Simulation of Potential Banana Photosynthesis in the Atlantic Zone of Costa Rica[1]

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ABSTRACT

For quantified evaluation of the suitability of soils for banana production, a simulation model would be useful. As a first step towards the design of such a model, a simulation model for potential photosynthesis of banana has been developed, based on a mechanistic approach. In the model, special attention is paid to leaf alignment of the banana plant, i.e. the position of the leaves and the daily movement of lamina halves of the leaf. The model was used to calculate potential banana photosynthesis for different sites in the Atlantic Zone of Costa Rica, using monthly averages of hours of sunshine at four weather stations in the area. Simulated potential photosynthesis appeared to be correlated with the actual production of banana plantations.

Key words: Model, banana canopy, climate, Atlantic zone, Costa Rica.

COMPENDIO

Para hacer una evaluación cuantitativa de la aptitud de la tierra para el cultivo del banano, sería útil disponer de un modelo de simulación. Por lo tanto, como primer paso para su diseño, se desarrolló un modelo de simulación de la fotosíntesis del banano, utilizando el método mecanístico. En él se da igual atención a algunas características típicas del cultivo, como la posición y el movimiento diario de las hojas. El modelo se utilizó para calcular la fotosíntesis potencial en varios sitios de la Zona Atlántica de Costa Rica, usando los promedios mensuales de brillo solar correspondientes a cuatro estaciones meteorológicas. Aparentemente la fotosíntesis simulada se correlaciona con la producción real de las plantaciones de banano.

Palabras claves: Modelo, dosel del banano, clima, zona atlántica, Costa Rica.

INTRODUCTION

Banana is an important export product for several tropical countries. The cultivated area is still being expanded in order to increase production. As the best banana soils are becoming scarce, plantations are being established in less suitable areas. Much capital is invested in land preparation, artificial drainage and infrastructure. Some systems exist for the determination of the aptitude of soils for banana growth (6), but so far a quantitative evaluation has not been undertaken. A mathematical model that simulates banana growth will enable analysis of various production alternatives and help indicate the viability of investments.

Various models have been developed to simulate plant growth, for example, SUCROS87 (10) and WOFOST (2); however they are usually restricted to annual crops.

One of the basic processes to be considered when modeling plant growth is photosynthesis. Based on De Wit's (13) mechanistic approach, a model to simulate potential photosynthesis of banana was developed which considers the position of the leaves, leaf area index, effects of light reflection and transmission, amount of diffuse and/or direct light, solar angle, and the photosynthetic function of single leaves.

The model was used to calculate potential photosynthesis for different sites in Costa Rica's Atlantic zone, and the results were compared with actual production data of banana plantations. This paper describes the model and presents the results of the study.

MATERIALS AND METHODS

De Wit's canopy photosynthesis model

Photosynthesis of a canopy depends not only on light intensity and the photosynthetic function of single leaves, but also on the distribution of light over the leaves of the canopy. The most important factors affecting the latter are:

— the number and the size of the leaves and their position with respect to a horizontal surface and to each other;

— the light transmission and reflection characteristics of the leaves;

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— the ratio between diffuse and direct light; and

— the solar angle.

De Wit (13) describes a model that simulates photosynthesis of some widely different canopies, considering each of these factors. The position of the leaves in space is described using a leaf distribution function, which divides the leaves of the canopy into inclination classes. Since most light is intercepted at the top of the canopy, the top leaves are of a greater importance for this function.

The canopy's light distribution function is then calculated to quantify how light is dispersed over the leaf inclination classes. This is carried out in two steps. First, light distribution functions are calculated for canopies with leaves at one inclination which are then combined with the leaf distribution function to obtain the canopy's light distribution function.

The canopy of the crop is assumed to consist of horizontal layers, with each having a specific leaf area index (leaf area of a layer per unit of soil area) that is so small that mutual shading within the layer can be neglected. The amount of diffuse and direct light intercepted in each layer declines exponentially with increasing depth in the canopy and is calculated in this model using a light penetration function. The scattered fraction of this light is obtained by means of a scattering coefficient. In the present model, a value of 0.2 is used for this coefficient (5). Ten percent of the light that is intercepted by the soil surface is estimated to be reflected and is absorbed by the leaf layers according to the penetration function.

