. Producing the distribution for a short time period (e.g., a single day), would require knowledge or assumptions about the nature of cloudiness during the time period considered.

## References

- Anderson, M.C. 1966. Some problems of simple characterization of the light climate in plant communities. *In* Light as an Ecological Factor. Eds. R. Bainbridge, G.C. Evans and O. Rackham. Blackwell Science Publishers, Oxford, pp 77–90.
- Bell, C.J. and D.A. Rose. 1981. Light measurement and the terminology of flow. *Plant Cell Environ.* 4:89–96.
- Cescatti, A. 1998. Effects of needle clumping in shoots and crowns on the radiative regime of a Norway spruce canopy. *Ann. Sci. For.* 22:89–102.
- Gates, D.M. 1980. *Biophysical ecology*. Springer-Verlag, New York, 611 p.
- Karttunen, H., P. Kröger, H. Oja, M. Poutanen and K.J. Donner. 1996. *Fundamental astronomy*, 3rd Edn. Springer-Verlag, Heidelberg, 532 p.
- Knyazikhin, Y., J. Kranigk, R. Myneni, O. Panfyorov and G. Gravenhorst. 1998. Influence of small-scale structure on radiative transfer and photosynthesis in vegetation cover. *J. Geophys. Res.* 103: 6133–6144.
- Larcher, W. 1995. *Physiological plant ecology*, 3rd Edn. Springer-Verlag, Heidelberg, 506 p.
- List, R.J. 1984. *Smithsonian meteorological tables*, 6th Edn. Smithsonian Institution, Washington, D.C., 572 p.
- Mandelbrot, B.B. 1983. *The fractal geometry of nature*. Freeman, New York, 468 p.
- Mann, J.E., G.L. Curry, D.J. Hartfield and D.W. Demichele. 1977. A general law for direct sunlight penetration. *Math. Biosci.* 34: 63–78.
- Nilson, T. 1971. A theoretical analysis of the frequency of gaps in plant stands. *Agric. Meteorol.* 8:25–38.
- Nilson, T. 1992. Radiative transfer in non-homogeneous plant canopies. *In* Advances in Bioclimatology, Vol. 1. Ed. G. Stanhill. Springer-Verlag, Berlin, pp 59–88.
- Nilson, T. 1999. Inversion of gap frequency data in forest stands. *Agric. For. Meteorol.* 98:437–448.
- Norman, J.M. 1980. Interfacing leaf and canopy light interception models. *In* Predicting Photosynthesis for Ecosystem Models, Vol. 2. Eds. J.D. Hesketh and J.W. Jones. CRC Press, Boca Raton, FL, pp 49–67.
- Norman, J.M. and P.G. Jarvis. 1975. Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.). V. Radiation penetration theory and a test case. *J. Appl. Ecol.* 12:839–877.
- Norman, J.M. and J.M. Welles. 1983. Radiative transfer in an array of canopies. *Agron. J.* 75:481–488.
- Oker-Blom, P. 1986. Photosynthetic radiation regime and canopy structure in modeled forest stands. *Acta For. Fenn.* 197:1–44.
- Press, W.H., S.A. Teukolsky, W.T. Vetterling and B.F. Flannery. 1992. *Numerical Recipes in FORTRAN*, 2nd Edn. Cambridge Univ. Press, Cambridge, 963 p.
- Robinson, N. 1966. *Solar radiation*, 1st Edn. Elsevier, Amsterdam, 347 p.
- Ross, J. 1970. Mathematical models of photosynthesis in a plant stand. *In* Prediction and Measurement of Photosynthetic Productivity. Ed. I. Setlik. Centre for Agricultural Publishing and Documentation, Wageningen, pp 29–45.
- Ross, J. and M. Sulev. 2000. Sources of errors in measurements of PAR. *Agric. For. Meteorol.* 100:103–125.
- Smith, N.J., J.M. Chen and T.A. Black. 1993. Effects of clumping on estimates of stand leaf area index using the Li-Cor LAI-2000. *Can. J. For. Res.* 23:1940–1943.
- Smolander, S. 1999. Sunray and forest. Master's thesis, Univ. of Helsinki, 46 p. In Finnish.
- Sprugel, D., J.R. Brooks and T.M. Hinckley. 1996. Effects of light on shoot geometry and needle morphology in *Abies amabilis*. *Tree Physiol.* 16:91–98.
- Stenberg, P. 1996. Simulations of the effects of shoot structure and orientation on vertical gradients in intercepted light by conifer canopies. *Tree Physiol.* 16:99–108.
- Stenberg, P., E.H. DeLucia, A.W. Schoettle and H. Smolander. 1995. Photosynthetic light capture and processing from cell to canopy. *In* Resource Physiology of Conifers. Eds. W.K. Smith and T.M. Hinckley. Academic Press, New York, pp 3–38.
- Stenberg, P., T. Kangas, H. Smolander and S. Linder. 1999. Shoot structure, canopy openness, and light interception in Norway spruce. *Plant Cell Environ.* 22:1133–1142.

- Stenberg, P., S. Palmroth, B.J. Bond, D.G. Sprugel and H. Smolander. 2001. Shoot structure and photosynthetic efficiency along the light gradient in a Scots pine canopy. *Tree Physiol.* 21:805–814.
- Stenberg, P., H. Smolander and S. Kellomäki. 1993. Description of crown structure for light interception models: Angular and spatial distribution of shoots in young Scots pine. *Stud. For. Suec.* 191: 43–50.
- Stenberg, P., H. Smolander, D. Sprugel and S. Smolander. 1998. Shoot structure, light interception, and distribution of nitrogen in an *Abies amabilis* canopy. *Tree Physiol.* 18:759–767.
- Stoer, J. and R. Bulirsh. 1980. Introduction to numerical analysis, 1st Edn. Springer-Verlag, New York, 609 p.
- Weiss, A. and J.M. Norman. 1985. Partitioning solar radiation into direct and diffuse, visible and near-infrared components. *Agric. For. Meteorol.* 34:205–213.
- Williams, D.L. 1991. A comparison of spectral reflectance properties at the needle, branch, and canopy level for selected conifer species. *Remote Sens. Environ.* 35:79–93.