On estimating canopy photosynthesis and stomatal conductance in a deciduous forest with clumped foliage

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Summary

The foliage in a fully-leafed deciduous forest canopy is clumped. Consequently, theory indicates that the probability of beam penetration will be estimated more accurately with a model based on the negative binomial distribution than with a model based on the Poisson distribution, incorporating an assumption of a spherical leaf inclination angle distribution. Flux densities of photosynthetically active radiation (PAR) were measured in and above a deciduous forest canopy and were computed with the canopy radiative transfer models based on the negative binomial and Poisson distributions. These radiation values were used to compute canopy photosynthesis and stomatal conductance. Canopy photosynthesis and stomatal conductance, based on the negative binomial model, over-estimated values computed from measured PAR profiles by 8 and 9%, respectively. The canopy photosynthesis and stomatal conductance values computed with the spherical Poisson model under-estimated measured values by 17 and 10%, respectively. Thus, the negative binomial radiative transfer model improves estimates of canopy photosynthesis and, to a lesser extent, stomatal conductance, inside a deciduous forest.

Introduction

Leaf photosynthesis and stomatal conductance are nonlinear functions of incident radiation. Since leaves inside a vegetated canopy are either sunlit or shaded, computations of canopy photosynthesis and stomatal conductance require the use of an accurate canopy radiative transfer model, i.e., a phytoactinometric model. Most canopy radiative transfer models that have been described were developed for uniform crop canopies (e.g., Lemeur 1973, Ross 1976, Norman 1979). Forest canopies, however, are heterogeneous in structure (Jarvis and Leverenz 1983). Therefore, phytoactinometric models developed for uniform canopies may not apply to forests.

Recently, Baldocchi et al. (1985) tested several phytoactinometric models against measurements of solar radiation components made above and within a deciduous, oak-hickory forest. These tests revealed that the foliage in that canopy was clumped. Consequently, phytoactinometric models developed for uniform crop canopies, based on the Poisson distribution (Lemeur 1973, Ross 1976, Norman 1979), underestimate beam penetration. A ramification of using such models to compute canopy photosynthesis and stomatal conductance will be a substantial underestimation in the magnitude of these biological processes, along with an error in the estimate of sunlit leaf area (Baldocchi et al. 1986).

Estimates of beam penetration in a canopy with clumped foliage can be improved using the negative binomial distribution (Acock et al. 1970, Nilson

1971, Baldocchi et al. 1985). Here, we modify the spherical Poisson canopy radiative transfer model of Norman (1979), developed for uniform crop canopies. We use the negative binomial distribution to compute the probability of beam and sky diffuse radiation penetration, scattering and sunlit leaf area. The objectives of this paper are: 1) to compare fluxes of photosynthetically active radiation (PAR) calculated by means of the spherical Poisson and the negative binomial phytoactinometric models against PAR measured in a deciduous forest; and 2) to compare estimates of canopy photosynthesis and stomatal conductance computed with these two phytoactinometric models and PAR profiles measured in a deciduous forest with clumped foliage.

Theory

Solar radiation inside a vegetated canopy consists of direct, sky-originated diffuse and scattered radiation. This radiation field is a function of the solar elevation angle and the density, spatial and angular distribution, and optical properties of the foliage (see Ross 1976). Below we discuss the model of Norman (1979), developed for a uniform crop canopy, and the modified model which is based on the negative binomial distribution.

Norman's canopy radiative transfer model

Norman's (1979) model is based on the assumption that foliage is randomly distributed in space and that the leaf inclination angle distribution is spherical. Based on these assumptions, the probability of beam penetration is computed as:

$$I_b(f) = \exp\left(-0.5\,f/\sin\beta\right) \qquad (1)$$

where f is the cumulative leaf area index, β is the solar elevation angle. The constant, 0.5, represents the value of the foliage area orientation function (G) for a canopy with a spherical leaf inclination angle distribution (Ross 1976). The foliage area orientation function represents the cosine of the angle between the solar beam and mean leaf normal (Ross 1976).

