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Effect of canopy structure on the diurnal interception of direct solar radiation and photosynthesis in a tree stand

Timo Pukkala & Timo Kuuluvainen

TIIVISTELMÄ: LATVUSTON RAKENTEEN VAIKUTUS METSIKÖN PÄIVITTÄISEEN SUORAN SÄTEILYN PIDÄTYKSEEN JA FOTOSYNTEESIIN

Pukkala, T. & Kuuluvainen, T. 1987. Effect of canopy structure on the diurnal interception of direct solar radiation and photosynthesis in a tree stand. Tiivistelmä: Latvuston rakenteen vaikutus metsikön päivittäiseen suoran säteilyn pidätykseen ja fotosynteesiin. Silva Fennica 21 (3): 237–250.

The utilization of direct radiation was studied in five model stands of Poisson-type tree distribution and cone-shaped crowns. The radiation extinction depended on the self-shading of the crown and the shading caused by other trees. The results indicate that at low sun elevation a stand populated by very narrow-crowned trees is most effective in light interception and photosynthesis. At high sun elevation a broad-crowned canopy is best illuminated and most favourable for photosynthesis. A stand with a two storey canopy is effective in all latitudes when the crowns are moderately narrow. In two-storey canopies the foliage of the lower storey can be better illuminated than in the lower parts of the upper storey, because of the smaller self-shading in the small crowns of the lower storey. A canopy where the crown volume is concentrated on few big crowns is less effective than a canopy consisting of many small crowns.

Metsikön kykyä hyödyntää suoraa säteilyä tutkittiin viidessä latvustorakenteeltaan erilaisessa mallimetsikössä. Puiden tilajärjestys oli satunnainen ja latvusmuoto kartio. Laskennassa säteilyn sammumistodennäköisyys riippui puun omasta varjostuksesta ja muiden puiden latvusten aiheuttamasta varjostuksesta. Pienellä auringon korkeuskulmalla hyvin kapealatvaisista puista koostuva metsikkö pidättää tehokkaimmin suoraa säteilyä ja tuotta parhaan säteilyilmaston fotosynteesiä ajatellen. Suurilla auringon korkeuskulmilla leveistä ja lyhyistä latvuksista koostuva latvusto on parhaiten valaistu ja suo parhaat edellytykset yhteyttämiselle. Kaksijaksoinen metsikkö pidättää säteilyä ja yhteyttää tehokkaasti kaikilla auringon korkeuskulmilla, jos latvukset ovat kummassakin jaksossa kapeahkoja. Kaksijaksoisessa metsikössä alemman jakson neulaset saattavat olla paremmin valaistuja kuin ylemmän jakson alaosassa, jossa suurten latvusten oma varjostus on voimakasta. Metsikkö, jossa neulasmassa on keskittynyt harvoihin suuriin latvuksiin, on nettofotosynteesin kannalta epäedullisempi kuin metsikkö, jossa neulaset ovat jakaantuneet moniin pieniin latvuksiin.

Keywords: radiation regime, interception, tree ideotype, crown form, simulation
ODC 181.21+161.32+181.62+53

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1. Introduction

The understanding of the interaction between solar radiation and canopy structure is becoming increasingly important for the understanding of growth processes and for the selection of optimum genotypes and stand structures. For this purpose models that predict the radiation conditions of canopies of a given structure are essential. The information about radiation distribution in forest canopies is needed for the calculation of photosynthesis and for the prediction of productivity. Radiation models can also be used for analyzing other processes, for example, light conditions for seedling establishment under forest canopies (Satterlund 1983, Kuuluvainen and Pukkala 1987).

The distribution of radiation in crops and trees or tree stands has for some time been studied intensively both empirically and theoretically. Since Monsi and Saeki (1953) published their general theory of light extinction in plant canopies the problem has been greatly elaborated and new methods have been developed in order to more reliably meet situations in reality (Ross 1975, 1981, Oker-Blom 1986). The importance and behaviour of different components of radiation in plant canopies, such as the penumbra effect (Miller and Norman 1971a, 1971b, Norman et al. 1971, Denholm 1981a, 1981b, Oker-Blom 1984) and diffuse light (de Wit 1965, Oker-Blom 1985) have been studied. Also empirical studies have added substantially to the knowledge of actual radiation conditions in forest stands (Anderson 1964a, 1964b).

