

Effects of needle clumping in shoots and crowns on the radiative regime of a Norway spruce canopy

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Abstract – The effects of hierarchical levels of needle clumping on the canopy transmittance of a conifer stand are examined using a 3D radiative transfer model. Canopy architecture in an experimental plot is described by the tree spatial distribution, crown shape, shoot geometry and needle morphology. Various assumptions about canopy structure (homogeneous or discontinuous; measured or random tree distribution) and basic foliage elements (needles or shoots) are tested. The vertical profiles of unintercepted direct and diffuse radiation, and the spatial variability of the fluxes within and between tree crowns are examined. In the case of a homogeneous canopy, most of the incoming radiation would appear to be absorbed when leaf area index (LAI) reaches a value of 5, while leaf clumping in crowns increases the average canopy transmittance at the base of the canopy (LAI 7.84) up to 4.9 % for direct and up to 10.9 % for diffuse radiation. The effect of needle clumping in shoots on light penetration rapidly decreases if needle clumping in crowns is also assumed. The impact of needle clumping on the indirect LAI estimates obtained by a LICOR LAI 2000 plant canopy analyser is quantified by simulating the device within the modelled tree canopies. Needle clumping in crowns induces an LAI underestimation of 54 % if the observed tree distribution is assumed, and this increases to 61 % in the case of a random distribution. In a homogeneous canopy, needle clumping in shoots induces an LAI underestimation of 36 %, while in discontinuous canopies the negative bias is only 4 %. (© Inra/Elsevier, Paris.)

canopy architecture / light interception / LAI / PCA / *Picea abies*

Résumé – Effet de l'agrégation des aiguilles dans les rameaux et les houppiers sur le régime radiatif d'un couvert d'épicéa commun. Les effets du niveau d'organisation de l'agrégation des aiguilles sur la transmittance d'un couvert de conifères ont été évalués à partir d'un modèle tridimensionnel de transferts radiatifs. L'architecture des houppiers a été décrite dans une parcelle expérimentale par la distribution spatiale des arbres, la forme de leurs houppiers, la géométrie des rameaux et la morphologie des aiguilles. Plusieurs hypothèses de structure des houppiers (homogènes ou hétérogènes, distribution réelle ou au hasard) ont été testées. Les profils verticaux de rayonnement direct et diffus, et leur variabilité spatiale à l'intérieur et entre les houppiers, ont été

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examinés. Dans le cas d'un couvert homogène, la plus grande partie du rayonnement incident et absorbée lorsque l'indice foliaire (LAI) atteint une valeur de 5, alors que l'agrégation des aiguilles dans les houppiers augmente la transmittance moyenne à la base du couvert (LAI = 7,84) de 4,9 % pour le rayonnement direct et 10,9 % pour le diffus. L'effet sur la pénétration du rayonnement de l'agrégation des aiguilles sur les rameaux décroît rapidement si l'agrégation des aiguilles est aussi réalisée au niveau des houppiers. L'impact de l'agrégation des aiguilles sur la mesure indirecte du LAI au moyen de l'analyseur LI-COR LAI 2000 a été simulé par le modèle. L'agrégation des aiguilles dans les houppiers entraîne une sous-estimation du LAI de 54 % dans le cas de la distribution réelle des tiges dans la parcelle, et ce biais passe à 61 % dans le cas d'une distribution des tiges au hasard. Dans un couvert homogène, l'agrégation des aiguilles sur les rameaux entraîne une sous-estimation du LAI de 36 %, alors que pour un couvert discontinu, l'écart n'est plus que de 4 %. (© Inra/Elsevier, Paris.)

architecture aérienne / interception lumineuse / indice foliaire / analyseur / *Picea abies*

1. INTRODUCTION

Total leaf area and its spatial distribution are crucial parameters in the description of tree canopies, as they determine radiation regimes and affect mass and energy exchange between vegetation and the atmosphere [17]. The relevance of these issues has encouraged the implementation of canopy models for the prediction of radiative fluxes within vegetation canopies, and the development of indirect methods for the estimation of leaf area index (LAI, half the total leaf area per unit ground surface area) by inversion of gap fraction data. Because specific knowledge of leaf spatial distribution is lacking, most of these methods and models are based on the assumption that canopies are homogeneous in horizontal layers, and that phytoelements are distributed randomly [18, 32]. But many natural or semi-natural tree canopies develop a non-random leaf distribution, as a response to genetic forces (e.g. shoot geometry and apical dominance in conifers), environmental factors (harsh weather condition), or human pressure (silviculture and agroforestry [5, 27, 29]). Conifers in particular present successive levels of leaf clumping which may be an architectural strategy for the optimisation of light absorption in dense canopies [8,

21, 27]. Consequently, in canopy models, the spatial distribution of leaf area should be taken into account because it significantly affects light interception and related phenomena such as photosynthesis, carbon balance and stand dynamics [2, 7, 13, 20, 34]. Furthermore, due to the close relationship between leaf distribution and canopy gap fraction, indirect methods used to estimate LAI should be corrected to eliminate errors introduced by the spatial arrangements of phytoelements [5].

