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Original article

Scaling up from the individual tree to the stand level in Scots pine. I. Needle distribution, overall crown and root geometry

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Abstract – We quantified and scaled up (from individual trees over average trees per diameter at breast height, DBH, class) various characteristics of canopy architecture such as leaf area index, needle aggregation, vertical and radial distribution of the foliage for a mature, even-aged Scots pine (*Pinus sylvestris* L.) stand in the Campine region, Brasschaat, Belgium. Both the vertical and radial needle distribution, scaled up to the stand level from destructive harvests of a limited number of trees, have been presented. Total leaf area index for the stand was 3.0 derived from the needle distribution in different canopy layers. The 'cloud' technique used to describe the position and aggregation of needles on branches, on branches in the crown and on crowns in the canopy has been described and applied. These clouds are well-defined spatial units, larger than clusters, on branches with between one and several clouds per branch. The regression equations used to relate needle properties, positions of clouds, needle distribution to stand- and tree-related parameters (such as diameter at breast height, frequency distribution) were developed, parameterised for the particular stand and applied for scaling up purposes. The fitted Rayleigh equation defined the midpoint of the canopy at a height of 19.6 m and the canopy depth as only being almost 5 m. The appropriate values for making conversions from needle mass to needle area were presented and discussed in relation to position in the crown. Overall crown and canopy geometry, as well as geometry and dimensions of the root system were also described and scaled up from individual trees to the stand level. The overall volume of the crown, of the root system and of the canopy were related to the volume of the clouds and the gaps in the canopy, and allowed us to quantify the 'space use efficiency' of the stand. (© Inra/Elsevier, Paris.)

Scots pine / vertical needle distribution / scaling up / leaf area index / canopy structure / root geometry / needle dry mass distribution / tree allometrics

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Résumé – Changement d'échelle de l'arbre au peuplement chez le pin sylvestre. I. Distribution des aiguilles, architecture aérienne et souterraine. Cet article quantifie et extrapole (de l'échelle de l'arbre individuel à celle des arbres moyens de chaque classe de diamètre) plusieurs variables de l'architecture du couvert, comme l'indice foliaire, l'agrégation des aiguilles, et la distribution verticale et radiale du feuillage, dans un peuplement équienne et mature de pin sylvestre (*Pinus sylvestris* L.) dans la région de Campine, Brasschaat, en Belgique. La distribution verticale et radiale du feuillage, extrapolée à l'échelle du peuplement, à partir d'analyses destructives de quelques arbres, est présentée ici. L'indice foliaire total du peuplement, évalué à partir de la distribution des aiguilles dans les différentes couches du couvert, était de 3,0. La technique des « volumes élémentaires » utilisée pour décrire la position et l'agrégation des aiguilles sur les branches, des branches dans les houppiers, et des houppiers dans le couvert, est décrite ici. Ces volumes élémentaires sont des unités spatiales bien définies, plus grandes que les agrégats foliaires, situées sur les branches, chaque branche étant constituée d'un ou de plusieurs de ces volumes. Des équations de régression reliant les propriétés des aiguilles, la position des volumes élémentaires, et la distribution des aiguilles, aux paramètres dendrométriques des arbres et du peuplement (diamètre à 1,3 m, distribution des tiges) ont été développées et paramétrisées, et utilisées pour effectuer le changement d'échelle. Le calibrage de l'équation de Rayleigh a permis de définir le point moyen du couvert à une hauteur de 19,6 m et sa profondeur à environ 5 m. Les valeurs utilisées pour convertir les masses foliaires en surfaces sont présentées et discutées, en relation avec le niveau considéré dans le houppier des arbres. La géométrie des houppiers et du couvert, comme celle des systèmes racinaires, ont aussi été décrites et extrapolées de l'arbre individuel au peuplement. Les volume totaux des houppiers, des systèmes racinaires et du couvert ont été mis en relation avec les volumes élémentaires et avec ceux des trouées dans le couvert, ce qui a permis de définir une « efficacité d'utilisation de l'espace » du peuplement. (© Inra/Elsevier, Paris.)

***Pinus sylvestris* / distribution des aiguilles / changement d'échelle / indice foliaire / structure du couvert / géométrie racinaire / relations allométriques**

1. INTRODUCTION

Measurements of leaf area index (LAI) and light penetration in forest communities are increasingly important for study of forest productivity, gas exchange and ecosystem modelling. Light penetration through a forest canopy is determined by leaf area (and/or leaf mass) and the spatial arrangement of canopy foliage, branches and stems [26]. The amount of leaf (or needle) area and branch biomass, and differences in the arrangement of canopy foliage and branches, are associated with stand structure and canopy architecture [19, 26, 34]. Architectural influences on light penetration through a forest canopy are LAI, vertical distribution of the foliage, leaf (or needle) inclination angles, leaf reflectance and transmittance, and degree of foliage aggregation. Thus, a quantitative description of tree crown geometry and canopy architecture is essential to study growth, productivity and dynamics of forest ecosystems [3, 27]. Traditional forest inventory data provide an important fundamental basis, but are not sufficient. A more detailed quantitative biometric description and the establishment of appropriate relationship data based on individual trees are necessary for scaling up from the tree to the stand level, as well as for comparing different forest stands with each other.

A number of studies have already yielded useful descriptions of canopy architecture and leaf area, as well as allometric relationships for pine *(Pinus)* [1, 15, 16, 26, 31, 33]. A strong relationship has, for example, been found between needle mass and sapwood basal area in single stands of Scots pine grown in central Sweden, but this relationship did not seem appropriate to aggregate the material into one overall regression, having sapwood basal area as the only independent variable [1, 34]. All in all, studies on the relationship between sapwood area, needle area and needle mass, and on the vertical distribution of the needle area in the crown have been rather few [1, 4, 16, 33]. However, it has been demonstrated that foliage aggregation and distribution in pine [13] is one of the key characteristics determining light penetration through the canopy, and is more important than leaf inclination angle, reflectance or transmittance [26].

Therefore, a detailed description of canopy architecture, including needle area and mass distribution, at the tree and stand level is essential in pine. Canopy architecture incorporates variation in LAI and in the spatial distribution of the canopy foliage, thereby determining foliage aggregation and light penetration [23]. Allometric relationships have been and are being widely used to generalize and scale up measured values of biomass, needle area, needle mass and other parameters from an individual branch or tree scale to the stand level, primarily by using stem diameter at breast height (DBH), basal stem area or another non-destructively measured forest inventory parameter [15, 24, 30].

The aims of the current study were 1) to describe in detail the spatial (vertical, radial as well as within individual trees) distribution of needle area and needle dry mass of a mature Scots pine stand, 2) to describe the overall crown and canopy architecture, and the root geometry of the stand using a destructive harvesting technique, and 3) to provide and evaluate the necessary scaling up tools and allometric relations for application to various parameters and processes of primary interest, as canopy carbon and water fluxes. An essential component of reliable estimates of canopy photosynthesis, conductance and water loss is an accurate knowledge of the spatial and temporal variation of the LAI of needles in different needle age classes and needle aggregates. We applied a novel, rather simple approach for describing and scaling up (after Cermak [7]) based on the form of the stem, on the position of the main branches in the crown and on the aggregation of needles in 'clouds'. This approach allowed us to collect in a relatively short time period enough results on a number of harvested trees with a sufficient precision for a reliable upscaling exercise and for further applications.

2. MATERIALS AND METHODS

2.1. Experimental site, location, climate and soil

The study was performed at the experimental plot of a Scots pine *(Pinus sylvestris* L.) forest plantation in Brasschaat, Campine region of the province of Antwerpen, Belgium (51°18'33''N and 4°31'14''E, altitude 16 m, orientation NNE). This forest is part of the regional forest 'De Inslag' (parcel no. 6, Flemish Region) located nearly 15 km northeast from Antwerpen. The site is almost flat (slope 1.5 %) and belongs to the plateau of the northern lower plain basin of the Scheldt river. Soil characteristics are: i) moderately wet sandy soil with a distinct humus and/or iron B-horizon (psammentic haplumbrept in the USDA classification, umbric regosol or haplic podzol in the FAO classification), ii) very deep (1.75–2.25 m) aeolian sand (Dryas III), somewhat poorly drained (neither receiving nor shedding water), and iii) rarely saturated but moist for all horizons with rapid hydraulic conductivity for all horizons [2, 32]. The groundwater depth normally ranges between 1.2 and 1.5 m and might be lower due to non-edaphic circumstances. Human impacts mainly include deep (up to 45 cm) forest tillage in the past. The occurrence of a *Rhododendron ponticum* (L.) shrub in the understorey layer causes (probably also because of allelopathic effects) an unfavorable O-litter characterized by very low biological activity. A mycelium and many ants are present in the litter layer. The climate of the Campine region is moist subhumid (C1), rainy and mesothermal (B'1). Mean (over 28 years) annual and growing season temperatures for the region are 9.76 and 13.72 °C, respectively. Mean annual and growing season precipitation is 767 and 433 mm, respectively. Mean annual and growing season potential evapotranspiration values are 670 and 619 mm, respectively.