The rate of photosynthesis of the entire canopy is computed by including the amount of absorbed light of each leaf layer in an equation that quantifies the instantaneous photosynthetic rate of individual leaves as a function of absorbed light; and by adding the individual rates of every layer.

Daily totals of photosynthesis are obtained by repeating the calculations substituting estimated or measured incoming radiation for different solar angles and by subsequential numerical integration of the rate of photosynthesis over the day.

Leaf distribution

Banana leaves are spirally arranged around the pseudo-stem, making an angle of approximately 156 between the petioles of successive leaves (1). At the time of florescence, the banana variety Valery has 12 photosynthetically active leaves (9). According to Stover (11), a leaf area index of between four and five encompasses most populations in permanent plantations of five years or older in Central America. In this study, a value of 4.5 has been used.

Banana leaves show a daily movement of the lamina halves. In the morning both laminas are situated in one plane, while as heat or drought increases, both halves will droop more and more, to rise later in the afternoon. The position of the lamina halves with time for the variety Gros Michel, according to Trelease (12), is given in Fig. 1.

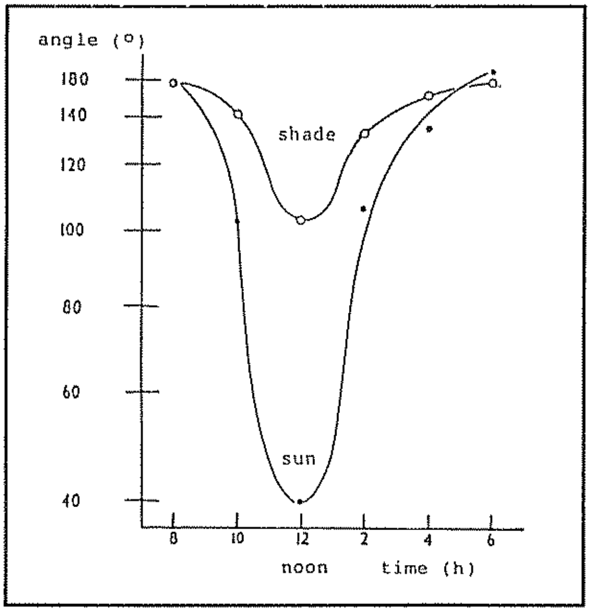

Fig. 1. Angle between the lamina halves as a function of time. (Source: Trelease).

In the model, the position of banana leaves in space is described by the azimuth and by the inclination of the lamina halves of the leaves (IB). IB is determined by the inclination of the midrib (IL) and the angle between both halves (2AL). Because of the rather constant angle between successive leaves, it is assumed that no preferred azimuth direction exists. At different times of the day IB is calculated with the equations shown in Fig. 2.

$$\tan(IB) = \frac{1}{\cos(IL) \cdot \tan(AL)}$$

if IL = 90° IB = 90°
if AL = 90° IB = IL

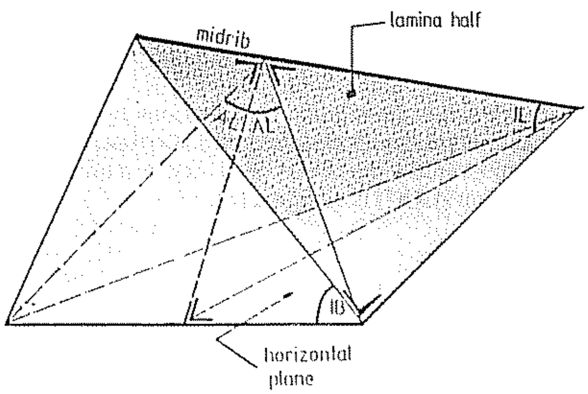

Fig. 2. Calculation of the inclination of the lamina (IB) from the inclination of the midrib (IL) and the angle between the lamina halves (2AL).

For the determination of the leaf distribution function only the upper seven leaves of the canopy are taken into account. Most light is intercepted by these leaves, as they form a complete crown that overshadows the remaining leaves of the canopy. For each of these leaves, IL was obtained from Champion and Charpentier (1) and the angle between the lamina halves was derived from Trelease (12) (Fig. 1). On an overcast day, this angle was assumed to be the mean of the angle of a shaded leaf and that of a leaf in hours of sunshine. The daily lamina movement is considered to be similar for each of the seven leaves.