As Anderson (1966) pointed out, radiation extinction is highly dependent on canopy structure. This question has received considerable attention in forest research (e.g. Warren Wilson 1965, Nilson 1971, Kimes et al. 1980). The problem of canopy modelling for forest trees is rather difficult because of the hierarchical grouping of foliage, which greatly influences light penetration and absorption (Norman and Jarvis 1975, Oker-Blom and Kellomäki 1983). The grouping of foliage in coniferous stands may be characterized at different levels:

(1) Shoot level
- shoot structure
- shape and size distribution of needles
- spatial distribution of needles within shoots

(2) Crown level
- crown shape
- spatial distribution of shoots inside crown

(3) Stand level
- spatial and size distribution of trees

No radiation model adequate to handling all these hierarchical levels has yet been developed. Research has concentrated on one level or some levels at a time by neglecting or making simplifying assumptions about the other levels. For example, Jahnke and Lawrence (1965) and Oker-Blom and Kellomäki (1982b) studied the influence of the aggregation of foliage in crowns of different shape on light absorption in individual trees, and Kellomäki et al. (1985) in tree stands by making simplifying assumptions about the actual inner crown structure. In the models of Norman and Jarvis (1975) and Oker-Blom and Kellomäki (1981) the grouping of needles into shoots is also taken into account. Also the influence of the structure of individual shoots has been examined by Oker-Blom et al. (1983) and Oker-Blom (1985). A more realistic stand model, where the grouping of foliage into shoots and shoots into crowns is taken into consideration, was outlined by Oker-Blom and Kellomäki (1982a, 1983).

Reviewed literature shows that adequate model descriptions of the interaction between entire stands and solar radiation are rather few. In this study we present a model which involves a method for generating stands with specified canopy structures. The momentary direct radiation conditions of the canopy are calculated by utilizing the light extinction model of Oker-Blom and Kellomäki (1982a).

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2. Calculation method

2.1 Outlines of the method

In the calculation method the foliage of the tree stand is assumed to be aggregated into conical crowns. The needles inside the crowns are clustered into shoots. The horizontal location of crowns and the spatial location of shoots inside crown is Poisson distributed. With this aggregation structure, the probability of a beam of radiation attaining the point is calculated at a great number of points in the canopy. Using these probabilities the irradiance and the potential potosynthesis are estimated at each point. Since each point represents a definite crown volume element, the potential rate of photosynthesis for the whole canopy can be estimated as a sum of products of point rates and volumes of crown space represented by the point. Integration over time is carried out by calculating the momentary interception and photosynthesis at one hour intervals.

The calculation unit of the simulation model is a forest stand plot. The first phase in the simulation is to generate individual trees on the plot so that the stand and its canopy has a specified structure.

2.2 Calculation of irradiance and photosynthesis

Radiation extinction

In the radiation extinction model (Oker-Blom and Kellomäki 1982a) the tree crown is illustrated as a cone having a Poisson shoot distribution inside. The spatial pattern of trees is Poisson. The probability that the solar beam attains a point inside the tree crown depends on two factors: self-shading of the crown and shading due to other trees. Let s=(x,y,z) be a point inside the crown cone and t(s) the distance that the beam must pass inside the crown before arriving at point s (Fig. 1). For self-shading the probability that a beam of radiation attains point s (p_w) is

$$p_w(s) = \exp(-L_p t(s)) \qquad (1)$$

where L_p is the projected leaf area density (number density of shoots in the crown multiplied by the mean projection area of a shoot). The value of L_p is taken as 1.86 m^2/m^3 (Oker-Blom and Kellomäki 1982a). It is assumed that L_p is independent of the elevation and azimuth of sun. The distance t(s) is calculated by equations of Oker-Blom and Kellomäki (1982b).

The probability that other trees do not inhibit the arrival of radiation at point s is approximately

$$p_b(z) = \exp(-A(z)) \qquad (2)$$

where A is the total projection area of the tree crowns on horizontal plane z. It is given by

$$A(z) = \sum_{j=1}^{N} n_j T(z)_j \qquad (3)$$

where N = number of tree classes (here also number of trees on the plot)
n_j = number of trees in class j (trees/m^2),
$T(z)_j$ = projection area of tree in class j (m^2).

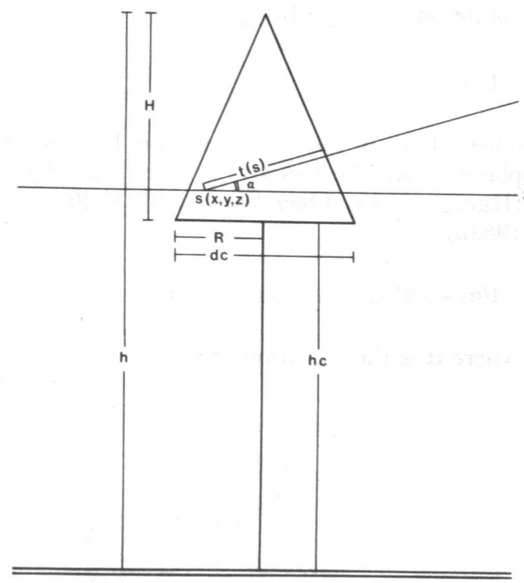

Fig. 1. Main measures of the radiation extinction model.

The projection area $T(z)_j$ is the total area of the shade which the shoots of a tree in class j cast on horizontal plane z, and is given by

$$T(z) = \iint_{V(z)} 1\text{-}\exp(-L_p t(s))\,dxdy \qquad (4)$$

where V(z) is the projection of the crown cone on the horizontal plane z. The projection area is calculated numerically by the method of Kuuluvainen and Pukkala (1987). In this method the probability that the shoots cast shade is calculated at several points on the horizontal projection area of the crown cone. The projection area of the tree (T(z)) is the sum of products which are obtained by multiplying the extinction probability at point (x,y) by the area represented by that point.