The aim of this study was to investigate the effects of different levels of leaf clumping on radiative regimes, using a 3D canopy model to generate different architectural scenarios, and a radiative transfer model to predict fluxes in the modelled canopies [3]. The importance of shoot clumping has been stressed in several previous studies concerned with conifer physiology and indirect LAI estimation [14, 25]. However, the quantitative influence of shoot clumping on light interception in non-homogeneous canopies has not been clarified, especially if additional levels of needle clumping (e.g. crown geometry and tree spatial distribution) occur simultaneously. This question has been addressed in this study by evaluating the consequences of single architectural assumptions on the interception of direct and diffuse radiation, and the

interactions between different levels of canopy architecture are highlighted. Furthermore, vertical profiles of direct and diffuse fluxes within and between tree crowns are predicted in order to quantify the importance of leaf clumping in crowns. The observed tree spatial distribution is compared with the assumption of random tree distribution often adopted in other canopy models [12].

The effect of successive levels of leaf clumping on indirect LAI estimates obtained by the LI-COR LAI 2000 plant canopy analyser (PCA) [33] is analysed by simulating the PCA readings of canopy transmittance within the modelled canopies. Errors induced by tree spatial distribution and leaf clumping in crowns and shoots are quantified; in addition, the correction of LAI estimates for shoot clumping proposed by Stenberg [25] is tested under different canopy scenarios.

2. MATERIALS AND METHODS

2.1. Study site

The experimental area is located in an even-aged Norway spruce (*Picea abies* Karst.) stand, 5 km from the Hyytiälä Forest Field Station (61°53' N, 24°13' E, Tampere, Finland). Accessory species include Scots pine (*Pinus sylvestris* L.) and silver birch (*Betula pendula* Roth.) accounting for 3 and 1 % of the specimens, respectively. The canopy structure was surveyed in a 90 × 90 m plot, relatively homogeneous with respect to species composition, canopy structure and ground vegetation. To avoid an edge effect, the torus edge correction was applied. As a consequence, trees on a given border have those on the opposite plot edge as neighbours [16].

2.2. Canopy architecture

Canopy architecture was described at different hierarchical levels, including tree spatial distribution, crown geometry, shoot archi-

ture and needle morphology. Because the number of pines and birches in the plot was limited, the stand was treated assuming that spruce is the only tree species.

The topographic position and height of each tree within the experimental plot were measured with an electronic tachymeter. The tree spatial pattern was estimated using the Clark and Evans index, corrected for edge effect by the algorithms developed by Donnelly [6], as reported in Fröhlich and Quednau [9]. In the case of a tree random distribution this index is equal to 1, while an index value larger or smaller than 1 indicates regular or clumped spatial patterns, respectively.

Crown geometry was described according to the crown shape model developed by Koop [11] and Cescatti [3]. For each tree, the following parameters were collected: total tree height, height at point of crown insertion and at the widest point of the crown, crown radii in four orthogonal directions, and shape coefficients of vertical crown profiles. Leaf biomass of single trees was estimated by the biometric equation reported by Marklund [15]. The leaf biomass was converted to half the total leaf area using a specific leaf area coefficient experimentally estimated in the study area ($5.54 \pm 1.05 \text{ m}^2\text{kg}^{-1}$). Needle clumping in shoots was quantified as the ratio of shoot silhouette to total needle area ($\overline{\text{STAR}}$) and equals 0.161 [28]. The spatial distribution of basic foliage elements within crowns (needles or shoots according to the architectural scenario) was assumed to be random; the leaf area density (LAD, half the total needle area per unit crown volume) was assumed to be uniformly distributed in the crown envelopes [1]; and the angular distribution of the needle and shoot normal was assumed to be spherical.