Light distribution

Even in canopies with leaves of the same inclination, the light is intercepted at various angles due to the difference in azimuth between the leaf's normal and the actual incident radiation. The sine of the angle of incidence (LS) on a leaf was given by De Wit (13).

$$\sin(LS) = A + B \cdot \sin(DA)$$
with
$$A = \sin(IS) \cdot \cos(IB)$$
$$B = \cos(IS) \cdot \sin(IB)$$

where IS is the inclination of the incoming light, IB is the inclination of the lamina half, and DA is the difference in azimuth between the lamina half's normal and the incident radiation. De Wit introduced a boundary angle (DAO) for DA, to distinguish between light falling on the upper side and on the under side of a leaf.

$$DAO = \arcsin(-A/B) \quad \text{for } IS < IB$$
$$DAO = -\tfrac{1}{2}\pi \quad \text{for } IS > IB$$

The probability (S) that light is intercepted by the upper side or the under side of a leaf is calculated with

$$S = (B \cdot \cos(DA) - A \cdot (\tfrac{1}{2}\pi + DA)) \cdot W \quad \text{for } DA < DAO$$

and

$$S = (B \cdot (2 \cdot \cos(DAO) - \cos(DA)) - A \cdot (2 \cdot DAO + \tfrac{1}{2}\pi - DA)) \cdot W$$

for DA > DAO

$$\text{with} \quad W = (W \cdot B \cdot \cos(DAO) - 2 \cdot A \cdot DAO)^{-1}$$

In the recent model, these equations are only used for the moments in which both lamina halves of the leaves are in one plane. When the lamina halves of a banana leaf hang down, light interception by the under side of a lamina half is impeded by the other half of this leaf. For these conditions, De Wit's procedure was adapted and the probability of light interception is hence calculated with

$$S = (A \cdot (DA - DAO) + B \cdot (\cos(DAO) - \cos(DA))) \cdot W$$

$$\text{with} \quad W = (A \cdot (\tfrac{1}{2}\pi - DAO) + B \cdot \cos(DAO))^{-1}$$

The principle that light interception by lamina halves with any inclination is proportional to the number of lamina halves with this inclination and their relative projected area in the direction of the sun, is subsequently used to calculate the light distribution function for the banana canopy.

Instantaneous rate of photosynthesis per leaf layer

The photosynthetic-light response of individual leaves is described by the exponential function

$$A = A_{max}\left(1 - e^{-\frac{H \cdot A_{max}/hc}{A_{max}}}\right)$$

where A is the photosynthetic rate of the leaf, A_{max} is the maximum assimilation rate and H is the intensity of absorbed light. The ratio A_{max}/hc represents the efficiency of light use by the leaves at low light intensity (5).

Gietema-Groenendijk (4) reports measurements of photosynthetic-light response curves for banana leaves of different ages. From these curves, the magnitudes of the parameters A_{max} and hc have been determined. It appears that they depend largely on the age of the leaves. To account for the age effect, the following procedure has been developed to obtain values for the parameters of the photosynthesis function for each leaf layer. This procedure is based on the observation that the oldest leaves are situated at the lowest positions in the canopy.

The canopy, with a total leaf area index of 4.5, is assumed to consist of 45 layers, each with a specific leaf area of 0.1. A_{max} is set to 17.9 kg CO_2 ha^{-1} h^{-1} for the top and to 5 kg CO_2 ha^{-1} h^{-1} for the lowest layer. For each intermediate layer, the value for A_{max} is calculated by linear interpolation over the depth of the canopy. A similar procedure is followed for hc, which has been set to 50 W m^{-2} for the top and to 30 W m^{-2} for the lowest layer.

Incoming radiation

The amounts of direct and diffuse light on a clear day at different solar angles are calculated according to procedures used by Diepen *et al.* (2). The transmission through the atmosphere is estimated to be 0.71. This value was derived from the values for A and B for the humid tropics in the Angström formula, according to Frere and Popov (3).

The proportion of diffuse light on a clear day is assumed to be 0.29, as estimated with an empirical relation (7). On an overcast day, the amount of light (all diffuse) that arrives at the earth's surface is assumed to be 20 per cent of the amount on a clear day.

