

6. D. E. Atkinson, J. H. Hathaway, E. C. Smith, *J. Biol. Chem.* **238**, 2875 (1963); D. E. Atkinson, *Ann. Rev. Biochem.* **35**, 85 (1966).
7. D. E. Atkinson, J. H. Hathaway, E. C. Smith, *J. Biol. Chem.* **240**, 2682 (1965).
8. H. Lineweaver and D. Burk, *J. Amer. Chem. Soc.* **56**, 658 (1934).
9. G. S. Eadie, *J. Biol. Chem.* **146**, 85 (1942).
10. J. E. Dowd and O. S. Riggs, *ibid.* **240**, 863 (1965).
11. B. L. Vallee and F. L. Hoch, *ibid.* **225**, 185 (1957); B. L. Vallee, R. J. P. Williams, F. L. Hoch, *J. Biol. Chem.* **234**, 2621 (1959).
12. R. B. Loftfield and E. A. Eigner, *Fed. Proc.* **24**, 216 (1965); ———, *J. Biol. Chem.* **244**, 1746 (1969).
13. I. W. Davie, V. V. Koningsberger, F. Lipmann, *Arch. Biochem. Biophys.* **65**, 21 (1956); A. N. Baldwin and P. Berg, *J. Biol. Chem.* **241**, 831 (1966); U. Lagerquist and J. Waldenström, *J. Biol. Chem.* **242**, 3021 (1967); H. George and A. Meister, *Biochim. Biophys. Acta* **132**, 165 (1967).
14. M. E. Krahf and G. H. A. Clowes, *J. Gen. Phys.* **43**, 1101 (1941); G. H. A. Clowes, *Ann. N.Y. Acad. Sci.* **5**, 1409 (1951).
15. C. T. Beer and J. H. Quastel, *Can. J. Biochem. Physiol.* **36**, 531, 543 (1958).
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Solar Radiation Profiles in Openings in Canopies of Aspen and Oak

Abstract. Vertical profiles of solar radiation in openings in forest canopies showed increasing solar radiation with depth in Colorado, but not in Minnesota. A model was developed and tested to calculate solar radiation in openings from the incoming direct and sky radiation and from the depth and diameter of the opening. The increase occurs only with high direct and low sky radiation. The model may explain the geographic and seasonal distribution of the solar radiation profiles and the lack of such observations previously.

Vertical profiles of solar radiation in vegetation canopies usually show decreasing intensity with increasing depth into the canopy. The decreasing intensity is largely a function of the decreasing probability of a continuous gap in the foliage to transmit the direct solar beam (1, 2). However, under certain conditions solar radiation was found to increase before decreasing with depth in the canopy, a previously unrecognized anomaly. A mathematical model is pre-

sented that accounts for the observations. This model appears to be generally applicable and important primarily in arid regions or at high altitudes.

In June and July 1966, near solar noon I measured vertical profiles of solar radiation in sunlit areas of four small aspen *Populus tremuloides* and two Gambel's oak *Quercus gambelii* stands in west central Colorado at about 2440 m, using the same radiometer at each level in the canopy. The number

of measurements which could be made was small. In the summer of 1967, I measured the solar radiation profiles with different solar radiometers, one mounted above and four mounted at different levels within the canopies of one oak and one aspen stand in west central Colorado and in one aspen stand in northern Minnesota. These measurements were made 15 to 20 times during 20 minutes of each daylight hour for periods of 1 to 5 days in each stand in late June and early July and in August. The radiometers were not moved during the measurements in a stand, so they were sometimes shaded during the 20-minute interval. Solar radiation profiles were constructed for each hour from the means of the 15 to 20 measurements at each level. In 1968, measurements were made to test the model proposed here. One radiometer was held manually in gaps in the canopy and repositioned at different levels. Two additional radiometers were permanently mounted outside the canopy, one to measure total downward solar radiation and the other to measure diffuse sky radiation. Signals from both the canopy radiometer and the stationary radiometers were recorded on a multipoint recorder within 10 seconds so that changes in the incoming solar radiation would be recorded. All radiometers were calibrated against an Eppley pyrliometer.