The penetration of diffuse sky radiation is computed assuming that the sky is of uniform brightness and that the azimuthal distribution of the leaves is symmetrical. The fractional penetration of diffuse sky radiation is computed by integrating Equation 1 over the solid angles of the sky hemisphere:

$$I_d(f) = 2 \int_0^{\pi/2} \exp(-0.5\,f/\sin\beta)\,\sin\beta\,\cos\beta\cdot d\beta \qquad (2)$$

Scattered radiation is generated by the reflection and transmission of intercepted radiation and enhances the flux densities of downward and upward directed diffuse radiation. Fluxes of downward and upward diffuse radiation are computed using a technique developed by Norman et al. (1971) and Norman (1979).

The canopy is divided into N layers defined as $F/\Delta f$, where F is the total leaf area index of the canopy and Δf is the leaf area index of the layer; Δf should be

less than 0.5 to minimize the probability of leaf overlap. The flux density of downward diffuse radiation at a layer j inside the canopy ($R_d(j)$) is the sum of transmitted diffuse and beam radiation received from the layer above ($j + 1$), downward directed sky diffuse radiation penetrating the canopy gaps and upward directed diffuse radiation (R_u) that is reflected downward. This relationship is expressed as:

$$R_d(j) = R_d(j + 1)(\tau(1 - I_d) + I_d) + R_u(j)(\rho(1 - I_d))$$
$$+ B\,I_b(j + 1)(1 - I_b)\tau \tag{3}$$

where τ is the leaf transmissivity, ρ is the leaf reflectivity, and B is the flux density of beam PAR radiation above the canopy. The flux density of upward directed diffuse radiation at layer $j + 1$ ($R_u(j + 1)$) is the sum of transmitted and penetrating upward directed diffuse radiation from layer j and upward reflected incoming diffuse and beam radiation from layer $j + 1$:

$$R_u(j + 1) = R_u(j)(\tau(1 - I_d) + I_d) + R_d(j + 1)(\rho(1 - I_d))$$
$$+ B\,I_b(j + 1)(1 - I_b) \tag{4}$$

Solving for Equations 3 and 4 requires knowledge of the flux densities of R_d and R_u in the adjacent layers. These values are initially unknown, but can be solved iteratively. The first iteration is performed by computing the ratio ($R_u(j + 1)/R_d(j + 1)$) for the case where the flux density of beam radiation is zero:

$$R_u(j + 1)/R_d(j + 1) = A(j + 1)$$

$$= \frac{[(\tau(1 - I_d) + I_d)^2 - (\rho(1 - I_d))^2]A(j) + \rho(1 - I_d)}{1 - \rho(1 - I_d)A(j)} \tag{5}$$

The computation of Equation 5 is initiated by setting $A(j = 1)$ equal to the albedo at the ground surface. Equations 3 and 4 are then re-expressed in terms of Equation 5 and solved for A in successive iterations. Convergence generally occurs after two to three iterations.

The negative binomial canopy radiative transfer model

In a canopy with clumped foliage, more than one contact between a light ray and a foliage element in a discrete layer of known leaf area is possible. Under such circumstances, the probability of beam penetration can be estimated in terms of the negative binomial distribution (Acock et al. 1970, Nilson 1971):

$$I_{nb}(f) = \exp(- f/g\,(\ln(1 + G\,g/\sin\beta))) \tag{6}$$

where g is the index of foliage dispersion.

The penetration of sky diffuse radiation is computed by integrating Equation 6 over the solid angles of the sky hemisphere:

$$I_{nd}(f) = 2 \int_0^{\pi/2} \exp(- f/g\,(\ln(1 + G\,g/\sin\beta)))\,\sin\beta\,\cos\beta\,d\beta \tag{7}$$

Flux densities of downward and upward diffuse radiation are computed by substituting I_{nb} for I_b and I_{nd} for I_d in Equations 3, 4 and 5.

Penumbral effects due to the finite size of the solar disk can influence the radiation field within a vegetated canopy (Miller and Norman 1971). Neither model considers penumbral effects, although they may be important in this forest canopy (Baldocchi et al. 1986).

Sunlit leaf area

Sunlit leaf area (L_s) can be estimated by integrating the probability of beam penetration (Equations 1 or 6) with respect to f. The resulting expressions are:

$$L_s(f) = (1 - I_b(f))\, 2 \sin \beta \tag{8a}$$

from the spherical model and

$$L_s(f) = (1 - I_{nb}(f))g/(\ln(1 + (G\, g/\sin \beta))) \tag{8b}$$

from the negative binomial model. Subsequently, shaded leaf area $L_{sh}(f)$ is computed as $(f - L_s(f))$.