2.3. Architectural scenarios

In order to generate alternative scenarios for the sensitivity analysis, the architecture of the experimental stand was modelled with various assumptions about canopy structure and basic foliage elements. With regards to canopy heterogeneity in horizontal space, the following three alternatives were compared: 1) the canopy is homogeneous in horizontal layers and has the same vertical LAI profile as the experimental stand (H); 2) the canopy is made heterogeneous by use of an array of crown

envelopes at the observed spatial location (O); 3) as for 2) but with a random tree distribution (R). For each of these three scenarios, the possibility that either needles (N) or shoots (S) are the basic foliage elements was tested. The significance of different canopy architectures on the radiative regime was evaluated separately for direct (D) and diffuse (d) radiative fields. Throughout the paper, individual simulations are identified by the symbols in parentheses. For example, (HNd) indicates the simulation concerning the diffuse flux in a homogeneous canopy of randomly distributed needles.

2.4. Radiative regime

Radiative fluxes penetrating the canopy were computed using FOREST, a model designed specifically to simulate the radiative transfer in heterogeneous canopies [3]. In this model, the probability of non-interception of a beam travelling through the canopy is computed by applying the Lambert-Beer equation to the beam paths in the crown array [20]. For each point investigated in the canopy space and for each intercepted crown, the beam path length and the LAD along the path in each crown were computed with an angular resolution of 1° for the whole upper hemisphere (360 by 90 directions). In scenario (N), extinction coefficients were estimated from the angular distribution of the leaf normal (0.5 for the spherical distribution; [1]), while in scenario (S), $2 \times \text{STAR}$ was used as the extinction coefficient, following Stenberg [26]. A comprehensive description and validation of the light interception model is reported in Cescatti [3, 4].

FOREST was used to calculate the mean canopy transmittance to direct and diffuse photosynthetic active radiation (PAR, 400–700 nm) during the vegetation period (1.5–15.9). The radiative field above the canopy was described from the 5 min spanned averages of global radiation recorded at the Hyytiälä weather station during 1995. Global radiation data were converted into direct and diffuse PAR fluxes according to Weiss and Norman [31]. During the investigated period, diffuse fluxes accounted for 65.5 % of the total PAR.

Radiative regimes for the different architectural scenarios were characterised by computing the unintercepted direct and diffuse fluxes reaching the nodes of a square, horizontal grid, consisting of 21×21 equally

spaced points, and a distance between two points of 4 m. The grid was repeated at 16 different levels within the canopy (every 2 m from a height of 0–30 m), so that 7 056 points were investigated in scenarios (O) and (R). Values of canopy transmittance at grid nodes falling within crown shells were used to characterise the radiative regime within crowns, and contrasted with those observed in the gaps between crowns. A further detailed analysis of the vertical pattern of light interception in discontinuous canopy scenarios (O, R) was made by sampling canopy transmittance to diffuse radiation at the nodes of a 90×30 m vertical grid, maintaining 0.5 m between points (11 041 nodes). Due to canopy homogeneity, in scenario (H) the variability of the radiative fluxes was limited to the vertical axis. For this reason, the radiative regime was characterised by the fluxes at 16 levels in the canopy. Each layer was characterised by the LAI observed in the real canopy, so that the vertical profiles of cumulative LAI were the same for the three scenarios (H), (O) and (R).

Within the FOREST model, a software simulator of the LI-COR LAI 2000 plant canopy analyser was implemented to test the performance of this device in estimating LAI. The behaviour of the PCA was simulated using the values of probability of non-interception (previously computed with 1° of resolution from each of the 7 056 investigated points) to calculate the canopy transmittance in the five concentric rings of the sensor [32]. Estimates of LAI were obtained from the values of canopy transmittance which were inverted with the uni-dimensional algorithm reported by Welles and Norman [32]. The correction factor proposed by Stenberg [25] to compensate for needle clumping in shoots was used to correct the LAI estimates in the (S) scenarios. Finally, the actual data and the PCA estimates of the vertical LAI profiles were compared, and the errors pertaining to individual architectural assumptions were quantified.

3. RESULTS

3.1. Stand statistics

Statistics of the experimental plot are summarised in *table 1*. The canopy appears

Table I. Stand statistics in the 90 × 90 m experimental plot.

Parameter	SI unit	
Density	(stem ha ⁻¹)	1045
Mean diameter	(cm)	21.8
Basal area	(m ² ha ⁻¹)	38.9
Top height	(m)	19.1
Crown projection	(m ² ha ⁻¹)	7338
LAI	(m ² m ⁻²)	7.84
Clark and Evans index		1.23

to be uniformly closed, with a stand density of 1 045 stems ha⁻¹ and an LAI of 7.84 m²m⁻². The vertical profile of the mean LAD in the 16 layers is an asymmetrical normal with a maximum of 0.71 m²m⁻³ at 15 m (*figure 1a*).