2.2. Forest stand

The original climax vegetation (natural forest) in the area was a Querceto-Betuletum [29]. The experimental pine stand was planted in 1929, and was thus 66 years old at the time of the present study. The original, homogeneous stocking density was very high (Van Looken, pers. comm.) and the stand had been frequently thinned, with the most recent thinning in 1993. The stocking density was 1 390 trees ha^{-1} in 1980, decreasing to 899 trees ha^{-1} in 1987, 743 trees ha^{-1} in 1990 and 716 trees ha^{-1} in 1993. Due to windfall a remaining 672 trees ha^{-1} were still present in 1994. A new detailed forest inventory was made in spring 1995 including the frequency distribution of stem diameter at breast height (DBH at 1.30 m above the ground), tree height to the top and to the base of the crown (i.e. the lowest green whorl). All the forest inventory data were collected in spring 1995 for the entire area of the experimental plot (i.e. 1.996 ha). The sparse pine canopy allowed a rather dense vegetation of only a few understorey species such as *Prunus serotina* (Ehrh.) and *Rhododendron ponticum* (L.) which were partially removed in 1993 until the present ground cover of about 20 % of the area was obtained. The herbaceous layer was composed of a dominant grass (*Molinia caerulea* (L.) Moench, covering about 50 % of the area), and some mosses *Hypnum cupressiforme* (L.) and *Polythrichum commune* (L.) that created a compact layer in about 30 % of the surface area.

2.3. Sample trees and tree harvests

Six sample pine trees were selected for harvest and for destructive measurements in the stand adjacent to the experimental plot where the understorey had been removed 3 years earlier. The stocking density and DBH frequency distribution were identical in both plots. Sap flow rates were measured in five of these trees and are described in an accompanying paper (Riguzzi et al., in prep.). The six study trees were selected as being representative of the entire stand based on their size (DBH) using the technique of quantils of the total [9, 10] so that each sampled tree represented the same portion of the stand basal area. Biometric data of the six sample trees, such as stem diameter at breast height including the bark (DBHb), diameter below the green crown including the bark (DGCb), corresponding bark thickness, total tree height, height of the base of the crown and crown projected area (*figure 1*) are summarized in *table I*. In the period from 15 July to 7 August 1995 each sample tree was cut and slowly put on the ground, using ropes, to prevent significant breakage of branches.

2.4. Tree architecture

Each tree was characterized by its stem form, the position and dimensions of the main branches, the total amount of large and small branches, and the dry mass of the needles (*figure 1*). The spatial needle distribution within the crown was analyzed in detail for three sample trees covering the whole range of tree sizes (i.e. trees 1, 3, 5). The total amount of needles and branches only was estimated in the other three trees (nos 2, 4, 6).

2.5. Overall root biometry

Roots were characterized in August 1995 on seven randomly chosen trees of different DBH (tree nos 7–13) that were wind-thrown between 1992 and 1993 in the same stand. After a rough excavation from the sandy soil the mean diameter of the root system, total rooting depth, mean length and diameter of the main roots were measured in the field using a taper. The overall form of the root tips was described in detail using photographic images. From the above parameters the bulk rooted volume (assuming the root system had the form of a paraboloid) and the enveloping surface area of the paraboloid interface (i.e. between the bulk rooted volume and the surrounding soil) were estimated. The upscaling of the root

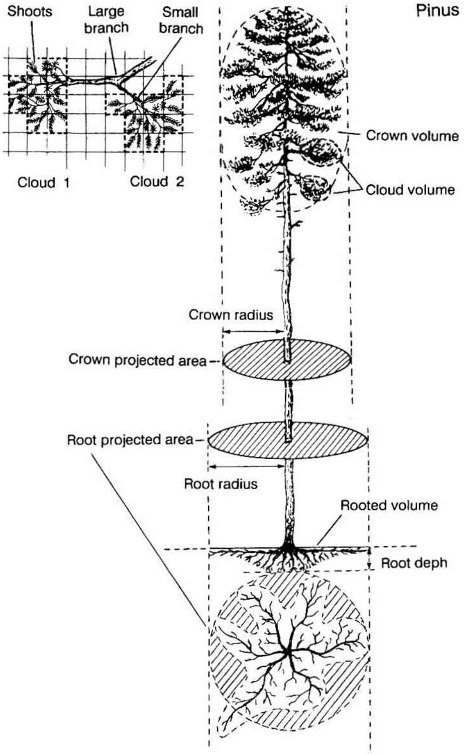

Figure 1. Schematic representation of an average Scots pine tree in the experimental forest stand at 'De Inslag' in Brasschaat (Campine region, Belgium) illustrating the various characteristics and parameters (above-ground as well as below-ground) that were measured or derived for the sample trees.

Table I. Biometric data of the six Scots pine sample trees that were used for destructive analysis at the experimental plot in De Inslag forest, Brasschaat, Belgium.

Tree no.	DBHb (cm)	Bark thick. (cm)	DGCb (cm)	Total height (m)	Height of crown base (m)	Crown depth (m)	Crown proj. area (m^2)	Crown characteristics
1	40.6	2.5	21.9	24.2	17.6	6.6	19.1	large, slightly asymetrical
2	30.5	1.5	—	22.0	17.3	4.7	10.9^{+}	medium, highly asymetrical
3	28.5	1.5	15.8	22.4	15.3	7.1	13.8	medium, mostly symmetrical
4	25.1	1.5	—	21.3	17.6	3.7	13.4^{+}	medium, mostly symmetrical
5	21.4	1.2	11.3	22.4	17.0	5.4	4.4	very small, symmetrical
6	26.3	2.4	13.8	22.2	14.6	7.6	—	medium, mostly symmetrical

DBHb, stem diameter at breast height with bark; DGCb, stem diameter below the green crown including the bark; bark thick: bark thickness. Values followed by + were not measured, but indirectly calculated.

biometric parameters from the individual trees to the entire stand was based on the basal area of the sample trees in proportion to the distribution of basal areas for the stand, as in the case of the foliage (see below). A single step approach was applied since only approximate linear relations were considered. The values derived for mean trees of different diameter classes were multiplied by the corresponding number of trees in the specific class to scale up to a 1-ha stand area. To obtain a rough estimate of the total volume and dry mass values of the root systems, the volume to dry mass ratio of the base of the stem was also used for the roots.

2.6. Needle distribution

The vertical and radial distribution of needles were destructively estimated using the 'cloud' technique on the harvested trees [7]. The position of needles was characterized as if they were located within 'clouds' on the tree, i.e. within certain more or less homogeneous, relatively uninterrupted spatial volumes along branches containing tens of clusters of needles *(figure 1)*. Within this regard we consider leafy shoots with 2-year-old needles as clusters. For each branch, the diameters at 10 cm from the main stem as well as just below the green parts with needles, the bark thickness, branch orientation (azimuth), vertical angles of the branch to the main stem and to the centre of the 'cloud', total branch length and length up to the green part of the branch were measured with a taper, caliper and protractor, respectively. On the same branch one to several individual 'clouds' were distinguished depending on the amount of needles.

For each individual cloud the volume was calculated as an ellipsoid ($V = 4*a*b*c/3$) from measurements of the length (along the branch, $2a$), width (horizontal, tangential $2b$) and depth (perpendicular to the branch axis, $2c$) of the cloud measured in their natural position in the crown. After the dimension measurements in the field all needles were picked, collected per cloud and brought to the laboratory. Needle dry mass of each cloud was estimated after drying for 48 h at 80 °C in a drying oven. The total needle area was calculated for each cloud from their dry mass to area ratio (DMAR, g m^{-2}) estimated on separate small sub-samples. Total needle area per cloud was calculated by applying an allometric relation (Riguzzi et al., in prep.) between needle dry mass and needle area for individual needle pairs (or fascicles). Only one single regression equation was applied for all classes of needles when converting needle dry masses to needle area values.