Irradiance

The relative irradiance or non-extinction probability (p) at point s(x,y,z) is

$$p(s) = p_w(s)p_b(z) \qquad (5)$$

where $p_w(s)$ is the relative irradiance due to the shading of the tree crown itself and $p_b(z)$ that caused by other trees.

The relative irradiance is converted to absolute one $(I(s,\alpha))$ by

$$I(s,\alpha) = p(s)I(\alpha) \qquad (6)$$

where $I(\alpha)$ is the irradiance on horizontal plane above the canopy. It is estimated by (Ducrey 1975, Oker-Blom and Kellomäki 1982b)

$$I(\alpha) = 3.92\exp(-0.23/\sin\alpha)\sin\alpha,\ \mathrm{MJm^{-2}h^{-1}} \qquad (7)$$

where α is the elevation of the sun.

Net photosynthesis

The net photosynthesis (P) is assumed to depend on irradiance (I) as follows (Chartier 1970)

$$P = \frac{aI+P_{max}-\sqrt{(aI)^2+P_{max}{}^2-aIP_{max}(4b-2)}}{2b},\ \mathrm{gCO_2m^{-2}h^{-1}} \qquad (8)$$

where P_{max}, a and b are parameters. The maximum photosynthesis was taken as 10 mg CO_2/h per 1 dm^2 of upper surface of needles, and the needle area was assumed to be 10 m^2/m^3 (Larcher 1980, p. 131, Oker-Blom and Kellomäki 1982a, 1982b). Parameters a and b were taken as 0.00577 and 0.386 respectively. They were estimated from Hari et al. (1982, p. 9). The parameters correspond to a situation where the water supply is sufficient and the tree is physiologically active.

2.3 Integration of interception and photosynthesis

The irradiance was calculated at one hour intervals for all hours when the sun was over horizon. At each time point the computations were carried out at 0.5 m vertical intervals. At each horizontal level the irradiance was calculated at 80 points in all crowns which cut the calculation plane. The crown volume represented by each point was also computed, which made it possible to calculate the potential photosynthesis for the whole stand. The total interception of radiation for a particular hour was calculated as a difference of the irradiance above and below canopy. The relative irradiance below canopy was calculated by Equation (2) for horizontal level z=0 m (see Fig. 1).

The results of this study concern the date June 30 and latitudes 25, 45 and 65°N but the procedure applies to any time interval and latitude, as well as for calculating momentary results.

3. Stands used in simulation

The interaction between the canopy structure and direct radiation was examined in five model stands with varying canopy structures (Table 1, Fig. 2). In three stands the diameter distribution was the same; only the crown shape varied. In the fourth stand the tree size varied considerably and the fifth stand consisted of two distinct canopy layers.

The size distribution of trees in each model stand was defined by the diameter distribution of the stand basal area which was described by a beta function:

$$f(d) = (d-d_{min})^{\alpha}\,(d_{max}-d)^{\gamma} \qquad (9)$$

where d = diameter at breast height,
f(d) = basal area of diameter d,
d_{min} = minimum diameter,
d_{max} = maximum diameter,
α and γ = constants which determine the shape of the distribution.

Trees for a sample plot of 30 m by 30 m were generated by using the diameter distribution defined by the beta function. The height of each tree sampled from the distribution was calculated by (Pukkala and Tahvanainen 1986)

$$h = c_1\,(1.3+d^2/(1.907+0.1672d)^2) \qquad (10)$$

where h = height (m),
c_1 = correction factor to obtain a specified height for average tree,
d = diameter (cm).

Table 1. Characteristics of model stands used in simulation examples.

Characteristic	Even stands 1	2	3	Uneven 4	2-storey 5 Over	Under
Diameter distribution						
– parameter α	1.70	1.70	1.70	0.77	1.08	0.41
– parameter γ	1.84	1.84	1.84	0.77	1.08	0.41
– stand basal area (m^2/ha)	25	25	25	25	20	5
– minimum diameter (cm)	24.5	24.5	24.5	5	20	5
– mean diameter (cm)	25	25	25	25	25	10
– maximum diameter (cm)	25.5	25.5	25.5	45	30	15
Correction factors						
– height (c_1)	1.38	1.38	1.38	1.38	1.38	1.10
– crown base (c_2)	3.10	2.05	0.21	2.05	2.05	0.74
– crown width (c_3)	1.03	0.74	0.54	0.74	0.74	0.77
Parameters for average tree						
– H/R-ratio	3	8	20	8	8	11
– height (m)	25	25	25	25	25	10
– crown base height (m)	18.3	12.1	1.27	12.1	12.1	1.5
– crown width (m)	4.47	3.22	2.37	3.22	3.22	1.5
Sum characteristics						
– stocking (stems/ha)	511	511	511	972	1222	
– total volume (m^3/ha)	303	303	303	284	275	
– leaf area index (m^2/m^2)	18.4	18.3	18.1	17.7	17.7	

The height of the crown base and the crown width were estimated by (Pukkala and Tahvanainen 1986)

Crown base

$$h_c = c_2(-1.336-0.1809d+0.9184h-0.01793d^2) \quad (11)$$

Crown width

$$d_c = c_3(0.25+0.3085d) \quad (12)$$

where h_c = height of crown base (m),
c_2 = correction factor to obtain a specified h_c for average tree,
h = height (m),
d = diameter (cm),
d_c = crown width (m),
c_3 = correction factor to obtain a specified d_c for average tree.

