

# This Week's Citation Classic

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Duncan W G, Loomis R S, Williams W A & Hanau R. A model for simulating photosynthesis in plant communities. *Hilgardia* 38:181-205, 1967.  
[Depts. Agronomy and Physics, Univ. Kentucky, Lexington, KY and Dept. Agronomy, Univ. California, Davis, CA]

The paper gives the mathematical logic for building a model for calculating the rate of photosynthesis of leaves of a uniformly distributed plant leaf canopy for any sun position. The parameters supplied in the input to the model are leaf angle, leaf area, leaf distribution, leaf reflectivity and transmissivity, solar elevation and brightness, skylight brightness, and the relationship between leaf illumination and photosynthetic rate. [The SCI® indicates that this paper has been cited over 165 times since 1967.]

W.G. Duncan  
Department of Agronomy  
Institute of Food and  
Agricultural Sciences  
University of Florida  
Gainesville, FL 32611

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"In a plant canopy each leaf is busily engaged in contributing its photosynthate at rates based on the amount of energy it is receiving from the sun, the sky, and reflected from surrounding leaves. The illumination of each leaf is affected by its attitude and location in the canopy as well as by the position of the sun. To complicate matters, the sun moves from horizon to a maximum altitude and the skylight varies with every passing cloud.

"Crop physiologists had long been aware of the fact that differences in canopy leaf display caused differences in photosynthesis per unit of land area and hence in crop yield, but the system appeared too complex to analyze quantitatively or to measure experimentally. When a computer became available at the University of Kentucky, I thought this problem might give me a good excuse to play with it. With the mathematical assistance of R. Hanau, and using earlier work by Warren Wilson,<sup>1</sup> I worked out a solution to the problem in the early-1960s, but our computer was too slow and cumbersome to handle it in any reasonable time so I put it back on the shelf.

"In 1966, I went to the University of California at Davis for a sabbatical and had the good fortune to work with Bob Loomis and Bill Williams. They appreciated the value of what I had been trying to do and gave me the help and encouragement needed to polish up the model. Also, the next computer generation had arrived on the Davis campus and it had enough speed to work through the calculations in a reasonable time. I went on from Davis to work with John Hesketh in the Phytotron at Canberra leaving the details of getting the model published to Loomis and Williams. They did all of the dirty work. Had it been left to me, the manuscript might still be gathering dust in my filing cabinet.

"It was a surprise to learn that the publication has been so widely cited. Considering its length and the mathematics it contains I strongly suspect that it may have been cited more frequently than it has been read. The work was one of the first attempts to develop a method for getting quantitative answers for an important problem. It couldn't have been done earlier because computers were not generally available. The model as published was based on sound mathematical principles and was free of arbitrary assumptions of any consequence so not much room was left for further progress. My fellow agronomists, however, have always had more faith in experimental results than in mathematical equations so at least two independent studies<sup>2,3</sup> were devoted to testing the accuracy of the model. Fortunately, no discrepancies were found so it has not been necessary to revise Euclid's geometry or the calculus.

"The 1950s and 1960s saw a great deal of activity by crop ecologists in quantifying the nature and photosynthetic performance of foliage canopies. The concept of leaf area index was widely employed but the geometry of this relative to sunlight was more difficult. Models came forth from Japanese, English,<sup>4</sup> Dutch, and Estonian workers. The *Hilgardia* paper is probably widely cited because it is perhaps the simplest complete solution."

1. Wilson J W. Analysis of the spatial distribution of foliage by two-dimensional point quadrats. *New Phytol.* 58:92-101, 1959.
2. Stewart D W & Lemon E R. *The energy budget at the earth's surface: a simulation of net photosynthesis of field corn.* Ithaca, NY: US Department of Agriculture, Agricultural Research Service, Water Conservation Division, December 1969. Microclimate Investigations Report 69-3. 145 p.
3. Keener M E. *A test of the Duncan model of photosynthesis in plant communities.* MS thesis. College Station: Texas A&M University, 1972.
4. Monteth J L. Light distribution and photosynthesis in field crops. *Ann. Bot.* NS 29:17-37, 1965.  
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