2.7. Projected vertical needle distribution

It was assumed that individual clouds of needles were composed of a set of cubical cells (20*20*20 cm, 125 cubes per m^3) containing different amounts of needles. These cells were projected on the vertical and on the horizontal plane with a 0.2*0.2 m matrix (25 squares per m^2). Each cloud was characterized by a certain number of squares covering the area of its projection. The total dry mass (correlates to the needle area of the cloud) divided by its ellipsoidal volume represented the actual spatial needle density of each of the k clouds (ρ_c). The sum of all (k) clouds represented the total needle dry mass (M_L) or the total needle area (A_L) for a tree. The total dry mass ($M_{L.k}$) or the needle area of the cloud ($A_{L.k}$), divided by the number of squares separately for the vertical (s_{kv}) and horizontal (s_{kh}) projection, represented the projected (vertical and horizontal) density of needles (ρ_{cpv} and ρ_{cph}, respectively). The cumulated values of both needle dry mass and needle area of all clouds in different vertical layers (i) of 0.2 m in the canopy represented the vertical profile of needle distribution, whereby the sum of all vertical layers represented the overall total of the tree

$$M_{LD.t} = \sum_{i=1}^{i=n} M_{LD.i} \quad \text{and} \quad A_{L.t} = \sum_{i=1}^{i=n} A_L \qquad (1, 2)$$

2.8. Projected horizontal needle distribution

Similarly, cumulated values above different annulets corresponding to discrete intervals (dr) of crown radii (r) of 0.2-m intervals (s_j) represented the radial profile of the needle distribution. The crown projected area on a horizontal surface of all clouds of the tree (including overlapping areas of clouds and small gaps in between clouds) represented the tree crown ground plan area (A_{grp}). The ground plan area is considered to be a circle *(figure 1)*. The tree leaf area index (LAI_t) was calculated by dividing the total one-sided needle area of the tree ($A_{L.t}$) by A_{grp}. The leaf area index used in the context of this study always refers to the one-sided needle area (length * width), as in broadleaved species. The vertical distribution of the needle area density for a tree (LAD_v) was calculated by dividing the relevant needle areas in the vertical layers of the canopy, by A_{grp}. The radial distribution of the needle area density (LAD_r) was calculated by dividing the appropriate needle areas, occurring above individual annulets around the main stem, by the corresponding areas of the annulets (A_{an}). The area of a particular annulet j ($A_{an.j}$) is the difference between the theoretically maximum ground plan area, $A_{grp.max}$ calculated from the maximum crown radius, r_{max} (corresponding to the projected length of the longest branch) and radii that gradually decreased by dr (= 0.2 m)

$$A_{an.j} = \sim r^2_{max} - \pi (r_{max} - dr*j) \qquad (3)$$

In reality $A_{grp.max}$ ($>A_{grp}$) only served for the calculation of LAD_r. As in the case of the vertical profile, the sum of all individual j annulets also represents in the radial profile the tree total, which is valid for particular areas

$$A_{grp.max} = \sum_{j=1}^{j=n} A_{grp.j} \qquad (4)$$

as well as for the needle parameters

$$M_{LD.t} = \sum_{j=1}^{j=n} M_{LD.i}\,, \quad A_{L.t} = \sum_{j=1}^{j=n} A_{L.i} \qquad (5, 6)$$

2.9. Scaling up total area and dry mass of needles

The total area ($A_{L.t}$) and dry mass ($M_{LD.t}$) of all needles per tree were generalized and scaled up from the individual sample trees to the average trees of all m diameter classes in the stand (with DBH intervals of 2 cm). This was based on the allometric relations of the above-mentioned needle parameters to the corresponding basal area of trees (A_{bas})

$$A_{L.tm} = f_1\,(A_{bas}),\ M_{LD.tm} = f_2\,(A_{bas}) \qquad (7, 8)$$

The total area and the dry mass of needles for a unit stand area (1 ha), A_L and M_{LD} were estimated by multiplying the values of the corresponding parameters for the average trees in the individual DBH classes with the number of trees in the respective classes, and summed as

$$A_{L.s} = \sum_{m=1}^{m=n} A_{L.tm} * n_m\,,\ M_{LD.s} = \sum_{m=1}^{m=n} M_{LD.tm} * n_m \qquad (9, 10)$$

2.10. Scaling up of needle distribution

The vertical distribution of needles was scaled up for the particular stand using a two-step approach (recommended by J. Kucera, pers. comm.) and by applying the concept of the limiting height of the top of the tree.

The needle distribution in different layers above the ground (h_i = height in m) was approximated by a basic equation for each sample tree separately. Canopy layers with a depth of 0.2 m (along the axis of the stem) were considered, so that the needle distribution (y_i) could be expressed in (kg per 0.2 m) and/or in (m^2 per 0.2 m).

For the basic scaling up equation four different equations were considered and evaluated, i.e. the Gaussian, Log-normal, Transitional and the Rayleigh equations [22], written as:

Gaussian

$$y = P_1 * \exp[-P_2 * (h_i - P_3)^2] \qquad (11)$$

Log-normal

$$y = [P_1/(P_2 - h_i)] * \exp\{-[\ln(P_2 - h_i) - P_3]^2/P_4\} \qquad (12)$$

Transitional

$$y = P_1 * (P_2 - h_i) * \exp[-(P_2 - h_i)/P_3] \qquad (13)$$

Rayleigh

$$y = \{[P_1 * (h_{top} - h_i)]/P_2\} * \exp\{[-(h_{top} - h_i)^{P4}]P_3\} \qquad (14)$$

The selected Rayleigh equation was modified by introducing the height of the top of the tree (h_{top}) in addition to the h_i.

Only the Rayleigh equation, where the best fit for Scots pine in this study was observed, was applied for further calculations.

Both the height of the top of the tree (h_{top}) and the height of the crown base (h_{bas}) (together encompassing the space occupied by the canopy) were derived from the relation of tree height to DBH (= x) characterizing all trees in the stand:

$$h = a\,[1 - e^{-x/b)}]^{c} \qquad (15)$$

Values of h_{top} of the sample trees were applied during the first step of the calculation of the needle distribution, but only the values of h_{top} that were derived as described above, were introduced into the Rayleigh equation during the second step of the calculation procedure to obtain the upscaled characteristics of the needle distribution for the whole stand.

During the first step of the approximation the coefficients of the basic Rayleigh equation (P_1, P_2, P_3 and P_4) were calculated for each of the sample trees and the resulting data were validated.

These coefficients were then plotted against the DBH of each of the sample trees and their values were scaled up by introducing additional equations with different coefficients (A, B and C), according to the type of equation that was used.

From the above-equations generalized coefficients for the basic equation were calculated for the sample trees and validated once more; only these generalized coefficients were used for further calculations.

From the above-mentioned additional equations, values of parameters of the main equation (P_1, P_2, P_3 and P_4) were derived for each DBH, i.e. the average tree of each class according to the diameter at breast height with 2-cm intervals. Using the parameters derived in this way, the distribution of needles in different layers of height above the ground was computed.

The total amount of needles on the entire tree was calculated by summing the values of the needle distribution along the vertical stem axis.

The total amount of needles on the average trees of the DBH classes was validated by comparing two models, i.e. a simple parabolic regression model and the above-described model of vertical distribution. These results were applied for further calculations to scale up to the stand level.

The values calculated for different layers in individual trees (of mean DBH) were scaled up to the entire stand (stand area unit of 1 ha) by multiplying the total amount of needles with the number of trees in the different classes, and consequently summed.

3. RESULTS AND DISCUSSION

3.1. Forest inventory

The forest inventory data (recorded in spring 1995), all expressed per ha of ground area, are summarized in *table II*. Stocking density was 542 trees ha^{-1}, basal area of the stand 31.24 m^2 ha^{-1}, mean DBH 26.8 cm, mean tree height 20.6 m and total stem volume 299 m^3 ha^{-1} *(table II)*. The mean annual volume increment for the site was around 7 m^3 ha^{-1} year^{-1}. The stand could be characterized as the average for a given region. The frequency distribution showed a skewed Gaussian distribution with a relatively high number of trees with a diameter below the mean *(figure 2)*.

The heights of the top of the mean trees of all DBH classes showed a rather small variation; a much larger variation was found when heights of the crown base were considered *(table II)*. The appropriate coefficients of the regression equations are given in *table III*. The upscaled distribution of the heights of the top and of the crown base showed a rather narrow green canopy layer *(figure 3)*. The entire green canopy in the stand was limited to a narrow zone between 16 and 24 m (maximum), and no active green needles were observed below 15 m. For the entire stand (from small to large trees) the base of the green crown was around 16 m *(figure 3)* and the mean depth of the canopy was close to 5 m (maximum 7 m). In comparison with the small trees, the large trees had a longer and much more extended live crown, but not a deeper crown. This might reflect the rather dense stand (with little light penetrating to the lower part of the crown) before the last thinning of the stand

Table II. Detailed forest inventory data for the experimental Scots pine stand in De Inslag forest, Brasschaat.

DBH class (cm)	Frequency (# ha^{-1})	Mean diameter (cm)	Mean basal area (m^2)	Total basal area (m^2)	Mean height (m)	Height of crown base (m)	Canopy depth (m)
16	2	16.6	0.022	0.033	17.5	15.4	2.1
18	14	18.6	0.027	0.367	18.3	15.7	2.6
20	44	20.3	0.032	1.428	19.3	16.5	2.8
22	63	22.2	0.039	2.424	19.6	16.5	3.1
24	92	24.2	0.046	4.235	20.1	16.7	3.4
26	94	26.1	0.054	5.024	20.5	16.8	3.7
28	83	28.0	0.062	5.134	20.8	17.0	3.8
30	64	30.0	0.071	4.507	21.1	17.0	4.1
32	20	31.5	0.078	1.562	22.3	17.5	4.8
34	28	33.9	0.090	2.538	22.3	17.4	4.9
36	19	36.1	0.102	1.949	22.0	17.0	5.0
38	11	38.1	0.114	1.198	22.8	17.2	5.6
40	3	39.4	0.122	0.305	21.9	17.1	4.8
42	2	42.0	0.139	0.208	23.2	15.9	7.3
44	1	43.8	0.150	0.151	22.2	17.6	4.6
46	1	46.0	0.166	0.083	20.9	16.8	4.1
48	1	48.4	0.184	0.091	23.3	15.4	7.9
Mean		26.8	0.058		20.6	16.9	3.7
Total	542			31.24			

For each DBH class the frequency distribution (number of trees per ha), mean diameter, mean and total basal area, mean tree height, height of the crown base and mean canopy depth are given. Overall mean (for the stand) and total values for all classes of the stand are also given and are weighted for the class distribution. All values are expressed per unit ground area (i.e. per ha) based on observations at a 1.99-ha surface area.