In 1966, with clear skies, solar radiation in gaps near the top of the canopy increased by 0.05 to 0.10 cal cm⁻² min⁻¹, or up to 4 to 7 percent greater than the total incoming solar radiation (3). The same radiometer was used at all levels, so unbalanced calibration of the radiometers was not the cause of the measured increase. No increase occurred with overcast skies, indicating that the increase was related to the ratio of direct to diffuse solar radiation. In 1967, even though the measurements were made with no effort to insure that the radiometers were in the sun during the measurements, 37 out of 123 profiles indicated higher levels of radiation at some level within the canopy than were recorded above the canopy. In Minnesota none of the 17 profiles measured showed an increase in solar radiation. In Colorado a greater percentage of profiles showed an increase in early summer than in the August measurements. In Colorado in June and early July, 12 of the 32 profiles measured in aspen and 17 of the 30 oak showed an increase; and in August, 5 of the 28 profiles in aspen and 3 of the 16 measured in oak showed an increase

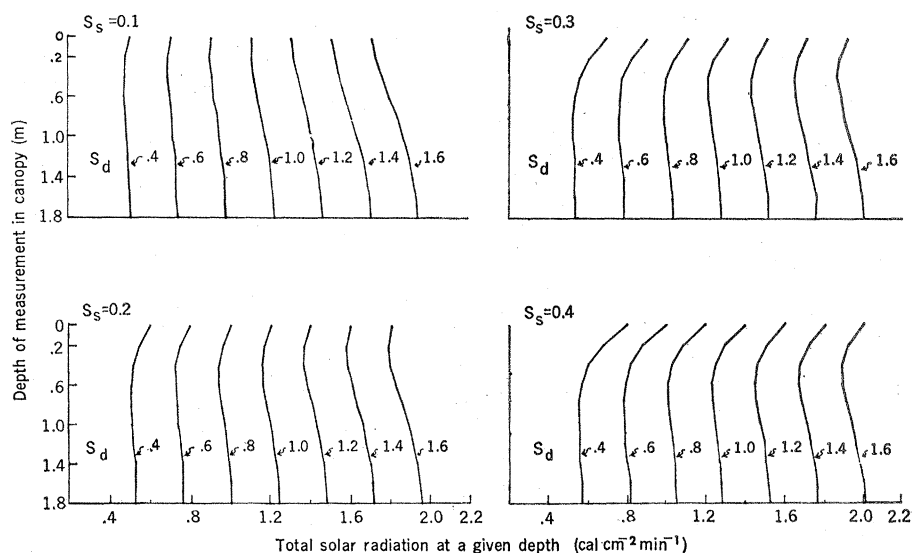


Fig. 1. Total solar radiation at different depths in openings near the top of the canopy calculated for different combinations of six intensities of the incoming solar radiation and four intensities of incoming sky radiation. The curves indicate an increase in total solar radiation in the canopy when the direct beam is high and the sky component is low.

Table 1. Observed and calculated solar radiation at different levels in openings near the top of the aspen canopy; S_T is total solar radiation, S_d is the direct beam, S_s is the solar radiation from the sky, and S_t is the reflected and transmitted component. Radiation is given in cal $\text{cm}^{-2}\text{min}^{-1}$. The diameter and total depths in meters of the four gaps were as follows; the diameter is given first: Gap No. 1, 0.5 and 0.5; Gap No. 2, 0.70 and 1.50; Gap No. 3, 0.85 and 1.50; Gap No. 4, 3.70 and 4.20.

Outside canopy			Within canopy					
S_T	S_d	S_s	Depth (m)	Observed	Calculated			
				S_T	S_T	S_d	S_s	S_t
Gap No. 1*								
1.36	1.17	.19	0.	1.35	1.36	1.17	0.19	0.00
1.36	1.17	.19	.25	1.37	1.45	1.17	.08	.20
1.36	1.16	.20	.50	1.46	1.46	1.17	.02	.27
Gap No. 2*								
1.50	1.22	.28	0	1.50	1.52	1.23	0.29	0.00
1.52	1.23	.29	.5	1.48	1.45	1.23	.05	.17
1.52	1.23	.29	1.0	1.52	1.52	1.23	.02	.27
1.53	1.23	.30	1.5	1.53	1.54	1.23	.01	.30
Gap No. 3*								
1.47	1.23	.24	0	1.48	1.47	1.23	0.24	0.00
1.47	1.23	.24	.5	1.48	1.45	1.23	.06	.16
1.49	1.24	.25	1.0	1.57	1.52	1.24	.02	.26
Gap No. 4†								
1.44	1.21	.23	0	1.48	1.44	1.21	0.23	0.00
1.44	1.21	.23	1.0	1.52	1.46	1.21	.13	.12
1.44	1.21	.23	2.0	1.55	1.49	1.21	.07	.21
1.44	1.21	.23	3.0	1.55	1.51	1.21	.04	.26
1.44	1.21	.23	4.0	1.53	1.53	1.21	.03	.29

* Three measurements at each level. † Four measurements at each level.

in total solar radiation within the canopy. Since the radiometers were not always located to receive the direct solar beam in the canopy, not all profiles could be expected to show an increase.