Canopy photosynthesis

Canopy photosynthesis (P_c) is computed by summing the weighted estimates of leaf photosynthesis according to the fractions of sunlit and shaded leaf area and the flux densities of PAR on the sunlit and shaded leaves (see Norman 1980):

$$P_c = \int_0^F (P_s(I_s(f))\, \Delta L_s(f) + P_s(I_{sh}(f))\, \Delta L_{sh}(f))\, \Delta f \tag{9}$$

where P_s is leaf photosynthesis at a given level of PAR, ΔL_s and ΔL_{sh} are the sunlit and shaded leaf areas, respectively, of the layer with a leaf area of Δf, e.g., $\Delta L_s(f) = L_s(f) - L_s(f + \Delta f)$, I_s is the flux density of PAR incident on the normal of the sunlit leaves and I_{sh} is the flux density of PAR incident on the shaded leaves. The flux densities, I_s and I_{sh} are computed as:

$$I_s(f) = B\, G/\sin \beta + I_{sh}(f) \tag{10a}$$

$$I_{sh}(f) = R_u(f) + R_d(f) \tag{10b}$$

Leaf photosynthesis (P_s) was computed using the model of Marshall and Biscoe (1980). This model takes the form of a nonrectangular hyperbola and is an improvement over models that express the response of C_3 leaf photosynthesis to PAR in terms of rectangular hyperbolic relationships. Leaf photosynthesis is expressed as:

$$a\, P_s^2 + b\, P_s + c = 0 \tag{11}$$

where $a = \mu$, $b = -(P_{max} + \alpha I - \mu R_d)$ and $c = \alpha I (P_{max} - (1 - \mu) R_d) - R_d P_{max}$. The symbol μ is the ratio of the total resistances to CO_2 exchange to the sum of the total and carboxylation resistances and acts as a curvature coefficient, α

denotes the photochemical efficiency (the initial slope of the photosynthesis-PAR response curve), I is the flux density of PAR, P_{max} is the maximum value of leaf photosynthesis and R_d is the rate of leaf respiration.

Canopy stomatal conductance

Like canopy photosynthesis, canopy stomatal conductance (g_c) is computed by summing the weighted estimates of leaf conductance (g_s) according to the fractions of sunlit and shaded leaf area and the flux densities of PAR on the shaded and sunlit leaves:

$$g_c = \int_0^F (g_s(I_s(f)) \, \Delta L_s(f) + g_s(I_{sh}(f)) \, \Delta L_{sh}(f)) \, \Delta f \tag{12}$$

The response of leaf stomatal conductance to PAR (I) is computed in terms of its inverse, stomatal resistance (r_s), using the relationship of Turner and Begg (1973):

$$r_s = r_{sm} + b \, r_{sm}/I \tag{13}$$

where r_{sm} is the minimum stomatal resistance and b is a constant equal to I at twice the minimum stomatal resistance.

Materials and methods

Biomass and environmental data used to drive the models were obtained above and within a fully-leafed, oak-hickory forest (*Quercus* and *Carya* sp.) located near Oak Ridge, TN. (35°57′30″ N; 84°17′15″ W; 365 m above mean sea level). The forest has a mean height of about 22 m, a leaf area index of about 4.9 and a silhouette woody biomass area index of about 0.6. The mean leaf inclination angle is about 40° above crown closure and 10° below crown closure. Further details regarding canopy structure are presented in Hutchison et al. (1986).

Vertical profiles of PAR and shortwave radiation (R_g) were measured above and within the canopy with silicon quantum sensors and pyranometers, respectively. The sensors were mounted on trams that traversed 30 m transects through the canopy. Diffuse (*D*) shortwave radiation was measured with pyranometers equipped with shadowbands. Since the spectral quality of direct radiation measured above the canopy is the same as that within, direct PAR was computed from measurements of R_g and D as 0.43 (R_g-D) (Ross 1976). Diffuse PAR was computed as the difference between PAR and direct PAR. Further information regarding the experimental measurements and instrumentation are provided in Baldocchi et al. (1984, 1985).