To estimate the relative contributions by different sky sections to the illumination of a horizontal surface from an overcast sky and a clear sky, a uniform sky distribution (UOC) is assumed (8).

Potential photosynthesis of the canopy for different locations in the Atlantic zone of Costa Rica

In Costa Rica's Atlantic zone banana is grown under different climatic conditions. It rains more near the lower slopes of the central mountain range and the sky is often overcast, while clear skies occur more frequently near the coast. These differences are clearly reflected in the monthly averages of daily hours of sunshine during 1988 at four weather stations in the zone (Table 1). "Los Diamantes" is located near the lower slopes of the mountain range, "Limón" is at the coast, and "La Mola" and "El Carmen" are between the two.

In the present model, daily totals of potential banana photosynthesis, for both a clear and an overcast sky, are simulated for every tenth day. The monthly averages of hours of sunshine from Table 1 are converted into values for intervals of ten days. Daily potential photosynthesis for each (partly overcast) interval is subsequently calculated by linear interpolation between the totals for a clear and an overcast sky.

Table 1. Daily average hours of sunshine, by month during 1988 at four weather stations in the Atlantic zone of Costa Rica.

Month	STATION (hours day^{-1}) "Los Diamantes"	"La Mola"	"El Carmen"	"Limón"
January	5.5	5.9	5.8	5.9
Februay	3.3	4.1	3.7	3.9
March	4.1	4.6	5.0	5.4
April	5.3	6.2	6.4	7.3
May	4.3	4.2	4.9	5.9
June	5.4	5.0	5.4	5.8
July	3.2	3.4	3.8	4.2
August	4.3	4.7	5.4	5.9
September	3.6	4.4	4.6	4.7
October	3.4	4.1	4.8	5.7
November	3.3	4.4	4.8	5.2
December	3.3	3.9	4.1	4.3
Average	4.1	4.6	4.9	5.3

Source: "El Carmen" and "La Mola"; BANDECO (pers. comm.); "Los Diamantes" and "Limon": IMN (pers. comm.).

RESULTS

Transmission of photosynthetically-active radiation through the canopy

The model has been used to simulate transmission of photosynthetically active radiation through the banana canopy. For the latitudes where banana is grown (between 30° northern and southern latitude) and a clear sky, a daily average of 15 per cent of transmission through a canopy with a leaf area index of 4.5 was computed.

Potential photosynthesis relating to the daily movement of the lamina halves

Figure 3 shows simulated daily totals of potential photosynthesis for different sky conditions for 10° northern latitude. The solid lines represent simulations according to the model described in this paper and the broken lines represent simulations of photosynthesis of banana, without taking into account the daily movement of the lamina halves.

For an overcast sky, there appears to be little difference between both curves. However, for a clear sky the movement of the lamina halves results in a somewhat higher simulated photosynthesis. The difference is a maximum of 20 kg CO_2 ha^{-1} day^{-1}, which is four percent of the daily total of 460 kg CO_2 ha^{-1} day^{-1}.

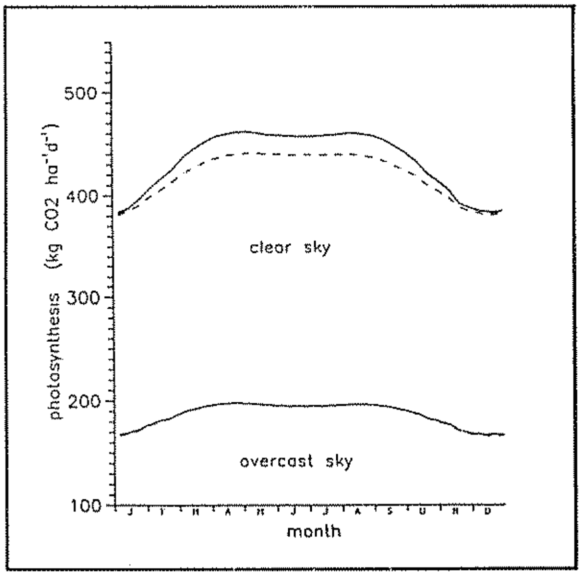

Fig. 3. Simulated daily totals of potential photosynthesis at 10° northern latitude for a clear and an overcast sky; with (solid line) and without (broken line) taking into account the daily movement of the lamina halves.