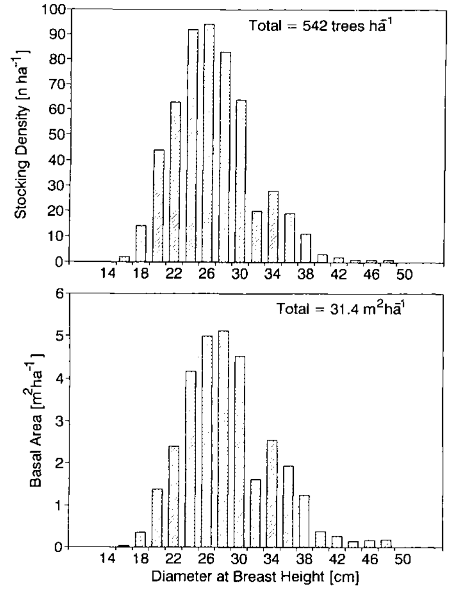

Figure 2. Tree stocking density and basal area for all DBH (diameter at breast height) classes in the Scots pine stand in Brasschaat.

Table III. Regression equations $y = a^*[1 - e^{(-x/b)}]^c$ for the relation between tree height (both height of the top of the tree and height of the base of the crown) and stem diameter at breast height (DBH) for Scots pine trees.

x and y variables	Regression equation	R^2
x = DBH, y= tree height to the top	$y = 24.8\ (1 - e^{-x/14.4})^{0.758}$	0.98
x = DBH, y = height of the crown base	$y = 16.9\ (1 - e^{-x/3.45})^{9.513}$	0.62

R^2 is the determination coefficient.

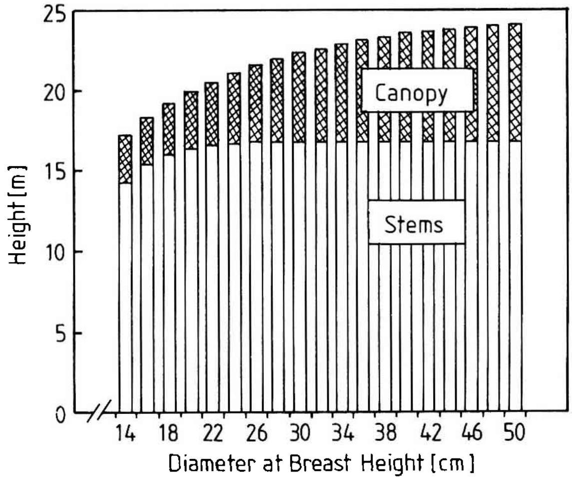

Figure 3. Height of the top of the tree and of the base of the crown (illustrating depth of the green canopy) for Scots pine trees in Brasschaat according to their DBH class as measured in June 1995. The dashed parts of the bars represent the live green canopy. Regression equations for scaling up purposes: height of tree top = $24.8\ (1 - e^{(-DBH/14.4)})$ with $R^2 = 0.98$; height of the crown base = $16.9\ (1 - e^{-DBH/3.45})$ with $R^2 = 0.62$.

in 1993. At present the stand is rather sparse and open, allowing deeper penetration of light *(figure 4)*; however, the trees are not able to develop new foliage in lower layers of the canopy, where they had previously lost their live branches.

3.2. Allometric relations at the cloud level

The biometric properties of needles were to a certain extent related to the properties of the clouds in which they were located (*table IV,* upper rows), irrespective of the open and sparse crowns of the pine trees. The multiple regression between DMAR in different clouds and directly measured cloud parameters, such as position of the cloud in the tree, branch length and branch cross-sectional area at the origin, was not significant ($R^2 = 0.12$). The relationship was improved ($R^2 = 0.46$) when some additional, derived parameters such as cloud needle dry mass and area densities (together 63 % of the sum of

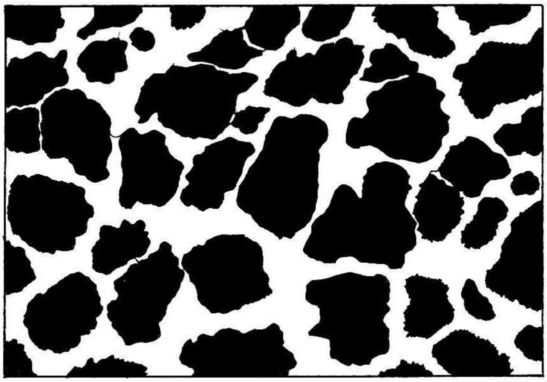

Figure 4. Schematic representation of stand density, overall tree crown form and spacing of the Scots pine trees in the experimental stand in Brasschaat reproduced from a photographic image taken at 20 m above the forest canopy.

Table IV. Results of multiple regression equations.

Independent variables	DMAR ratio (g m^{-2})	Cloud Area Density (m^2 m^{-3})	
		Tree no. 3	Tree no. 5
Constant	5.38 (0.05)	153.9 (75.7)	6.77 (0.84)
(Mean cloud distance from the ground in m)^2	—	0.075 (0.038)	
Ln (mean cloud distance from the ground)	—	–60.86 (30.37)	–1.23 (0.39)
Branch cross-sectional area at the stem (BCAS) (in cm^2)	—	–0.48 (0.14)	
(BCAS)^2	—		0.045 (0.014)
Branch cross-sectional area at the green part (BCAG) (in cm^2)	—		–0.35 (0.11)
Ln (BCAG)	—		1.34 (0.21)
Total branch length (in m)	—		–2.10 (0.54)
Ln (total branch length)	0.11 (0.04)	–1.17 (0.37)	
Ln (length of green part of branch)	—		1.38 (0.23)
Ln (absolute angle) (= azimuth – 180)	—		–0.083 (0.036)
Cloud needle area (in m^2)	0.02 (0.005)		
Cloud needle number (* 10^{-6})	–8.26 (1.67)		
Cloud dry mass density (kg m^{-3})	0.012 (0.02)		
Cloud area density (m^2 m^{-3})	–0.011 (0.002)		
Number of observations	33	26	24
R^2 (%)	45.9	37.6	78.7

Regression coefficients for the dry mass to area ratio (DMAR) and the cloud area density (independent variables) as a function of various dependent variables of the clouds in two Scots pine trees (nos 3 and 5). R^2 is the determination coefficient (expressed as %). Natural logarithms of dependent variables. Values within brackets are standard errors.

squares), needle area (5 % of the sum of squares) and number of needles (12 % of the sum of squares) were included in the regression model. A significant relationship (with $R^2 = 0.73$) was obtained between cloud area density and the mean distance from the cloud above the ground plus some branch parameters such as length of the green part of the branch and the cross-sectional area at the origin of the branch (together 29 %) *(table IV).* The fact that very few differences in DMAR were found with position of the cloud on the tree, could be explained by the rather limited crown depth and the small gradient in the light profile, which resulted in rather uniform needle characteristics within the tree crowns of this study.

3.3. Cloud properties in relation to their position

The volume of clouds per tree increases exponentially with DBH (volume = $1.086^{(DBH-1)}$, $R^2 = 0.984$). When characteristics of clouds, such as cloud needle area and cloud dry mass density, were considered in relation to their respective position within the crown, better results were obtained than for needle properties. However, in all cases the best or optimal fit was obtained using non-linear regression equations (*table IV,* lower rows). Three alternative indices were used as the independent variables for the relationship with cloud area density: an 'index of illumination' (i.e. the average distance of the cloud from the ground surface) and two branch-related indices, i.e. an 'active sapwood index' (expressed as the ratio of the branch cross-sectional area at the green part to this at the stem) and a 'length index' (expressed as the ratio of the green branch length to the total branch length). These relations explained 15 and 70 % of the sum of squares for the largest and the smallest sample tree, respectively. R^2 values ranged from 0.52 for the smallest and the largest trees to 0.74 for the smallest tree. For the medium tree no parameters of the green part of the branches were available. For the largest, well-illuminated tree the cloud area density was significantly correlated to the branch orientation (resulting in 30 % of the sum of squares). Branch orientation (azimuth) was defined here as the mean absolute deviation from the north. The cloud area density was significantly (at least for the largest tree) smaller at the northern and at the bottom parts of the crown, as well as on longer branches with smaller green parts. The relationship between cloud area density and distance of the cloud from the ground surface was more complex and not monotone, showing a minimum for the medium sample tree. This was also confirmed by an analysis of the internal coherence of biometric parameters within clouds (by the sums of R^2). If the internal coherence in the smallest sample tree was taken as the reference (i.e. 100 %), the value reached 152 % in the medium sample and 126 % in the largest sample tree. Thus, the cloud properties were more dependent on external parameters in smaller trees than in larger trees. The position of the needles or of the clouds in the crown has no significant effect on the differences in DMAR between needle age classes, confirming the findings of van Hees and Bartelink [33].