The index of foliage dispersion, g, was calculated to be 2.42 from an empirical fit of the vertical profile of direct shortwave radiation to Equation 6. The foliage area orientation function (*G*) was computed as a function of solar elevation with a technique described by Lemeur (1973), using measured values of the leaf inclination angle frequency distribution. Parameters used to compute light scattering, photosynthesis and conductance were either obtained from the literature or from

measurements made at the experimental site. Parameter values used in the computations are listed in Table 1.

Table 1. Parameters used in the computation of canopy photosynthesis and stomatal conductance.

Variable	Unit	Element	Value	Reference
ρ	–	*Quercus alba*	0.11	Baldocchi et al. (1985)
τ	–	*Q. alba*	0.16	Baldocchi et al. (1985)
ρ	–	forest floor	0.033	Baldocchi et al. (1985)
μ	–	typical forest	0.8	Jarvis and Leverenz (1983)
α	mg J^{-1}	*Q. alba*	0.012	Hinckley et al. (1978)
P_{max}	mg m^{-2} s^{-1}	*Q. alba*	0.41	Dougherty et al. (1979)
R_d	mg m^{-2} s^{-1}	C_3 species	0.08	Dougherty et al. (1979)
b	W m^{-2}	*Q. alba*	22	Baldocchi and Hutchison (unpublished)
r_{sm}	s m^{-1}	*Q. alba*	145	Baldocchi and Hutchison (unpublished)

The following analysis was conducted using data measured on day 272, 1981. The canopy was fully leafed at this date and represented the phenological conditions typically observed between late spring and early autumn (Baldocchi et al. 1984). Vertical profiles of PAR, canopy photosynthesis and stomatal conductance are presented as normalized daily means and were derived from hourly-averaged data obtained between 0800 and 1700 h EST. Model computations were performed on the basis of twenty canopy layers of equal leaf area.

Results and discussion

PAR radiation regime

Direct PAR estimated with the spherical Poisson model significantly underestimated observed values throughout the canopy (Figure 1). This underestimation was in the order of 10 to 25 W m^{-2}. The PAR profile computed with the negative binomial phytoactinometric model, on the other hand, agreed reasonably well with the measurements. A small discrepancy was observed between measured values and those computed with the negative binomial model. This was an artifact of using the coefficient 0.43 to estimate beam PAR; Ross (1981) reports that values between 0.35 and 0.45 are observed for solar elevations between about 30 and 50°. The results in Figure 1 show that the negative binomial model, with a calibrated index of dispersion, g, provides a better estimate of the beam PAR regime in a deciduous forest with clumped foliage than the spherical Poisson model.

Calculated and observed profiles of diffuse PAR are presented in Figure 2. Above crown closure (LAI < 3.0), the negative binomial model improved upon the estimation of diffuse PAR made with the spherical Poisson model. However, both computations from models underestimated observed models. Failure to account for penumbral effects in tall canopies can partially account for the underestimation in diffuse PAR above crown closure (Oker-Blom 1984, Baldocchi
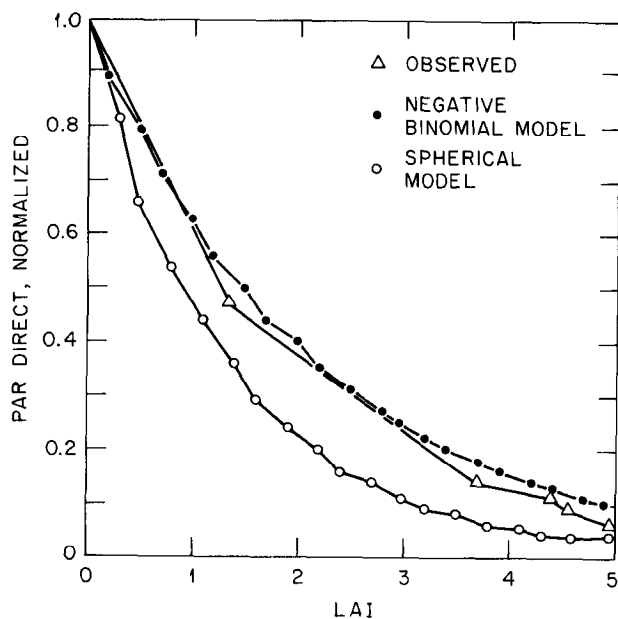
Figure 1. Normalized mean daily profile of direct PAR measured above and within an oak-hickory forest on day 272, 1981. The mean flux density of incoming direct PAR was 207 W m^{-2}.
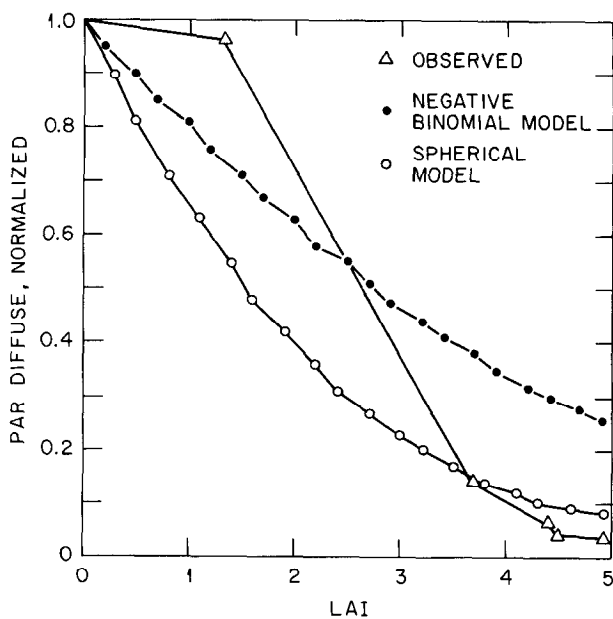