The Clark and Evans index is estimated as 1.23, indicating a regular spatial pattern of trees; this result is significantly different from the hypothesis of random tree distribution (*t*-test; *n* = 846, *t* = 39.9, *P* < 0.01). Regular patterns of tree distri-

bution affect the spatial arrangement of the leaf area and may influence the relationship between LAI and radiative regime. Previous investigations on this topic have assumed a random tree distribution [12, 22], but this assumption is not always valid. In fact, competition-driven self-thinning and silvicultural treatments often induce regular tree distributions in even-aged stands [10], while typical gap dynamics of natural, uneven-aged forests may produce clumped distributions [9, 30].

3.2. Canopy architecture and radiative regimes

3.2.1. Canopy heterogeneity

Vertical profiles of mean canopy transmittance, using needles as basic foliage elements, are shown for direct and diffuse radiation in *figure 1b, c*, respectively. Canopy heterogeneity appears to affect both the shape of the profiles and the absolute values of gap fraction. In scenarios (HND, d), most of the incoming direct and

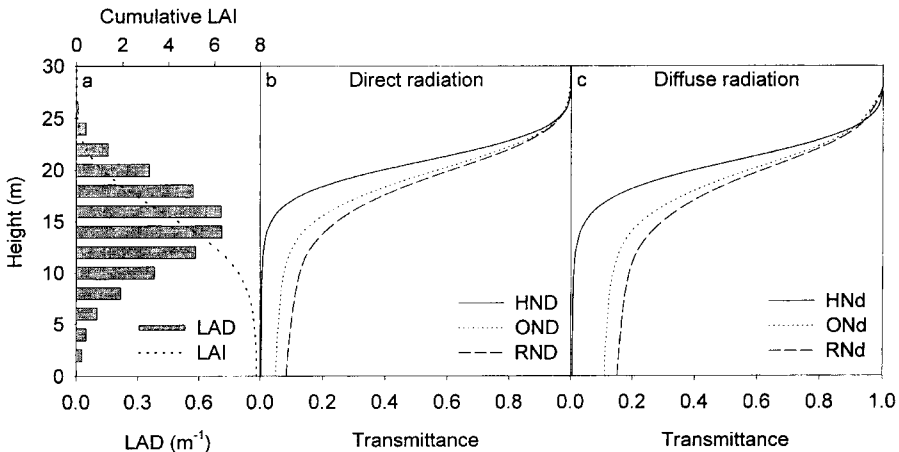


Figure 1. Vertical profiles of LAD (m²m⁻³), cumulative LAI (m²m⁻²) (a) and of canopy transmittance to direct (b) and diffuse (c) radiation, assuming a homogeneous canopy (H) and discontinuous canopies with observed (O) or random (R) tree spatial distribution.

diffuse radiation is apparently absorbed at LAI 5, so that deeper layers would not receive enough radiation to support the photosynthesis. On the other hand, leaf clumping in crowns increases the average canopy transmittance at the bottom of the canopy (LAI 7.84) up to 4.9 and 10.9 % for scenarios (OND) and (OND), respectively. Assuming a random tree distribution (RN), the canopy transmittance increased about 3 % with respect to the (ON) scenario (8.4 and 15.2 % for RND and RNd, respectively), with an overall reduction in the canopy interception efficiency. The differences in canopy transmittance between scenarios (HND, d) and those assuming canopy heterogeneity (OND, d and RND, d; *figure 2*) are maximised in the upper part of the canopy (15–20 m from the ground), where leaf area and physiological processes are concentrated. In the bottom canopy layers, the difference between (H) and (O, R) decreases as a consequence of low canopy transmittance and increased uniformity in

the spatial distribution of leaf area in the (O, R) scenarios.

Due to the isotropic distribution of diffuse fluxes in the sky hemisphere, canopy transmittance to diffuse radiation is higher than the transmittance to direct radiation, and this difference increases with the depth in the canopy. Both high canopy transmittance to diffuse radiation and the predominance of diffuse fluxes in the above-canopy PAR (65.5 % during the investigation period) support the hypothesis that the lower layers of coniferous canopies are acclimated to diffuse fluxes, which are evenly distributed both in time and in space [14, 24].