3.4. Allometric relations at the branch level

A very good relationship was observed between branch cross-sectional area and needle leaf area (as well as needle dry mass) on the branch level. The regression equation derived for two sample trees is given in *table V.* Since all of the total needle area estimates in the further part of this study were basically derived on a 'cloud' basis rather than on a single branch level, this equation was not further applied. Similarly a significant relation was observed between branch diameter and

Table V. Allometric relations and regression equations for branches, stems and root systems of the Scots pine trees used for scaling up.

x and y variables	Regression equation	R^2
Branch		
x = Branch cross-sectional area (m^2)	$y = 0.003\,x^2 - 0.08\,x$	
y = Needle area (m^2)		
Stem: x = DBH (cm)		
y = Needle DM (kg $tree^{-1}$)	$y = -0.0003\,x^2 + 0.0433\,x - 0.4908$	0.956
y = Needle area (m^2 $tree^{-1}$)	$y = 0.0608\,x^2 + 0.3537\,x$	0.900
y = Crown proj. area (m^2 $tree^{-1}$)	$y = 0.0067\,x^2 + 0.2126\,x$	0.833
Stem: x = basal area (m^2)		
y = Needle DM (kg $tree^{-1}$)	$y = 22.032\,x^2 + 198.42\,x$	0.942
y = Needle area (m^2 $tree^{-1}$)	$y = -1290.7\,x^2 + 1037.4\,x$	0.908
y = Crown proj. area (m^2 $tree^{-1}$)	$y = -595.81\,x^2 + 225.86\,x$	0.865
y = Number of needles (thousands $tree^{-1}$)	$y = 1.887\,x$ (x in cm^2)	0.987
Root: x = Stump diameter (cm)		
y = Diameter of root system (cm)	$y = 64.83 + 9.406\,x$	0.751
y = Rooting depth (cm)	$y = 77.17 + 1.037\,x$	0.246
y = Root volume (m^3)	$y = -11.36 + 1.060\,x$	0.797
y = Projected root area (m^2)	$y = -13.71 + 1.711\,x$	0.762

Allometric relations between branch cross-sectional area and needle area (on the branch), between stem diameter at breast height (DBH, cm) or basal area (m^2) and total needle dry mass (DM) per tree, total needle area per tree, crown projection area per tree and total number of needles, as well as between stump diameter and root diameter, rooting depth, volume of the root system and projected root area. Regression equations at the stem level were derived from total values of five experimental trees, at the branch level for two experimental trees and equations for the root systems were derived from seven wind-thrown trees in the stand. R^2 is the determination coefficient.

projected branch length (compare with Ceulemans et al. [12] for poplar). From this relation we could estimate for two of the sample trees (i.e. tree nos 2 and 4) their crown dimension (assuming a circular projection of the crown on the ground surface; *figure 1*) through the calculation of the projected branch length based on measurements of branch diameter.

3.5. Allometric relations at the stem level

In agreement with some other studies [1, 15, 20, 33] significant regression relations were observed between basal area (or DBH) on one side and needle area, needle dry mass or crown projection area on the other side. The relationship between crown projection area on the ground and basal area of the tree was based on five experimental trees *(table V)*. Although this relation is without any doubt non-linear when very small trees (i.e. DBH below 10 cm) and very large trees (i.e. DBH above 50 cm) are included, the regression was linear within the limits of the DBH classes of the experimental stand of this study (i.e. DBH between 14 and 48 cm) and passed through the origin. The regression equation was used to estimate the ground projection area of the average tree for all DBH classes, resulting in an approximate estimation of the overall crown dimension and crown volume. This allowed us to scale up the crown volume of the individual trees to the entire stand. A similar relationship between needle dry mass and (sapwood) basal area was found for single Scots pine stands in Sweden, but the needle biomass per unit of sapwood basal area varied with mean annual ring width in the sapwood [1]. However, the needle leaf area to sapwood area ratio as well as many other relationships and ratios are influenced by site and climate differences differences in Scots pine [5, 20].

3.6. Allometric relations at the root level

The allometric relations between the stump diameter and various characteristics of the root system showed results with an acceptable error for approximative calculations *(table V)*. The low correlation coefficient ($R^2 = 0.246$) obtained for the relationship between stump diameter and maximum rooting depth *(table V)* might indicate that trees of different stem diameters reached almost the same rooting depth in the stand limited by the underground water table.

3.7. Radial needle distribution of individual trees

The radial profile of the needle distribution (rotated to one side of the tree and thus neglecting orientation of the branches to cardinal points) showed a higher concentration of needles close to the main stem and a lower concentration toward the edges of the crown *(figure 5)*. This was more pro-

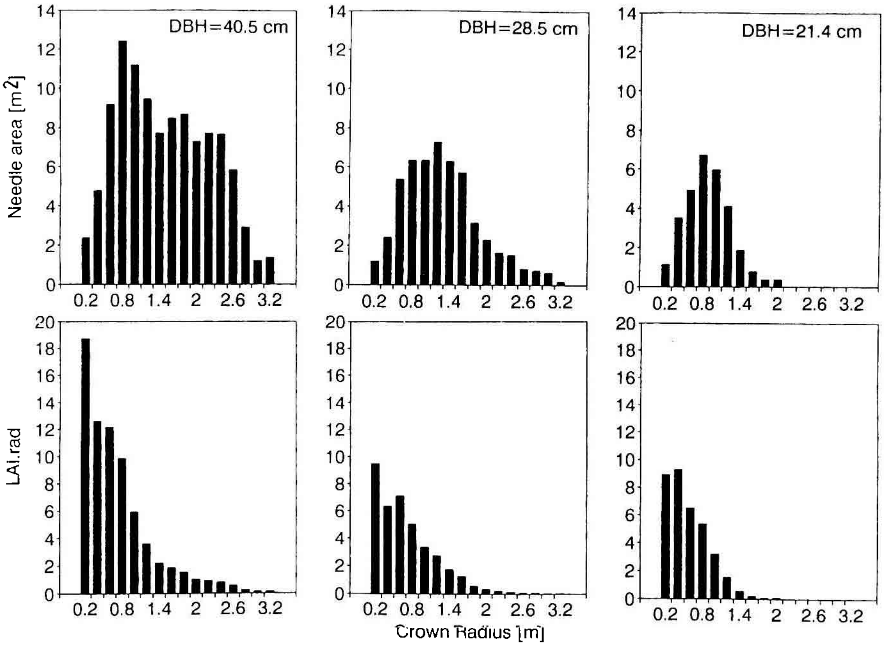

Figure 5. Radial profiles of needle area distribution and of the 'radial leaf area index' (LAI.rad) in three sample Scots pine trees of different diameter at breast height (DBH) in the forest at Brasschaat. The diagrams represent the total needle area above different 0.2-m wide annulets around the axis of the crown, rotated onto one plane (top diagrams) and the radial leaf area index (LAI.rad) above the same annulets (bottom diagrams).

nounced when we considered the radial LAI (LAI.rad), i.e. the needle area above certain annulets divided by the area of these annulets. The needle area itself was highest not far from the main stem *(figure 5)*, which is similar to observations on broadleaved species [21]. These results are highly relevant for the interpretation of data from remotely sensed images since tree crown patterns are inequal in space, but have regularly distributed properties *(figure 4)*.

3.8. Vertical needle distribution of individual trees

Profiles of foliage distribution in the canopy are often described by normal curves, although distribution of needle area on individual trees can appear bimodal [4]. The application of the various mathematical equations used here to approximate the vertical needle distributions in the Scots pine trees showed that both the Gaussian and the Log-normal equations fitted rather well for the central part of the crown, but that they significantly underestimated the upper part of the crown and simulated unrealistic values above the top of the tree *(figure 6)*. The transitional equation was too asymmetric; it overestimated the top of the tree and underestimated the lower parts of the crown. The Rayleigh equation was found to be the most appropriate to describe the vertical distribution of the pine needles,

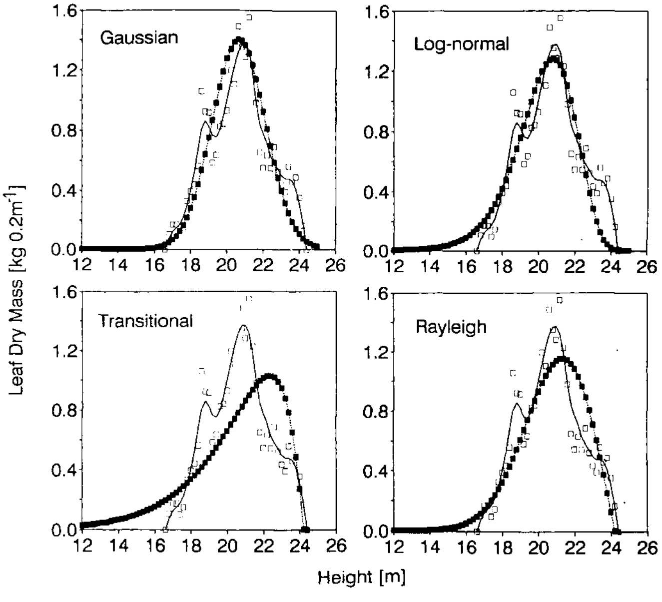

Figure 6. Vertical (axial) profile of needle dry mass distribution in a sample Scots pine tree (sample tree no. 1). The observed needle dry mass (expressed per layer of 0.2 m thick) as a function of tree height is shown as well as its simulation (or approximation) using four different mathematical equations, i.e. the Gaussian, Log-normal, Transitional and Rayleigh equations. The measured needle dry mass data for the individual layers are represented by the empty squares (□); the running average calculated through the measured data is represented by the full line; and the derived data are represented by the dotted line and filled square symbols (■). The differences between the overall totals of the four approximations were less than 0.5 %.

since it had the most realistic umbrella-like shape, which is typical for adult Scots pine trees and fitted best for all parts of the crown (*figures 1* and *6*). The coefficients of the various equations have been listed in *table VI*. The vertical needle distribution in the three harvested sample trees is illustrated in *figure 7* and agreed rather well with those presented by van Hees and Bartelink [33] for Scots pine trees in the Netherlands, who used a generalized logistic model to describe the cumulative distribution of the needle area.