Figure 2. Normalized mean daily profile of diffuse PAR measured above and within an oak-hickory forest on day 272, 1981. The mean flux density of incoming diffuse PAR was 77 W m^{-2}. The values of diffuse PAR within the canopy are comprised of sky diffuse and downward scattered radiation.

et al. 1986). Below crown closure, diffuse PAR computed with the negative binomial model strongly overestimated observed values. Although the relative differences between calculated and observed values were large, the absolute differences were only in the order of 20 W m^{-2}. On the other hand, the agreement between diffuse PAR computed with the spherical model and observed values below crown closure was improved. Diffuse PAR computed with the spherical Poisson model, however, overestimated measured values at LAI $>$ 4.

A possible reason why the negative binomial model overestimated diffuse PAR in the subcanopy is that clumping causes the optical properties of discrete layers to be lower than that of individual leaves. This is because clumps of leaves can trap light, through multiple scattering, and reduce the reflectance and transmittance of the layer. It is unclear why the spherical Poisson model improves the estimate of diffuse PAR below crown closure.

Total PAR computed with the negative binomial model agreed well with observed values above crown closure (Figure 3). Below crown closure, values computed with the negative binomial model overestimated observed values by 50 to 140%; the absolute difference was about 20 W m^{-2}. Computations of PAR made with the spherical Poisson model underestimated observed values throughout the canopy; the underestimation was about 15% above crown closure and 30 to 40% below crown closure.

Canopy photosynthesis

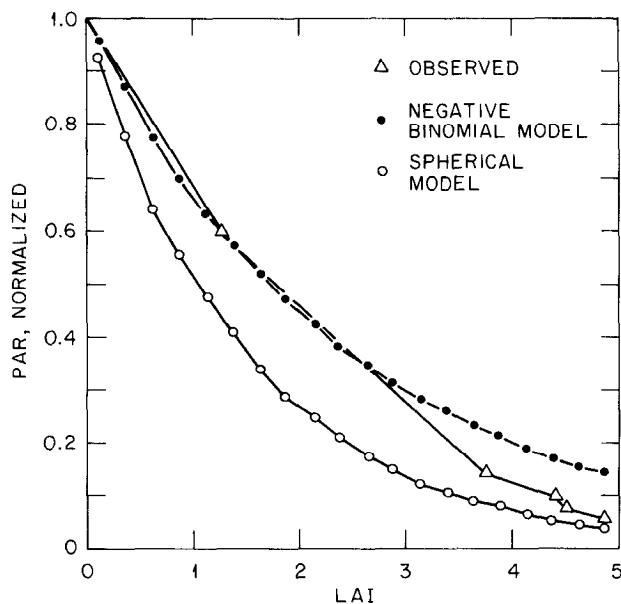The previous analysis demonstrates that the two radiative transfer models differ in