A normally distributed random number was added to the estimates of equations (10) . . . (12). The standard deviation of the random number was 5 % of the estimate. The purpose of the random term was to mimic the natural variation occurring in a real stand.

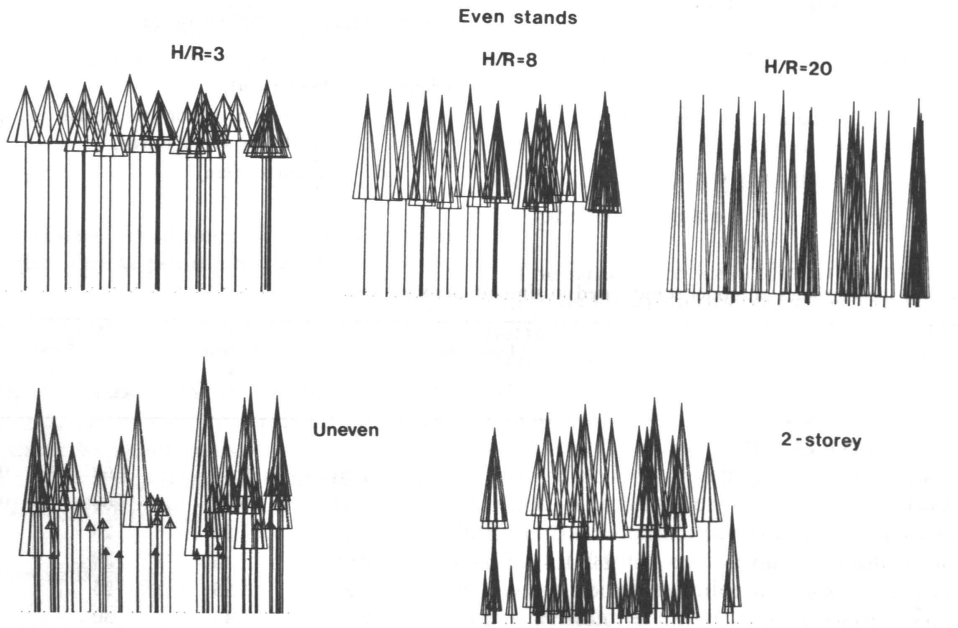

Fig. 2. Canopy structures used in calculation examples.

4. Results

4.1 Interception

The irradiance above forest canopy at solar noon is about 30 % higher in latitude 25°N than in 65°N. However, the time when the sun is over the horizon is longer in the north (Fig. 3). The proportion of interception of direct radiation is usually highest at low sun elevations.

Differences between canopy structures in the amount of intercepted radiation are negligible during low solar elevations, but they become evident with increasing sun elevation (Fig. 4). In latitude 25°N there is typically a remarkable drop in interception at noon in all canopy structures, because the sun elevation is so high that a considerable amount of radiation attains the forest floor through gaps between the tree crowns. An even stand with very narrow crowns intercepts radiation most effectively during the morning and evening hours, but the drop at noon is also greatest in this stand. The drop of an even stand is smallest when the crown shape is broad.

In the north, in latitude 65°N, the sun elevation is never so high that there would be a decline in the interception at noon (Fig. 4). A canopy of very narrow, vertically extended crowns is for the whole day best in intercepting direct solar radiation. Also a canopy structure consisting of two distinct layers with moderately narrow crowns in both layers gives efficient interception, which is higher than in an even stand with crowns of about the same average H/R-ratio.

The total interception on June 30 is in all canopy structures highest in high latitudes because of the length of the day and relatively