The variation in the vertical pattern of canopy transmittance produced by canopy heterogeneity was interpreted in terms of efficiency of light interception; an interception efficiency index is defined as the reduction in canopy transmittance per unit of LAI. The vertical profiles of this index in *figure 3* show the interception patterns of homogeneous canopies (i.e. crops and broad-leaved forests) in comparison to heterogeneous ones. While the homogeneous canopy (H) presents a high interception efficiency in the upper layers, which rapidly decreases beneath LAI 4, the efficiency reduction with depth is lower in heterogeneous canopies, which means that photosynthesis could be supported in the deeper layers. In fact, in *figure 3b*, the interception efficiency in scenarios (ONd) and (RNd) is quite stable for LAI larger than 5. These vertical profiles would probably be smoother if the angular distribution of the phytoelements and the shoot architecture were free to change with depth in the canopy model and if the penumbra effect were considered [25, 26]. In terms of light interception, maintaining inefficient upper layers produces an even distribution of the irradiance on the leaf area, and seems to be an architectural strategy of spruce canopies to sustain an LAI of 10 or more [13, 23, 26].

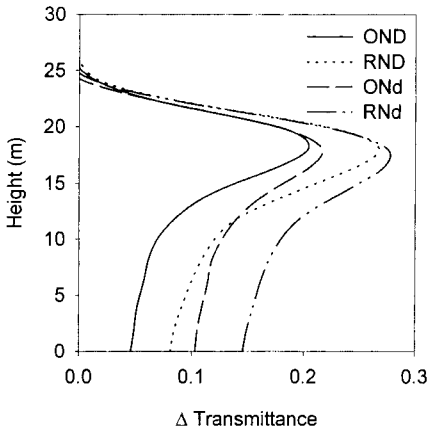


Figure 2. Differences in canopy transmittance to direct (D) and diffuse (d) radiation between the discontinuous canopies (O, R) and the homogeneous scenario (H) along the vertical canopy profile.

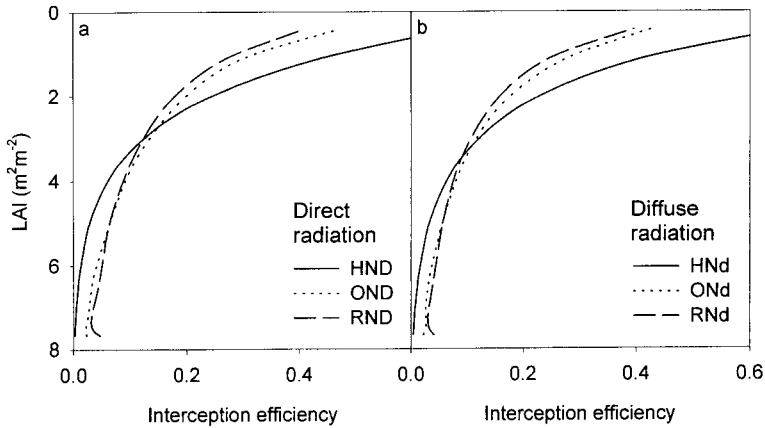


Figure 3. Reduction in canopy transmittance per unit of LAI (interception efficiency) for direct (a) and diffuse (b) radiation for three architectural scenarios (H, O, R).

As a whole, these results highlight the importance of horizontal canopy heterogeneity on radiative regimes. Consequently, canopy architecture at the crown level should be considered an essential feature of coniferous stands, and in all the canopies with a clearly recognisable crown geometry.

3.2.2. Within and between crown radiative regimes

Discontinuous canopies are composed of two media: the space within and the space between crowns, both of which are spatially organised into three-dimensions. Because they show different optical properties, these two media are characterised by distinct radiative regimes [20]. Therefore, in order to describe the light microclimate of heterogeneous canopies, it is necessary to investigate the radiative regimes of both the media [12]. In this study, the mean and standard deviation of vertical profiles of canopy transmittance were computed separately for the points within and between crowns in the archi-

tectural scenarios (OND, d) and (RND, d) (figure 4). The frequency distribution of the canopy transmittance at three different heights in the canopy (10, 16 and 22 m; figure 5) quantifies the spatial variability of both the direct and diffuse fluxes, in contrast with the single values predicted by the homogeneous canopy model (HND, d). Crown overlapping in the random tree distribution (RN) reduces the canopy cover, which may explain why the interception efficiency decreases, and spatial variability of the fluxes increases (figure 4). On the contrary, the observed regular crown distribution with clumping of leaf area within crowns seems to be an efficient strategy to distribute the light in dense canopies ([22]; figures 4 and 5).