Figure 3. Normalized mean daily profile of total PAR measured above and within an oak-hickory forest on day 272, 1981. The mean flux density of incoming PAR was 284 W m^{-2}.

their ability to simulate the measured PAR regime. The effect that these differences have on the estimate of canopy photosynthesis is shown in Table 2. Mean canopy photosynthesis, derived from the negative binomial model (P_{nb}), overestimated that derived from the observed PAR distributions (P_m) by 8%. The difference between P_{nb} and P_m, however, was significantly different from zero ($P < 0.05$). On the other hand, canopy photosynthesis derived with the Poisson phytoactinometric model (P_{sph}) underestimated that derived from measured profiles (P_m) by 17%, on the average. This difference was also significantly different from zero ($P < 0.05$).

The sources of the disagreement between P_m and P_{nb} and P_{sph} can be investigated by examining the mean profile of photosynthetic rates (Figure 4). In the upper canopy (LAI < 2), both P_{nb} and P_{sph} underestimated P_m. This underestimation of P_m may be an artifact of penumbral effects providing more PAR to the light unsaturated shaded leaves (see Baldocchi et al. 1986). As shown in Figure 5a, P_s is very sensitive to changes in PAR at levels below light saturation. Thus, a slight increase in PAR on light unsaturated shaded leaves due to penumbral effects can result in a significant increase in canopy photosynthesis (Oker-Blom 1984). In the region LAI < 1, P_{sph} was greater than P_{nb} even though the spherical radiative transfer model underestimated PAR (Figure 3). This difference in estimating canopy photosynthesis is probably due to the overestimate of sunlit leaf area by the spherical Poisson model in this portion of the canopy. Furthermore, differences in the estimation of PAR on sunlit leaves should be relatively inconsequential since the sunlit leaves are typically exposed to PAR levels exceeding

Table 2. Computations of canopy photosynthesis derived from vertical profiles of PAR measured in a deciduous forest and those derived from the negative binomial and spherical Poisson radiative transfer models. The relative differences, and the paired Student's t statistic for the difference between the photosynthetic rates based on the measured and simulated PAR profiles are also presented. These data were obtained above and within an oak-hickory forest on day 272, 1981.

Time	P_m	P_{nb}	P_{sph}	$(P_{nb} - P_m)/P_m$	$(P_{sph} - P_m)/P_m$
h	mg m⁻² s⁻¹	mg m⁻² s⁻¹	mg m⁻² s⁻¹		
0800	0.87	1.03	0.70	0.18	−0.20
0900	1.23	1.30	0.97	0.057	−0.21
1000	1.15	1.42	1.12	0.23	−0.026
1100	1.57	1.47	1.19	−0.063	−0.26
1200	1.16	1.44	1.19	0.24	0.026
1300	1.50	1.45	1.18	−0.033	−0.21
1400	1.36	1.37	1.07	0.007	−0.21
1500	1.07	1.22	0.89	0.14	−0.17
1600	0.81	0.90	0.59	0.11	−0.27
mean	1.19	1.29	0.99	0.084	−0.17
s.d.	0.24	0.19	0.21		

P_m vs P_{nb}, t paired = −2.22

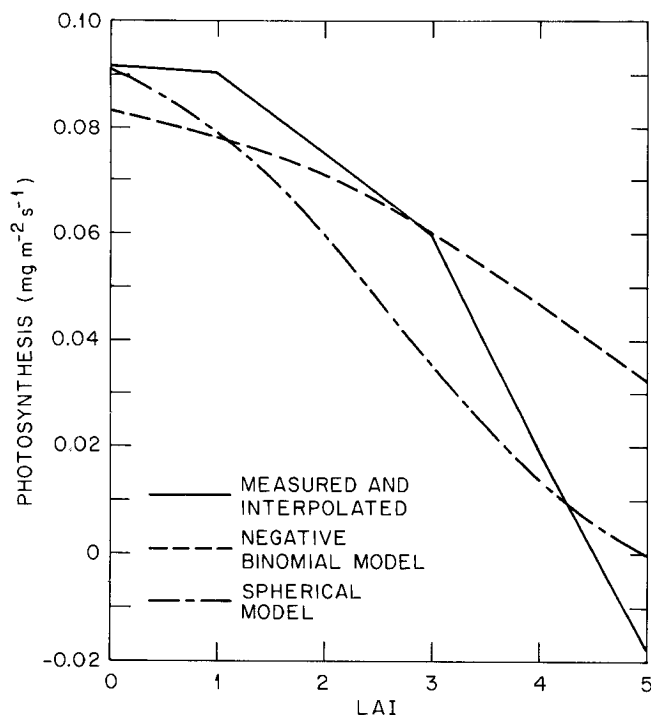P_m vs P_{sph}, t paired = 4.55

t, 0.05, 8 df = 1.86

Figure 4. Mean daily vertical profile of canopy photosynthesis computed from PAR profiles measured and computed with the negative binomial and spherical canopy radiative transfer models.

light saturation.