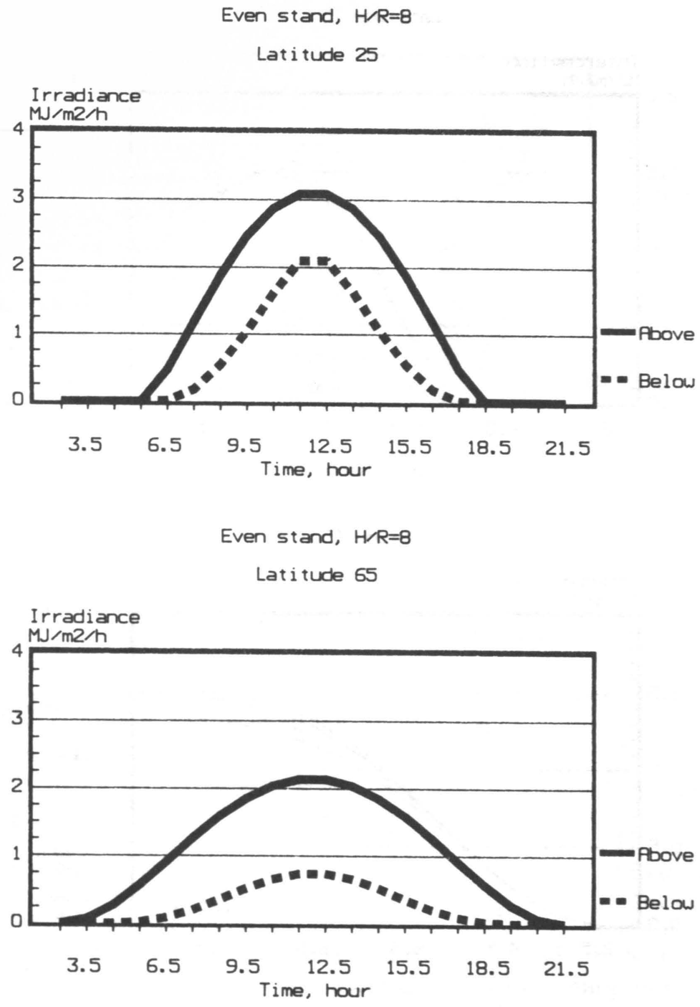

Fig. 3. Examples of the daily course of irradiance above and below canopy on June 30.

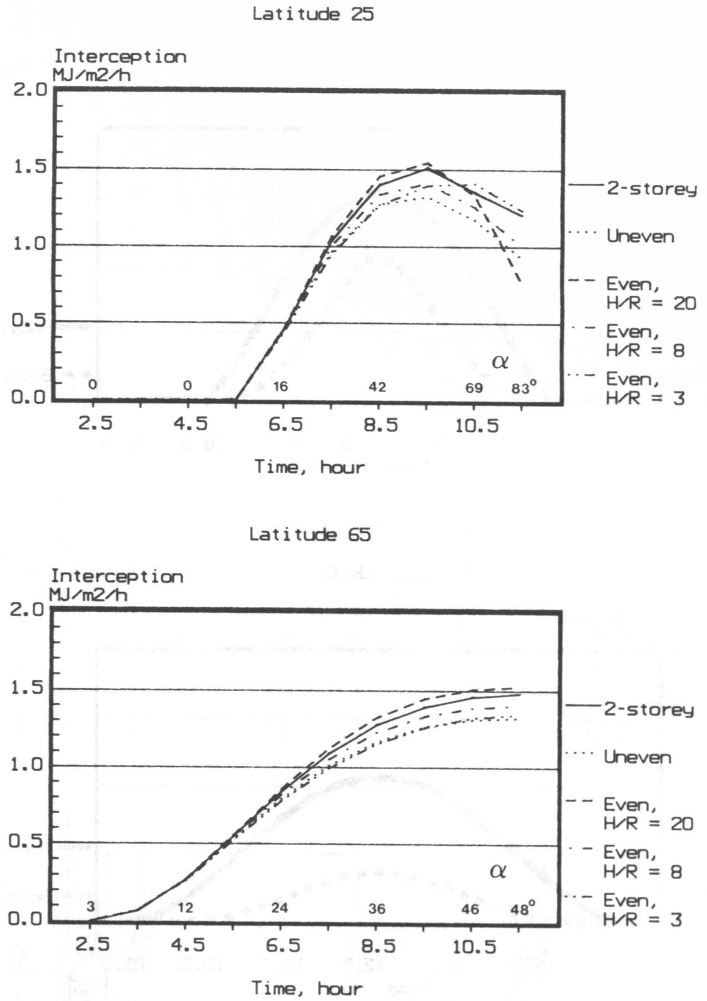

Fig. 4. Dependence of interception rate on time in different model stands in two latitudes on June 30. The smaller numbers on the x-axis show the elevation of the sun.

low sun elevation, which prevents the midday drop in interception (Fig. 5). In low latitudes both broad and narrow crowns (H/R=3 and 20) give equal radiation interception, which is obviously because the broad crown shape is good at noon and the narrow shape in the morning and afternoon. In low latitude the two-storey structure gives the highest total interception, but differences to the broad- and narrow-crowned even stands are small.

In higher latitudes the total interception of an even stand is the higher, the narrower the crown. The two-storey structure maintains its good efficiency also in higher latitudes, although an even stand with very narrow crowns is slightly more efficient in both latitudes 45 and 65°N.

4.2 Photosynthesis

The total interception alone does not determine the effectiveness of a canopy for photosynthesis, because it does not take into account the temporal and spatial variation in the illumination of foliage. Since the dependence of the rate of photosynthesis is of concave type, the best radiation environment for photosynthesis is attained when the irradiance distribution within the canopy is as even as possible, both in terms of time and space.

The calculations show that in low latitude (25°N) there is a midday drop in potential net photosynthesis in all canopy structures except that consisting of broad and short crowns (Fig. 6). This canopy structure has a clear peak in the potential photosynthesis at the highest sun elevations. The reason for this phenomenon is that at noon the whole upper surface of a broad cone-shaped crown with H/R-ratio 3 is illuminated causing a very favourable within crown radiation environment.