The vertical profiles of canopy transmittance reported in figure 6 clearly show how light penetrates heterogeneous canopies. In the case of regularly distributed trees, needle clumping in cone-shaped crowns generates vertical gaps through which columns of light can penetrate the deeper canopy layers (figure 6, scenario ONd). In the case of random tree

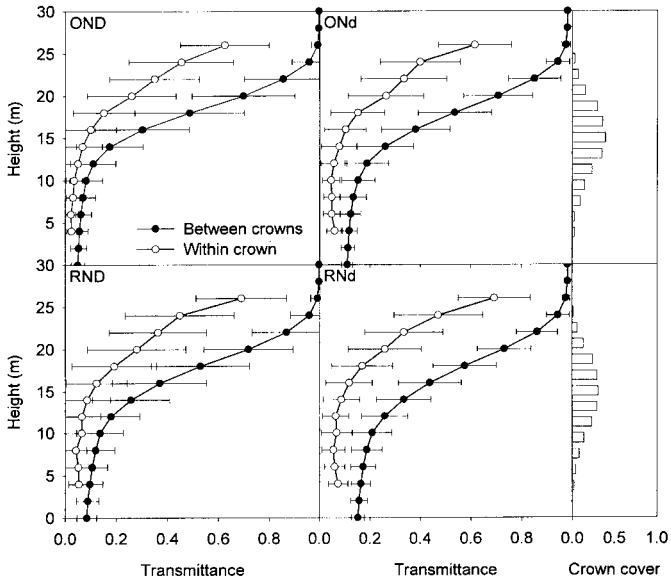


Figure 4. Mean and standard deviation of canopy transmittance for points within and between tree crowns; the assumptions of observed (O) and random (R) tree distribution are compared in terms of canopy cover, direct (D) and diffuse (d) radiative regime.

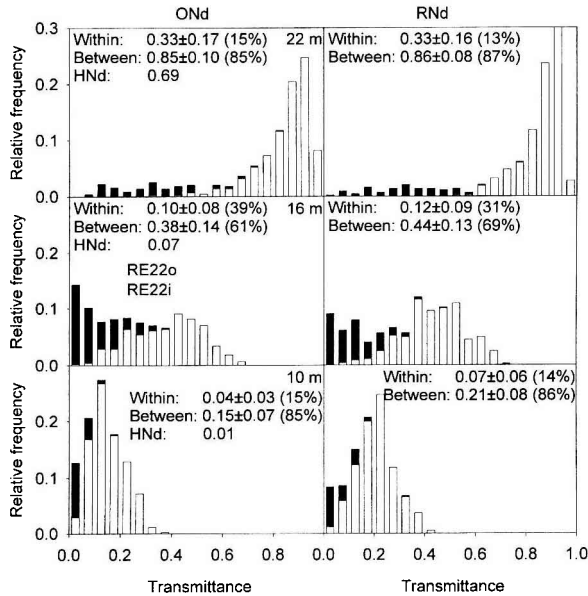


Figure 5. Frequency distribution of the canopy transmittance to diffuse radiation within and between tree crowns at three heights in the canopy (10, 16 and 22 m). Mean and standard deviation of canopy transmittance are reported for each canopy scenarios (H, O, R) together with the percentage of canopy space within and between crowns.

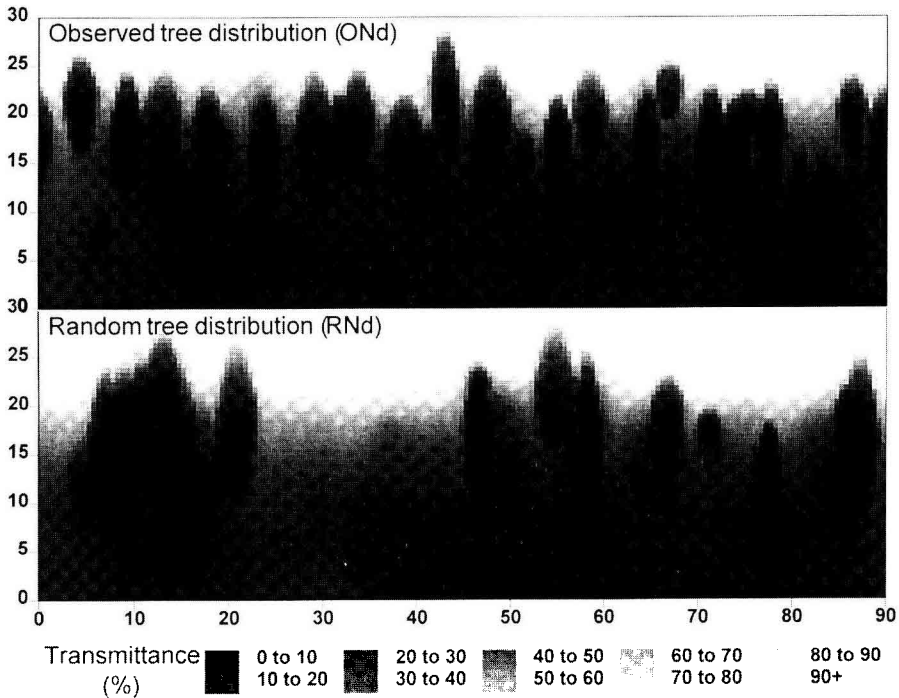


Figure 6. Percentages of canopy transmittance to diffuse radiation at the nodes of a vertical grid (90×30 m, 0.5 m space step, 11 041 sampled points) for the canopy scenarios (O) and (R).

distribution, the succession of dense tree clumps and large gaps increases the spatial variability of the fluxes and reduces the interception efficiency of the canopy (*figure 6*, scenario RNd).