Below crown closure (LAI > 3), P_{nb} overestimated P_m. Large differences in the estimates of photosynthetic rates existed even though the absolute differences in PAR were not great. These large differences stem from the shape of the P_s-PAR response curve under low PAR levels (Figure 5a); P_s is very sensitive to PAR under the low light levels typically observed deep inside the canopy. On the other hand, the agreement between P_{sph} and P_m, in the region, was better due to the closer agreement between measured and calculated values of PAR. In view of these results, it is especially critical to simulate PAR accurately deep inside the canopy, where P_s is very sensitive to changes in PAR.

Canopy stomatal conductance

Table 3 shows that canopy stomatal conductance computed with the negative binomial model (g_{nb}) overestimated that computed from the measured PAR profiles (g_m) by 9% on the average. Stomatal conductance computed with the spherical Poisson canopy radiative transfer model (g_{sph}) underestimated g_m by 10%. Both estimates of canopy conductance were significantly different from g_m ($P < 0.05$). The magnitudes of the differences between stomatal conductance derived from measured and estimated PAR profiles are smaller than the differ-
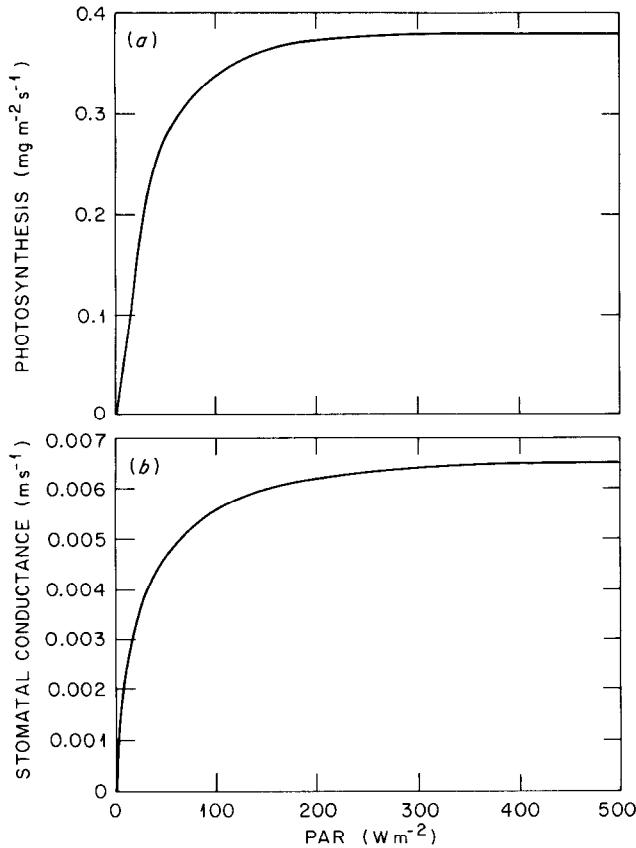
Figure 5. a) The leaf photosynthesis-PAR response curve for a *Quercus alba* L. leaf. The curve was computed using the Marshall-Biscoe model (1980). The parameters used to compute the curve are listed in Table 1.
b) The leaf stomatal conductance-PAR response curve for a *Q. alba* leaf. The curve was computed using the relationship of Turner and Begg (1973). The parameters used to compute this curve are listed in Table 1.

ences for canopy photosynthesis. This fact is owed to differences in curvature between the P_s-PAR and g_s-PAR response curves (See Figure 5).