3.9. Using the Rayleigh equations for scaling up

The coefficients of the Rayleigh equation as a function of DBH (= x) of the sam-

Table VI. Coefficients of the various equations used to approximate the needle dry mass distribution on a Scots pine sample tree with DBH (diameter at breast height) of 40.6 cm in 'De Inslag' forest at Brasschaat, Belgium. The various equations are described in the text.

Coefficients	P_1	P_2	P_3	P_4
Gaussian	1.5	24.2	1.86	—
Log-normal	1.4	0.23	20.65	—
Transient	8.3	27.1	1.9	0.122
Rayleigh	1.88	2.98	23.1	22.2

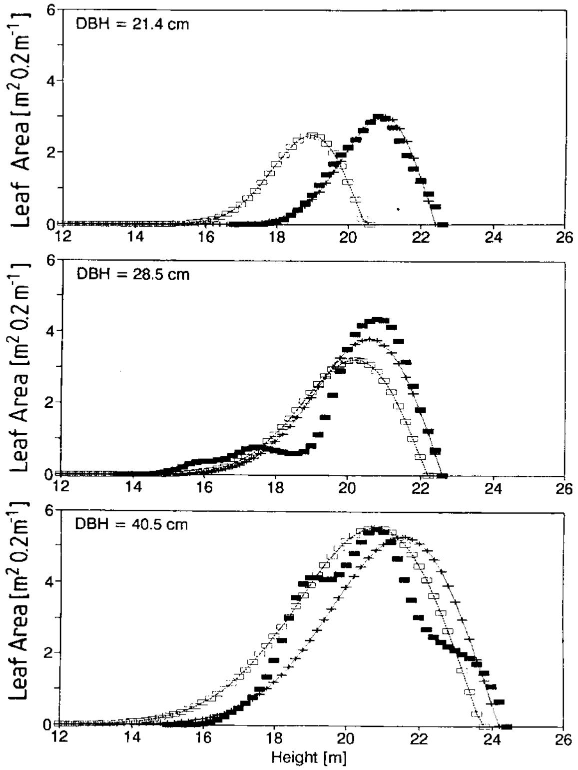

Figure 7. Vertical profile of needle area distribution for Scots pine trees in the experimental forest at Brasschaat represented as the needle area per 0.2-m-thick layers as a function of tree height for three sample trees of different DBH (diameter at breast height). Filled squares (■): running average of the original data points; + line: approximation of the vertical distribution using the Rayleigh equation (see text) calculated from the original data; dotted line and empty squares (□): Rayleigh equation after upscaling for the entire stand based on the corrected, upscaled tree heights (see *figure 3*) and the generalized coefficients of the main equation.

ple trees that were used to scale up the main equation to the stand level are shown in *table VII*. For the needle dry mass the best fit was found in P_1 and P_3 using the parabolic equation, and for P_2 and P_4 for the linear equation. For the needle area the best fit was found in P_1 in the parabolic equation, for the linear equation in P_3, and the values of P_2 and P_4 were constant. The original curves as well as the generalized, derived curves of the needle distribution are shown in *figures 7* and *8*.

Table VII. Values of the coefficients P_1 to P_4 for the basic Rayleigh equation (see text) describing the vertical needle distribution in layers above the ground (in kg per 0.2 m or m^2 per 0.2 m) derived on the basis of DBH (= x) from upscaling equations (parabolic or linear) using additional coefficients A, B and/or C.

Variable	Coefficient	A	B	C	R^2
Needle dry mass	P_1	0.003023	-0.21855	6.065	0.99
	P_2	3.53	-0.013	—	0.99
	P_3	0.017033	0.14593	-6.0495	0.99
	P_4	2.51	-0.0018	—	0.99
Needle area	P_1	0.00455	-0.2952	10.252	0.99
	P_2	1.81 (constant)	—	—	—
	P_3	0.6143	-8.448	—	0.99
	P_4	2.1 (constant)	—	—	—

R^2 is the determination coefficient.

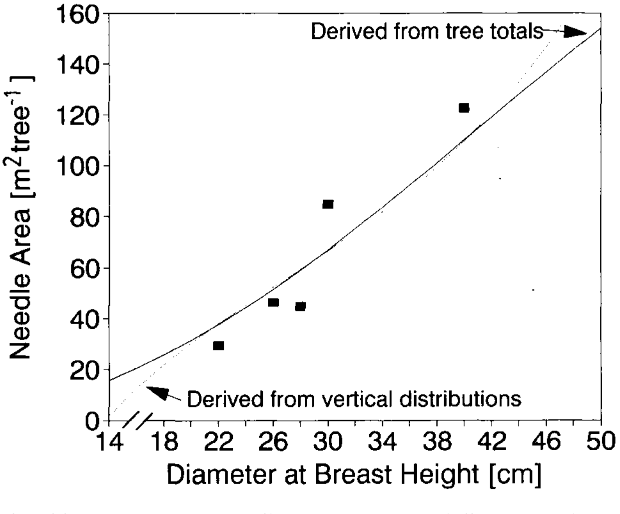

Figure 8. Relationship between total needle area per tree and diameter at breast height (DBH) for Scots pine in Brasschaat, Belgium. Measured data on five sample trees are represented by filled square symbols (■). The full line represents the upscaled needle area data (m^2 tree^{-1}) using a simple regression to basal area ($x = A_{bas}$ in cm^2; needle area = $-1290.7\ A_{bas}^2 + 0.3537\ A_{bas}$ with $R^2 = 0.91$; leaf dry mass = $22.03\ A_{bas}^2 + 198.42\ A_{bas}$ with $R^2 = 0.94$). The dotted line represents the upscaled data derived by the more complicated procedure using the upscaled vertical needle area distributions of *figures 6* and *7*. Full (simple upscaling approach) and dotted (more complicated upscaling approach) lines differ significantly only for extreme trees outside the range of DBH classes observed at the experimental stand in Brasschaat.

When the generalized equations were applied for upscaling of the vertical needle distribution, the differences between the real and the derived data (totals for trees) observed in the sample trees were slightly higher than the originally derived curves (see *figures 7* and *8*), but they never exceeded 0.25 % for both needle dry mass and needle leaf area, and thus were considered as acceptable. Some small shifts in the height of the crowns along the stems were visible *(figure 7)*; these were caused by minor discrepancies between the real heights of the sample trees and the corrected heights scaled up from the abovementioned curves that are valid for the entire stand (see *tables III* and *V*). The largest difference was found in the height of the crown of the smallest sample tree.

When we compared the results of the two models applied to obtain the total amount of needles per tree for the average trees of the individual DBH classes, only very minor differences were observed within the range of the tree sizes at the experimental stand of this study *(figure 8)*. This observation was valid when the most extreme values on both ends of the range were not taken into account, but confirmed that we could apply both models for further scaling up calculations.