3.2.3. Needles clumping in shoots

The effect of needle clumping in shoots on the radiative regimes of the different canopy scenarios (H, O) is shown in *figure 7* for direct and diffuse radiation. The increase in canopy transmittance due to shoot clumping seems to be maximised in the upper part of the canopy (18–22 m), while the effect in the deeper layers is rather limited. However, the relevance of

shoot architecture on canopy transmittance depends on the spatial structure of the canopy: the homogeneous canopy shows a maximum difference in canopy transmittance of 0.18 at 20–22 m, while for a heterogeneous canopy, the maximum difference is 0.06 at 18–20 m. These results highlight the complex interplay between canopy architecture and radiative regimes, through which the canopy structure at one architectural level (e.g. crowns) can influence the effect of needle clumping on light interception at a second level (e.g. shoots). As a consequence, the marked effect of shoot architecture on light penetration in a homogeneous canopy rapidly decreases when the canopy is characterised by other

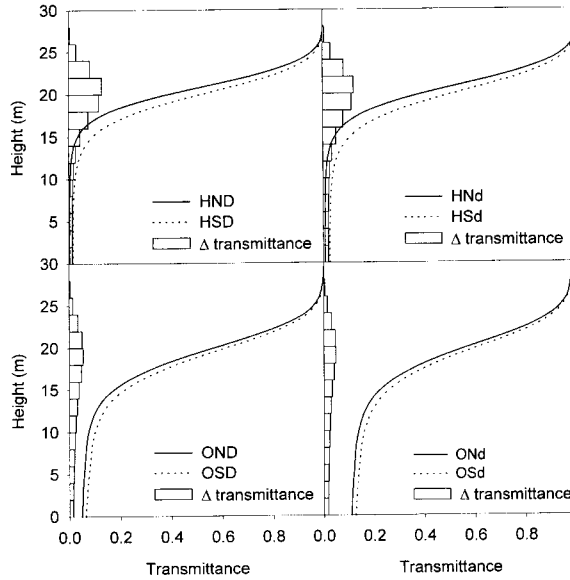


Figure 7. Vertical profiles of canopy transmittance assuming needles (N) and shoots (S) as foliage basic elements in the homogeneous (H) and discontinuous (O) scenarios.

levels of needle clumping (i.e. crowns). These considerations should be taken into account when shoots instead of needles are chosen as basic foliage elements of coniferous canopies, as suggested by Chen [5] and Stenberg [25, 26].

3.3. Canopy structure and indirect LAI estimation

Indirect methods for the estimation of LAI are based on experimental measurement of gap fraction and on the inversion of the radiative transfer equation, assuming a homogeneous canopy structure and a random leaf distribution [32]. Because of the non-linearity in the relationship between LAI and canopy transmittance, small errors in the gap fraction data produce large variations in the LAI estimates; therefore, the non-random leaf distribu-

tion, which affects the gap fraction, becomes an important source of error in the indirect LAI estimation [5, 25].

To evaluate the influence of canopy heterogeneity at different architectural levels (tree spatial distribution, and needle clumping in crowns and shoots) on the PCA estimates, real LAI values were compared with those predicted by the PCA simulator. In *figure 8*, the vertical profile of the cumulative LAI is plotted together with values predicted by the PCA simulator for the canopy scenarios (ON) and (OS). Results show that the error due to needle clumping in crowns (the differences between actual [LAI] and [ON]) is larger than that induced by needle clumping in shoots (the differences between [ON] and [OS]).