As with canopy photosynthesis, difference in the estimates of canopy stomatal conductance can be explained with profiles of stomatal conductance computed from the two models and from the measured PAR profiles. Figure 6 shows that g_{nb} and g_{sph} underestimated g_m above crown closure. Again, this result stems from penumbral effects. In the subcanopy, both g_{nb} and g_{sph} overestimated g_m. This is a result of the models overestimating PAR deep inside the canopy where the response of g_s to PAR is strong.

Conclusions

The negative binomial canopy radiative transfer model is better than the spherical Poisson model in estimating direct PAR in an oak-hickory forest. The negative
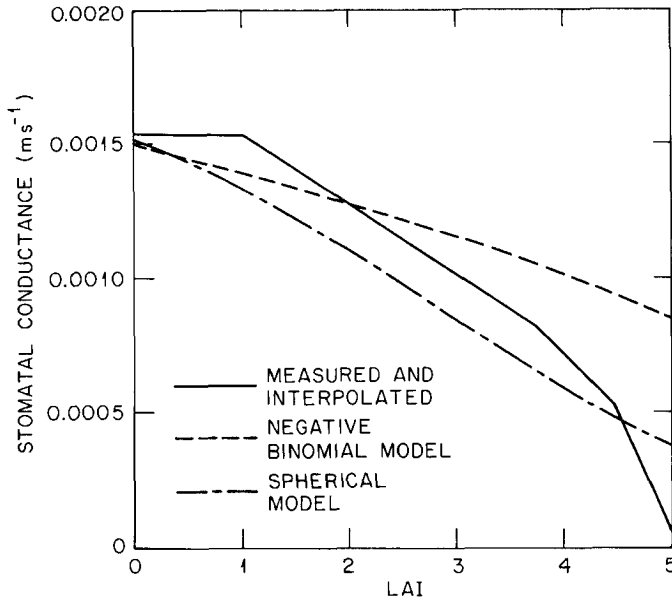
Figure 6. Mean daily vertical profile of canopy stomatal conductance computed from PAR profiles measured and computed with the spherical and negative binomial canopy radiative transfer models.

Table 3. Computations of canopy stomatal conductance derived from measured profiles and those computed with the Poisson spherical and negative binomial canopy radiative transfer models. The paired Student's t statistic and the relative differences between the means are also presented. These data are based on PAR measurements made above and within a fully-leafed oak-hickory forest on Day 272, 1981.

Time	g_m	g_{nb}	g_{sph}	$(g_{nb} - g_m)/g_m$	$(g_{sph} - g_m)/g_m$
h	$m\ s^{-1}$				
0800	0.0183	0.0219	0.0160	0.20	-0.10
0900	0.0231	0.0246	0.0198	0.065	-0.14
1000	0.0216	0.0258	0.0216	0.19	-0.00
1100	0.0269	0.0263	0.0225	-0.022	-0.16
1200	0.0217	0.0262	0.0224	0.21	0.032
1300	0.0264	0.0261	0.0223	-0.015	-0.16
1400	0.0244	0.0253	0.0210	0.037	-0.14
1500	0.0206	0.0237	0.0188	0.016	-0.087
1600	0.0175	0.0204	0.0150	0.17	-0.15
mean	0.0223	0.0245	0.0200	0.094	-0.10
s.d.	0.0031	0.0020	0.0025		

g_m vs g_{nb}, t paired $= -3.48$

g_m vs g_{sph}, t paired $= 4.02$

t, 0.05, 8 $df = 1.86$

binomial canopy radiative transfer model, improves the estimation of canopy photosynthesis, relative to computations made with a spherical Poisson phytoacti-

nometric model. However, we do not discount the spherical Poisson radiative transfer model because it is easier to use and estimates made with it are within the typical range of experimental error. Estimates of canopy stomatal conductance made with the two phytoactinometric models are not significantly different from estimates based on measured profiles of PAR, although g_{nb} overestimates g_m and g_{sph} underestimates g_m.

Errors in the prediction of P_c and g_c, with the negative binomial phytoactinometric model, result from ignoring penumbral effects and an inability to predict diffuse PAR well below crown closure where PAR levels are low and the PAR response curves for photosynthesis and stomatal conductance are very sensitive to changes in PAR.

Relative errors in the estimation of g_c were smaller than those associated with P_c. This effect results from differences in the nonlinearity of the respective PAR response curves. Consequently, relative errors in the estimates of nonlinear, light-dependent processes will decrease with reductions in curvature of the light response curve.

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