In high latitude (65°N) the very narrow-crowned even stand and the two-layered canopy have the greatest potential photosynthesis and the uneven stand the smallest (Fig. 6). There are no midday declines or peaks in the photosynthesis. The within-crown radiation climate is best at noon in all canopy structures.

In low latitude (25°N) the potential photosynthesis of June 30 is highest in the broad-crowned stand because of the midday peak (Fig. 7). In medium latitude (45°N) the even stand with either broad or very narrow crowns and the two-storey canopy display nearly equal total photosynthesis. In the north, in latitude 65°N, the narrow-crowned and two-storey canopies are clearly the most effective. A canopy where the crown is of medium type (H/R=8) is never the best one for radiation interception or photosynthesis (cf. Kellomäki et al. 1986).

An uneven canopy appears to be clearly the poorest irrespective of latitude and solar elevation, both in terms of interception and photosynthesis. This is probably because most of the crown volume is concentrated on the big crowns of the dominating trees, in which self-shading is considerable.

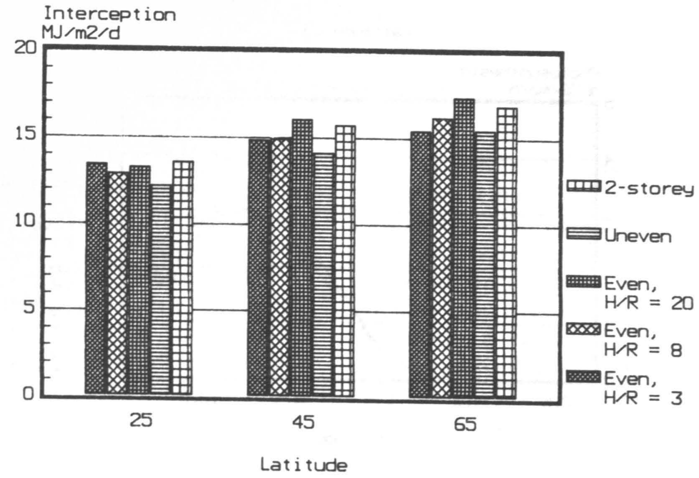

Fig. 5. Total interception of radiation on June 30.

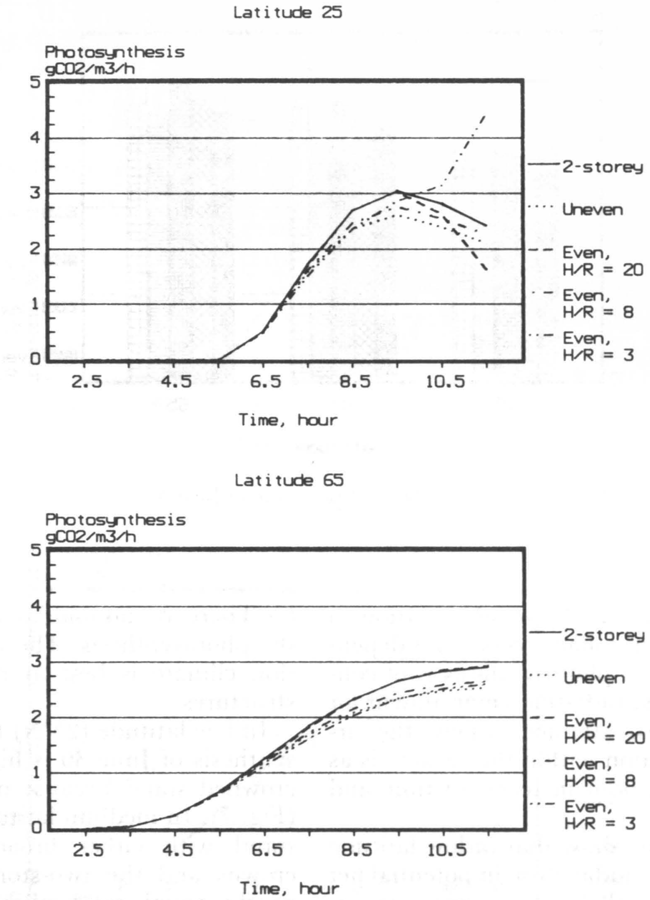

Fig. 6. Dependence of the rate of potential net photosynthesis on time in different model stands in two latitudes on June 30. The daily photosynthesis is expressed in terms of gCO_2 per one cubic meter of crown volume.

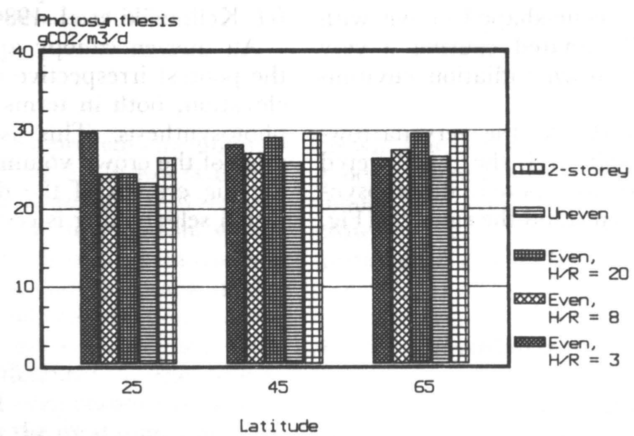

Fig. 7. Total amount of potential net photosynthesis on June 30.