The upscaled values of needle area for the average trees of all DBH classes and for the entire stand by multiplying the values with the corresponding numbers of trees in each class, are shown in *figure 9*. This upscaling results for the Scots pine stand of this study in a LAI of 3.0 and a total needle dry mass of 6250 kg ha^{-1}. The LAI of the plot estimated directly by destructive sampling and upscaling regressions as outlined above, was twice as high

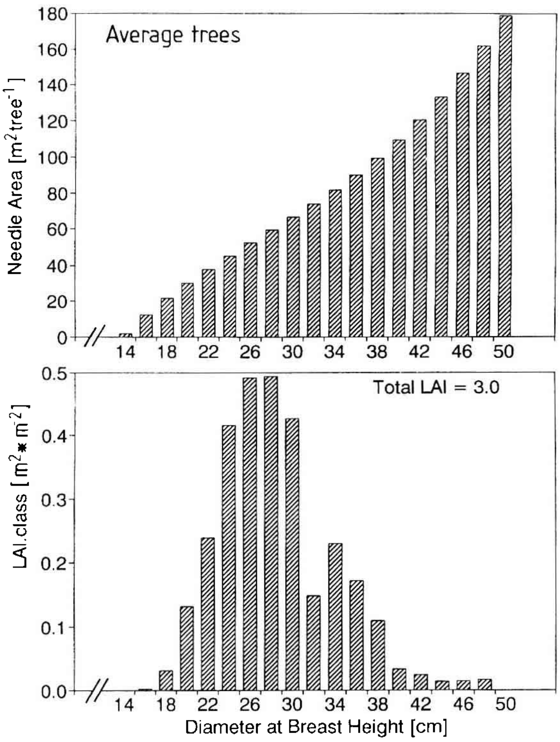

Figure 9. Total needle area per tree for the average tree of all DBH (diameter at breast height) classes (upper panel) and leaf area index (LAI) of each DBH class (lower panel) for the Scots pine stand in Brasschaat, Belgium. In the lower panel each bar represents the LAI of a DBH class, which was obtained by multiplying the total needle area per average tree by the number of trees in each class. Both figures were scaled up to the entire stand using the more detailed approach via the vertical needle distribution.

as the one measured indirectly with an LAI-2000 plant canopy analyzer (data not shown), similar to the observations of Sampson and Allen [25]. Further upscaled biometric characteristics of the stand and for the average tree of the stand are given in *table VIII.*

3.10. Vertical distribution of needle area density scaled up to the stand

The vertical profile of the needle area distribution was an almost symmetrical Gaussian-type curve, irrespective of the slightly asymmetrical, umbrella-type form of the large Scots pine trees (as expressed in the Rayleigh equation) *(figure 10).* The maximum needle density occurred at about 19.6 m high. The tallest tree height at which an agglomeration of needles was observed was at almost 24 m, and the lowest at about 15 m high. However, 95 % of the needles are present within the 4.4-m-thick layer between the lower height of 17.2 m and the upper height of 21.6 m *(figure 10).* These two heights marked out the space occupied by the canopy in the pine stand. Interestingly, we found in a

Table VIII. Biometric parameters of needles of Scots pine trees scaled up to the stand level (and expressed on a 1-ha basis) and for the average tree (expressed in totals per tree) in the 'De Inslag' forest in Brasschaat, Belgium.

Parameter	Forest stand	Average tree
Dry mass (kg)	6 286	11.6
Needle area (one-sided, m^2)	29 912	55.2
Surface needle area (m^2)	59 498	109.8
Total needle length (km)	27 451	50.6
Total needle volume (m^3)	7.774	0.014
Number of needles (10^3)	593 393	1 095

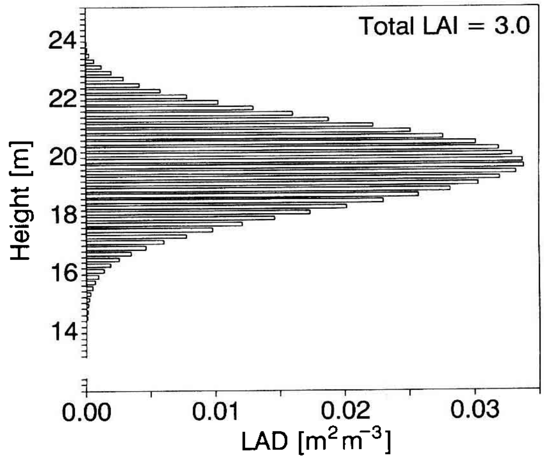

Figure 10. Vertical distribution of needle area index (LAD), expressed in horizontal layers of 0.2 m thickness, scaled up to the stand level for Scots pine in Brasschaat, Belgium. The total LAI for the stand adds up to 3.0.

very dense, young broadleaf forest (LAI of 7.8, leaf area density of 1.4 m^2 m^{-3}) a canopy layer of 5.5 m thick [21], while in an old floodplain forest with a LAI of 5.0 (and leaf area density of 0.14 m^2 m^{-3}) the canopy layer was about 30 m thick [8].

When the total number of trees of the stand was divided into three groups that each contained one third of the total number of trees (roughly representing a group of suppressed, co-dominant and dominant trees), these three groups contained respectively 16.8, 29 and 54.2 % of the total stand needle area *(figure 11)*. The vertical distribution of the needle area on an average tree of each of these groups is shown in *figure 11*. The total amount of needles roughly doubled from one group to another. The base of the crown remained approximately at the same depth in all trees. However, the height of the top of the trees increased by about 2 m in each group. This means that a relatively large amount of needles in the larger trees occurred under higher illumination; this fact further enhanced the differentiation processes within the stand *(figure 11)*. Similar differences in vertical needle area distribution between (co-)dominant trees of different sizes have already been reported [33]. In the latter study the mode of needle biomass distribution moved upwards in suppressed trees.

3.11. Scaling up biometry of root systems

Overall the root systems had more or less an inverse bell-shaped form. There were about six (± 2) large surface roots and also about six (±2) large, deep roots per tree. Surface roots with diameters of 5–12 cm at the stump were located in the

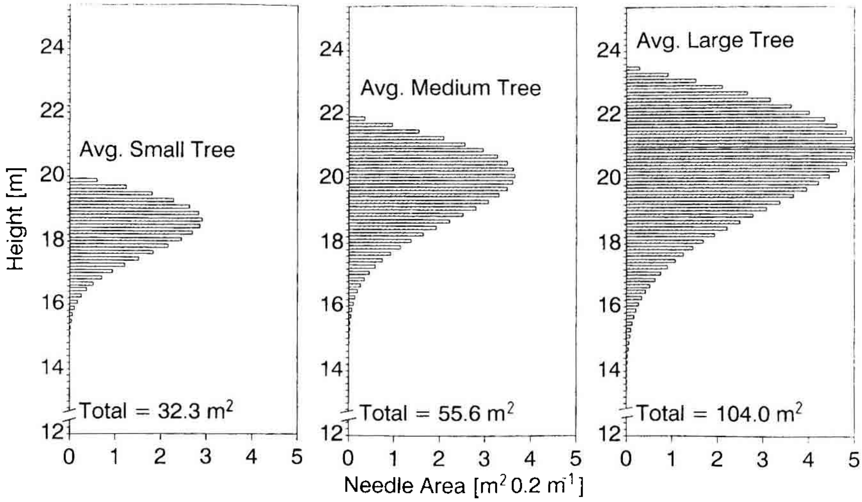

Figure 11. Vertical distribution of needle area (expressed in horizontal layers 0.2 m thick) for three 'typical' trees in the Scots pine forest at Brasschaat, Belgium. The diameter of each 'typical' tree has been calculated as the average for each third of the total number of trees per ha (3 × 181 = 543 trees ha^{-1}), i.e. small (DBH of 20.6 cm), medium (DBH of 26.9 cm) and large (DBH of 38.9 cm) trees. The overall mean tree of the entire stand has a DBH of 27.2 cm and a total needle area of 56.5 m^2. For each 'typical' tree the total needle area has also been indicated in the figure.

medium to upper soil layers (from 0.2 to 0.5 m) and were long. The mean length of these surface roots (L_r) ranged from 1 to 3 m for trees of different sizes and represented the radius of the root system (r_r), assuming that the roots had a uniform distribution around the trees *(figure 1)*. The total length of all main roots, horizontal and vertical, amounted on average to about 18 and 6 m, respectively. The average projected (circular) root area (A_r) was ca 30 m^2, while the bulk volume of the (parabolic) root system was ca 16 m^3, with a rooting density of about 0.8 m m^{-2} or 2.5 m m^{-3} *(table IX)*. The upper or surface roots ended in the soil in a prolonged, mostly horizontal branching pattern. The very fine active root tips (diameter less than 0.2 cm) could not be retrieved nor quantified in the wind-thrown trees, but the ends of the surface roots were rather thin (about 0.2–0.3 cm in diameter). The vertically oriented roots were found at a maximum depth ($h_{r.max}$) of about 1.1 m for the entire stand. They were about 3–6 cm in diameter at the origin, i.e. at the below-ground part of the stump. The mainly vertical branching ends of the vertical roots occurred below 0.5 m, were rather stout (0.5–1 cm) and short (about 10 cm), which gave them an irregular brush-like form. The overall form of the root system is schematically shown on *figure 1*. The biometric parameters of the root systems and of the largest roots of the sample trees are represented in *table IX*, while the coefficients of the corresponding allometric equations were represented in *table V*. The allometric relations were accurate enough (i.e. relatively small standard errors) to allow confident upscaling calculations. The scaling up exercise for root volume and biomass has for Scots pine also been performed using electrometric methods and by multiplying the corrected data by the stand density [31].

3.12. Above- and below-ground space use efficiency of the pine stand

An important characteristic of the forest stand that can be derived from the

Table IX. Biometric parameters and allometric relations of the root systems of seven Scots pine trees in the experimental stand at Brasschaat, Belgium.