The PCA estimates of LAI at ground level and the percentage error of the predictions under the different architectural

assumptions are summarised in *table II*. In the hypothesis of needle clumping in crowns, LAI is underestimated by 54 % if the observed tree distribution (ON) is assumed; this underestimation increases to 61 % if tree distribution is assumed ran-

dom (RN). Needle clumping in shoots increases these figures by a further 4 % (58 and 63.9 % for scenarios [OS] and [RS], respectively), while in a homogeneous canopy (HS) clumping in shoots induces an LAI underestimation of 36 %. These results support the hypothesis that shoot architecture is less relevant if the canopy presents other levels of needle clumping. The correction factor proposed by Stenberg [25] to compensate for needle clumping in shoots is effective when the canopy is homogeneous, but it cannot account for the error induced by crown architecture and spatial tree distribution (*table II*). These results highlight the need for new developments in inversion techniques in order to handle the effects of crown architecture on gap fraction.

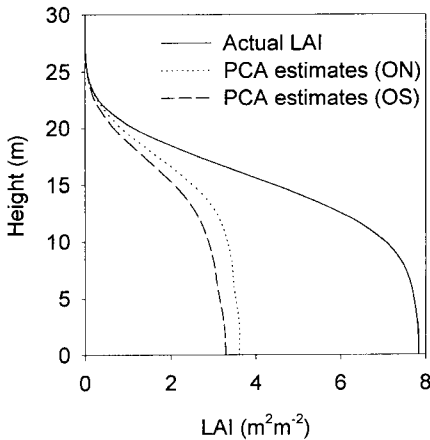


Figure 8. Actual values of cumulative LAI compared with the predictions of the PCA simulator, obtained in the discontinuous canopy scenario (O) assuming needles (N) and shoots (O) as basic foliage elements.

4. DISCUSSION

Results of the analyses on leaf spatial distribution demonstrate that the assumptions of canopy homogeneity and of random leaf distribution are not valid in the examined spruce canopies. In fact, ignoring leaf clumping leads to an underesti-

Table II. LAI predictions obtained by simulating the PCA readings in 441 regularly spaced points on the forest floor of the modelled spruce canopy under different architectural assumptions. In the hypothesis of shoots as basic foliage elements, the correction factor proposed by Stenberg (1996a) was applied (*). The percentage error is computed with respect to the actual LAI value (7.84).

Canopy structure	Basic foliage element	Scenario estimate	LAI (m^2m^{-2})	Percentage error (%)
Homogeneous canopy	Shoot	HS	5.04	-35.8
	Shoot*	HS*	7.82	-0.3
Observed tree distribution	Needle	ON	3.61	-54.0
	Shoot	OS	3.29	-58.0
Random tree distribution	Shoot*	OS*	5.11	-34.8
	Needle	RN	3.06	-61.0
	Shoot	RS	2.83	-63.9
	Shoot*	RS*	4.39	-44.0

mation of the canopy transmittance and, consequently, to an inaccurate prediction of radiative regimes.

Previous investigations into the relationship between crown architecture and radiative regimes were based on a random tree distribution [12]. Apparently this assumption need to be verified for individual plots, because it is not generally valid. In fact, even-aged stands usually present a regular tree distribution as a consequence of natural mortality and thinning [10], while gap dynamics generate a typical clumped pattern in uneven-aged forests [30]. The spruce canopy investigated here shows a regular tree distribution and clumped leaf area within crowns. Due to the cone-like shape of spruce crowns, columns of light can penetrate the vertical gaps between crowns, which may support photosynthesis in deeper layers. In addition, the regular tree distribution maintains a high interception efficiency of the canopy, which could be reduced by a random tree distribution [22].

The present results show that homogeneous canopies have a high interception efficiency in the upper layers but cannot support an LAI larger than 6 [23], while a random crown distribution creates high leaf clumping which reduces the canopy interception. A regular distribution of tree crowns with clumped leaf area within crowns represents the best compromise between these two extremes, because this canopy architecture, together with penumbra effects, smooths the irradiance distribution in dense canopies, maintaining most of the leaf area in the linear part of the photosynthetic light response curve [26]. Considering that the photosynthetic performance of spruce canopies depends on the uniformity in the distribution of the irradiance on the leaf area [7], the succession of regular (i.e. crowns, branches, whorls) and clumped (i.e. shoots) architectural levels may be interpreted as a structural strategy to optimise the within-

crown radiative regime and thus productivity of dense canopies [8, 14, 23].

These results also indicate that the close relationship between canopy architecture and gap fraction should be taken into account in the indirect estimation of LAI from canopy transmittance measurements. The underestimation of LAI due to shoot architecture can be corrected effectively through the coefficient proposed by Stenberg [25], even if the relevance of this error in discontinuous canopies is rather limited. A major problem is the correction of bias produced by crown clumping, which depends on stand density, tree spatial pattern and crown geometry. Several methods have been proposed [5, 19], but further developments on the inversion of the radiative transfer equation are required for the effective use of the PCA in discontinuous coniferous canopies.

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