5. Discussion

Using the developed calculation method, the interception of radiation, the distribution of leaf area into different irradiance classes, and the net potential photosynthesis, can be calculated for stands with different characteristics. Besides photosynthetic investigations, the calculation method may also be useful, for exmaple in studies concerning natural regeneration and micrometeorology of tree stands.

Most of the parameters used in the calculations apply to a restricted area, time and tree species. Usually they concern pine or spruce crowns or stands in southern Finland. Since we were interested in relative differences between theoretical canopy structures only, this deficiency does not reduce the validity of the results of this investigation.

The present version of the simulation program calculates only the relative irradiances for direct radiation; the inclusion of diffuse radiation into the model would increase considerably its applicability.

One way to increase the reliability of the model would be to make the extinction rate dependent on the distance from the edge of the crown (Koppel and Oja 1984). For this purpose the inner structure of the crown should be illustrated more thoroughly than in this investigation: the average shoot projection area should be expressed as a function of the distance from the crown periphery. It appears, however, that at least in young pine crowns the assumption of constant extinction rate everywhere in the crown is justified (Oker-Blom et al. 1986). It is more probable that the inner crown structure depends on the crown form. However, a careful documentation of the structure of tree crowns is needed for the assessment of these relationships.

When calculating the net photosynthesis it was assumed that the whole leaf area represented by one calculation point has the same irradiance. This gives a slight overestimate of photosynthesis. Because the extinction probabilities were for direct radiation, one would expect that if the relative irradiance is e.g. 0.4, 40 % of leaves is in full sunlight and 60 % gets only diffuese radiation. However, because of the remarkable penumbra effect typical of conifers, this assumption is also wrong and would underestimate the photosynthesis. One method to take the penumbra effect into account would be calculate the irradiance distribution of direct radiation for each calculation point (Oker-Blom and Kellomäki 1982a, their Appendix 4). However, because the main emphasis of this study was on relative photosynthetic capacities of different canopy structures, this was considered unnecessary.

The present model makes it possible to study the effects of stand location, stand density, crown form and size distribution of trees on direct radiation conditions in forest stands with a Poisson type spatial distribution of trees. For evaluating radiation conditions in stands with other spatial distributions another approash is needed: e.g. Kuuluvainen and Pukkala (1987) presented a method where standwise shading probability surfaces are constructed by combining surfaces calculated for individual trees. By this method the shading probability could be calculated at various horizontal levels, after which it would be possible to determine which parts of the surfaces are inside tree crowns; because the crown volume represented by one calculation point is known, the distribution of the crown volume into irradiance classes could be derived.

A theoretically optimal stand structure for productivity maximizes the light interception and minimizes the variation in irradiance on needle surface (Kellomäki et al. 1985). In general, the self-shading of trees appears to have considerable effect on the total shading in a tree stand (Oker-Blom and Kellomäki 1983). Consequently, light interception and the within-crown irradiance distribution is to a high degree a logical result of the self-shading properties of the crowns in relation to the prevailing angular distribution of direct solar radiation: an umbrella-like crown structure is beneficial in low latitudes characterized by high solar altitudes, whereas a columnar-like crown is beneficial for photosynthesis in high latitudes where low solar