Because such an increase in solar radiation apparently had not been observed before, a model based on the components of the solar radiation was developed to describe and explain the observed increase in solar radiation. The model assumed that an opening at the top of the canopy can be described by an inverted cone, the sides of which are formed by leaves. The leaves were assumed to form a continuous cover and not to reflect downward. The model applies to openings near the top of the canopy, and is less valid near the bottom where the leaves receive less unattenuated incoming direct and sky radiation. In the model, radiation is given in calories per square centimeter per minute and the depths and diameters of openings in the canopy are in meters.

Total downward solar radiation in a gap was divided into three components: a direct beam from the sun (S_d), a diffuse component from the sky (S_s), and a reflected and transmitted component (S_t) from the leaves immediately above. A small downward reflected component which would be reflected upward by leaves at the level of the radiometer and then reflected downward by leaves above the radiometer was ignored. The intensity of the direct beam in gaps was assumed constant through-

out the canopy. The diffuse beam from the sky decreases as the area of the sky "seen" by the radiometers decreases. Assuming that the radiometer "sees" the sky through an inverted cone formed by the gap in the canopy, the fraction of the sky "seen" (f) depends upon the diameter of the opening of the cone (D) and the depth of the radiometer (z_r) within the gap. The fraction of sky "seen" (f) was calculated from

$$f = 1 - 2z_r/(4z_r^2 + D^2)^{1/2} \quad (1)$$

This fraction is comparable to the view factors discussed previously (2, 4). Assuming a uniformly overcast sky, the intensity of sky radiation at a given depth was obtained by multiplying the fraction of sky radiation "seen" by total sky radiation above the canopy. As the diameter of the opening decreases, the extinction of sky radiation with depth increases.

The intensity of the downward reflected and transmitted solar radiation, S_t , was given by the transmitted fraction of the intercepted direct and sky beams and was calculated from:

$$S_t = t (\Delta \% \text{ sun}) (S_d + S_s) \quad (2)$$

where t has a value of approximately 0.2 (5). The downward reflected component was assumed negligible. The term " $\Delta \% \text{ sun}$ " is the fraction of solar radiation at the top of the canopy which is intercepted by leaves above the level of measurement, and it was calculated as the difference in the cross-sectional

areas of the cone at the top of the canopy and at the level of measurement. Thus

$$(\Delta \% \text{ sun}) = 1 - [(z_c - z_r)/z_c]^2 \quad (3)$$

where z_c is the total depth of the cone or opening, and z_r is the depth of the radiometer.

The total solar radiation (S_T) at any level in the gap was given by:

$$S_T = S_d + [1 - 2z_r/(4z_r^2 + D^2)^{1/2}] S_s + 0.2\{1 - [(z_c - z_r)/z_c]^2\}(S_d + S_s) \quad (4)$$

Results of measurements made in July of 1968, to test Eq. 4, are given in Table 1. The predictions agreed with the observations, considering the simplifying assumptions. Gap 1 was formed by small trees, and the leaves did not form a continuous cover. Thus, the model predicted greater solar radiation than was observed at a depth of 0.25 m. In gap 2 the model predicted a decrease at a depth of 0.5 m before an increase at lower depths. In gap 4 the model predicted a continuous increase in radiation which was observed except for the lower levels.

The solutions of Eq. 4 for different sky and direct-beam conditions for a gap of diameter equal to 1.0 m and a depth of 2.0 m are given in Fig. 1. The model describes increasing total solar radiation with depth in the canopy only when the intensity of the direct solar beam is high and scattered radiation from the sky is low. The restriction of this increase to solar radiation conditions which are more common at high altitudes and in subtropical deserts may partially explain why such an increase has not been observed before. Much of the work on radiation profiles in vegetation has been done in humid climates with lower ratios of direct to diffuse radiation. This restriction may also explain the geographic and seasonal variation observed in the 1967 profiles.

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References and Notes

1. M. Monsi and T. Saeki, *Jap. J. Bot.* **14**, 22 (1953); J. L. Davidson and J. R. Phillip in *Climatology and Microclimatology* (UNESCO, Paris, 1958), p. 181; M. C. Anderson, *J. Appl. Ecol.* **3**, 41 (1966).
2. W. G. Duncan, R. S. Loomis, W. A. Williams, R. Hanau, *Hilgardia* **38**, 181 (1967).
3. P. C. Miller, *Oecol. Plant.* **2**, 241 (1967).
4. W. E. Reifsnnyder and H. W. Lull, *U.S. Department of Agriculture Technical Bulletin No. 1344* (Government Printing Office, Washington, D.C., 1965).
5. R. Birkebæk and R. Birkebæk, *Ecology* **45**, 646 (1964).
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