Sample tree no.	Stump xylem diameter (cm)	DBH (cm)	Maximum rooting depth (cm)	Average radius root system (cm)	Volume of root system (m^3)	Projected root area (m^2)	Surface parabolic area (m^2)
7	19	15.9	110	220	8.4	15.2	24.1
8	21	17.6	90	310	13.6	30.2	73.1
9	21	17.6	90	240	8.1	18.1	33.0
10	27.5	23.0	115	340	20.9	36.3	77.6
11	29.2	24.4	100	320	16.1	32.2	72.9
12	30	25.1	110	360	22.4	40.7	96.8
13	30.5	25.5	110	340	20.0	36.3	80.7
Mean	25.5	21.3	104	304	15.6	29.9	65.5

Stump diameter without the bark (stump xylem diameter), stem diameter at breast height (DBH), maximum depth and average radius of the root system, volume of the root system (assuming the root system had a parabolic form), projected area and surface area of the parabolic envelope of the root system. The stump xylem diameter was taken equal to 1.195 * DBH. All parameters were measured on wind-thrown trees.

allometric relations and the upscaled needle distribution described above is the 'volume or space use efficiency', i.e. the proportional use of the volume occupied by the trees by various tree organs or tree parts. For the available volume aboveground a column of 1 ha soil surface from the ground up to the height of the top of the trees was considered *(figure 12)*. For the below-ground part a surface of 1 ha from the ground surface down to the maximum rooting depth was taken. Within this volume the green canopy or phyllosphere layer represented 23 % of the stand volume. Within the canopy volume only, the cylindrical volume of the crowns (corresponding to the crown projection area, *figure 1*) represented 59 %, the (ellipsoidal) enveloping volume of the crowns occupied 19.6 % and the clouds of needles (assuming the clouds had an ellipsoidal volume) occupied 9.8 % *(figure 12)*. Half (i.e. 50 %) of the crown volume only was occupied by clouds with needles, which represented 0.486 m^3 m^{-2} of cloud volume per crown projected area. The total leaf area in the stand was about 1 000 times the total stand basal area. And if we take into account the annual timber volume increment, there was around 4 270 m^2 of needle area per m^3 of timber volume. The ellipsoidal volume of the crowns occupied about 0.965 m^3 m^{-2} of the crown projected area *(table X)*. This reflects the fact that the amount of aggregation in pine canopies is largely determined by crown branching patterns [14, 26]. The foliage is aggregated within clouds, clouds and branches are aggregated within crowns, and crowns are aggregated within the canopy [17, 26]. Thus, the crown aggregation depends on the spatial distribution of individual trees and the formation of canopy gaps [19].

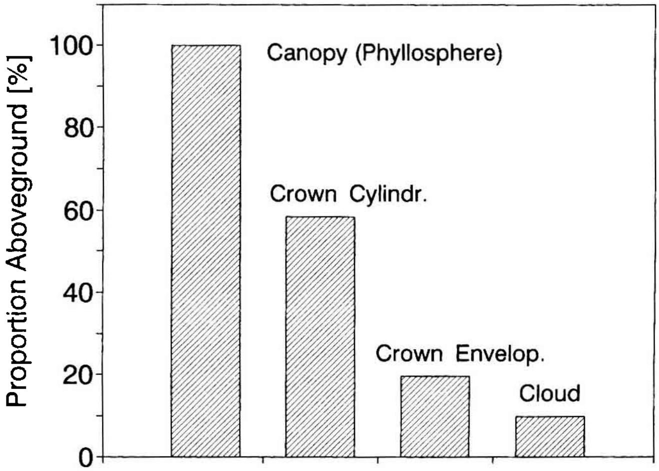

Figure 12. Volume use efficiency of the above-ground stand volume by the needles in the Scots pine stand at Brasschaat, Belgium. Different volumes occupied by the needles were considered as illustrated by the different bars: 1) the volume of the green canopy layer including the open gaps between the tree crowns (the latter represent 22.8 % of the stand volume); 2) the total crown volume (assuming the crowns were cylinders) including the gaps between the clouds; 3) the total crown volume (assuming the crowns were ellipsoids) including the gaps between the clouds; and 4) the total cloud volume of needles (also assuming the clouds were ellipsoids, see *figure 1*).

Table X. Space use efficiency of different parts of the Scots pine trees.

	Total estimated volume (m^3)	Needle dry mass density (kg m^{-3})	Needle area density (m^2 m^{-3})	Proportional use of total volume (%)			
Above-ground							
Stand (up to top of trees)	216 645	0.029	0.138	100	439	750	2245
Canopy (phyllosphere)	49 314	0.127	0.607	23	100	171	511
Crown (cylinder)	28 855	0.218	1.037	13	59	100	299
Crown (ellipsoid)	9 652	0.651	3.099	5	20	33	100
Cloud (ellipsoid)	4 856	1.295	6.160	2	10	17	50
Below-ground							
Roots (rhizosphere)	11 000				100	43	180
Roots (cylinder)	23 392				234	100	422
Roots (parabole)	6 096				55	24	100

Proportions of the above-ground (crowns, green canopy) and below-ground (root system) volume occupied by different parts of the pine trees in 'De Inslag' forest in Brasschaat, Belgium. Data are to be read and compared within columns.

From the total available below-ground volume, the rhizosphere (thus of 11 000 m^3; *table X*), the cylindrical volume occupied by the roots (corresponding with the root projected area, *figure 1*) represented 234 %. This is an evidence for the fact that the pine root systems were not just uniformly circular, but produced an irregular, star-shaped form. Coarse roots were longer than large branches and reach significantly oustide the projected area of the tree crown (*figure 1*). When the circle on *figure 1* is considered as the projected root area, only 43 % of this projected area could be used by the roots without overlap. When the bulk paraboloidal rooted volume was considered, the enveloping volume of the root systems occupied 55 % of the volume represented by the rhizosphere (*table X*). With regard to the above-mentioned reduction in the real or true volume, this value was maximum.

3.13. Ecological significance

Let us assume that the pine trees would have grown very closely together, i.e. filled the total available area and that the crown projected area (i.e. the ground plan area) could be considered as the stand area. In that case the LAI would have been equal to 5.1 (instead of the real LAI = 3.0), the LAD would have been 1.031 m^2 m^{-3} (instead of the actual 0.607 m^2 m^{-3}) and the DMAR 1.07 kg m^{-2} (instead of the actual DMAR of 0.625 kg m^{-2}) (*table X*). In this hypothesis the needle density of the 'compressed' canopy would approximate the density within the crowns and would limit the penetration of light into deeper canopy layers. This can also be illustrated by the LAD within individual clouds. Most clouds had a LAD of 6 m^2 m^{-3}, but the maximum value reached up to about 25 m^2 m^{-3} (*figure 13*). This could be considered as the maximum density of a (relatively small) cloud growing in the

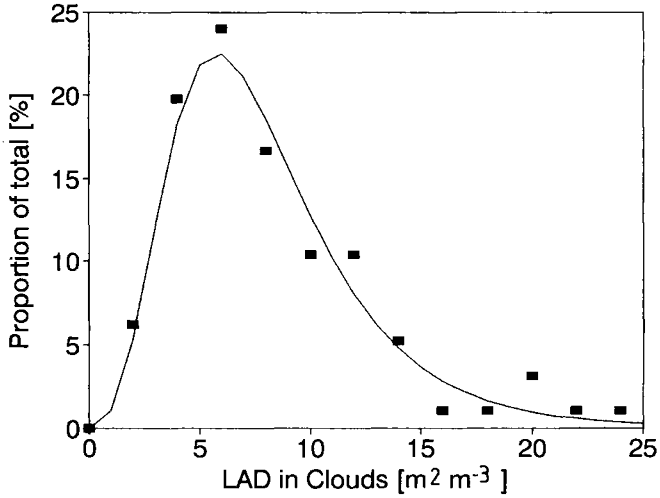

Figure 13. Frequency distribution of needle area density (LAD) in different clouds of the sample Scots pine trees in the experimental stand at Brasschaat, Belgium. Observed data (full square symbols) are approximately described with the Log-normal equation $y = [180/(25.5-x_i)]* \exp\{-[\ln(25.5-x_i)-2.17]^\wedge 2/0.37\}$.

open (and not shaded by its neighbours), which would enable the needles to still obtain sufficient light for survival. A coniferous stand can maintain a high productive LAI by means of a large ratio of silhouette area to projected needle area [27, 28] of shade-acclimated shoots [18]. This is in accordance with the observations of Stenberg et al. [28] that an increase in the silhouette area to projected needle area ratio implied more efficient light interception by shoots in the lower crown, where little light is available.

3.14. Conclusions

The general context of the present paper was one of a scaling up excercise for parameters of crown architecture and needle distribution. Scaling up techniques require both detailed information and the appropriate allometric relations to scale up given parameters to higher hierarchical levels. The 'cloud' technique used to describe and quantify needle aggregation, needle mass and needle area, as well as the vertical and radial distribution patterns of these parameters, proved to be a valuable and reliable method. It can also be applied for three-dimensional distribution models of trees. The allometric relations and mathematical equations described here (e.g. *table V*) are valid for the particular, even-aged Scots pine stand of this study. They are being used in further applications and scaling up procedures, for example to scale up sap flow rates from individual trees to the entire stand (Riguzzi et al., in prep.) and to scale up carbon fluxes. These allometric relations might also be useful for applications in experimental stands of the same species at other sites, although they need to be carefully evaluated or validated for their applicability, and modified accordingly when necessary.

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