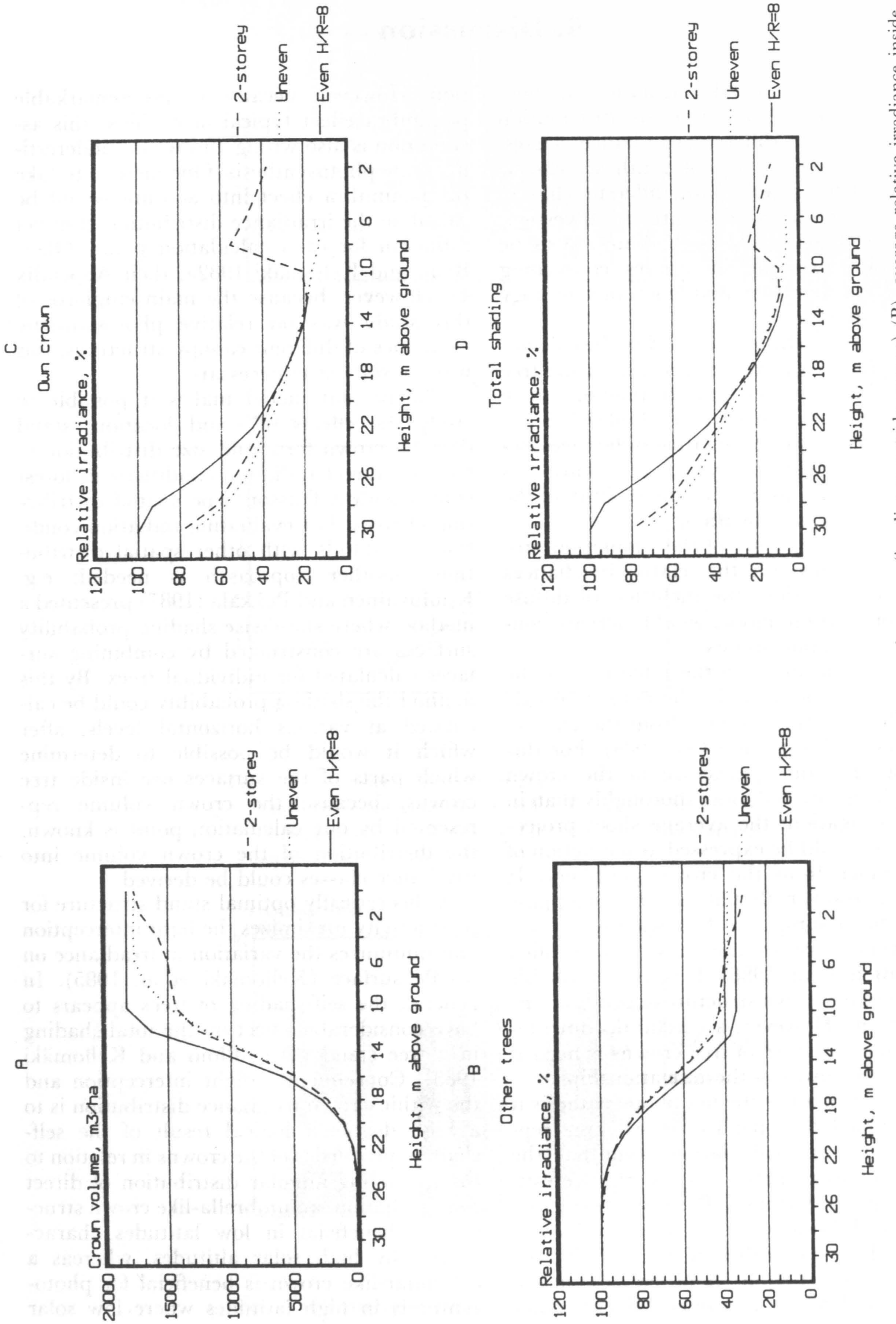

Fig. 8. Accumulation of crown volume (A), average relative irradiance due to other trees (irradiance outside crowns) (B), average relative irradiance inside crown due to self-shading (C) and average total shading inside crowns (D) as a function of canopy deepness expressed as distance from the ground level. In even stand the H/R-ratio is 8. Results apply to June 30 at 12 o'clock in latitude 65°N, or when sun elevation is 48.3°.

altitudes are common (Kellomäki et al. 1986).

Since self-shading in a tree crown decreases with crown size, a canopy of many small crowns is more beneficial for photosynthesis than a canopy of few big crowns with the same total canopy volume. For the same reason, the radiation conditions in dominated small-crowned trees can be better than those in the lower parts of the crowns of dominating trees (Fig. 8). Accordingly, Kellomäki and Hari (1980) found higher growth rates per unit of needle mass in suppressed Scots pine trees than in other tree classes.

In low latitudes the interception appears to increase towards both narrow and broad crowns, indicating an existing minimum within the range of the examined crown shapes, whereas in medium and high latitudes the diurnal light interception increases towards narrow crown shapes within the range of H/R values from 3 to 20. However, it is clear that a crown shape for minimum interception exists also in medium and high latitudes, although it falls beyond the range of crown shapes examined in this study (Oker-Blom and Kellomäki 1982b. Kellomäki et al. 1985).

In high latitudes the potential net photosynthesis was closely related to the amount of intercepted radiation. However, differences in the amount of intercepted radiation do not necessarily correspond to differences in the potential net photosynthesis. For example, the net photosynthesis per unit of intercepted light of the broad crown was greater in low and medium latitudes than in latitude 65°N, due to the beneficial shading properties of broad, horizontally extended crowns at high solar elevations. Accordingly, broad crowns are obviously more efficient in photosynthesis than narrow crowns with equal interception.

Though differences in diurnal interception of radiation and photosynthesis between the highly different canopy structures were clear, they were rather small. This can be related to the shading dynamics in tree stands. For example, at low solar elevations self-shading is obviously low in columnar-like crowns and high in umbrella-like crowns. A canopy of columnar-like crowns has, however, high between-tree shading, while a canopy of umbrella-like crowns has not. At high sun elevation, in turn, a narrow crown is characterized by high within-tree shading, and a broad and short crown by low within-tree shading. Thus, when self-shading in a crown is low, between-tree shading is usually high and vice versa. It is probably due to this opposite and compensative effect of self-shading and between-tree shading on the total shading, that differences between the different canopy structures in light interception and photosynthesis are not very distinct. However, in low latitudes the umbrella-like crown form appears to be clearly more favourable than other crown forms, because at high solar elevations, exceptionally, both self-shading and between-tree shading are small in a canopy of broad crowns.

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