The simulated photosynthesis for an overcast sky is approximately 43 per cent of the amount for a clear sky, whereas the incoming radiation is only 20 per cent of the amount arriving under a clear sky.

Potential photosynthesis in the Atlantic Zone of Costa Rica

The photosynthesis model was run using the monthly averages of daily hours of sunshine during 1988 of four weather stations of the Atlantic zone of Costa Rica. Table 2 gives values for the average duration of hours of sunshine, the cumulative simulated photosynthetic rate and the average exportable banana productivity of three cantons.

A correlation factor $r^2 = 0.99$ was found with linear regression analysis with the average productivity as the dependent and the simulated potential photosynthesis as the independent variable.

The mentioned high totals of photosynthesis can only be realized when the photosynthesis of the leaves is not adversely affected by shortages or excesses of water in the soil, deficiencies of nutrients, pests, diseases or by low or high temperatures.

DISCUSSION

The present model is based on physical principles and relationships that quantify the underlying processes of canopy photosynthesis. Because these relationships are valid for a wide range of circumstances, the model has a more widespread utility than models of the regression type, which need to be calibrated for each area under consideration. Any model, however, is a simplification of reality and its designer makes choices for the type of input data, the level of aggregation and the internal structure.

Furthermore, the data that were used to simulate the photosynthetic response of the banana canopy concern a number of varieties, since based on the literature a complete data set of just one variety could not be realized. Consequently, the model presented here has to be validated externally, before far-reaching conclusions can be made on the simulated results.

The simulated transmission of photosynthetically active light through the banana canopy falls within the range measured in Honduras, where 14-18 per cent of the incident photosynthetically active light is transmitted through the canopies of older plantations of the varieties Valery and Grand Nain (11). Hence, the overall light interception by the canopy is modeled appropriately.

Table 2. Average duration of hours of sunshine, simulated photosynthesis and average exportable banana productivity during 1988.

Canton (station)	Hours of sunshine ($h\ day^{-1}$)	Average productivity ($kg\ ha^{-1}\ year^{-1}$)*	Photosynthesis ($kg\ CO_2\ ha^{-1}\ year^{-1}$)
Pococí		44.7 . 10^3 (n=27)	
(Diamantes)	4.1		97 . 10^3
(La Mola)	4.6		100 . 10^3
Siquirres		49.5 . 10^3 (n=16)	
(El Carmen)	4.9		103 . 10^3
Limón		51.8 . 10^3 (n=6)	
(Limón)	5.3		106 . 10^3

The number of plantations for which data are available is given in parentheses.
The exportable part of gross banana production can vary between 70 and 85 per cent.
Source: * ASBANA (pers. comm.).

The daily movement of the lamina halves of banana leaves has a relatively small effect on simulated potential photosynthesis. Simulated photosynthesis is somewhat higher when this movement is taken into account, as light is more equally distributed over the depth of the canopy when the lamina halves of the leaves hang down.

The simulated potential photosynthesis appears to be correlated ($r^2 = 0.99$) with the actual productivity of banana plantations in the Atlantic zone of Costa Rica. Although there are other major factors that influence banana growth, for example pests, diseases and soil conditions, it seems plausible that the amount of radiation explains part of the variation in banana productivity between the three cantons.

CONCLUSIONS

The presented model appears to be consistent. Results obtained are not contradicted by available empirical data, not only with regard transmission through the canopy but also Costa Rica's banana plantation productivity in the Atlantic zone.

The model could be useful for research towards evaluating location suitability for banana. However, its external validation is a prerequisite to this model's application.

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RESEÑA DE LIBROS

LUC, M.; SIKORA, R.A.; BRIDGE, J. (EDS.). 1990. Plant Parasitic Nematodes in Subtropical and Tropical Agriculture. CAB International, Institute of Parasitology. 629 p.

This book contains a total of 19 chapters authored by 33 nematologists from different geographical areas of the world. Some aspects of the morphology, anatomy and biology of plant-parasitic nematodes, as well as techniques used to extract and process them, are covered in the first two chapters, sometimes in a rather superficial way. These are followed by 16 chapters dealing with major and minor nematode problems of rice, cereals (corn, sorghum, wheat, barley, millets), root and tuber crops (potato, sweet potatoes, yams, taro, *Xanthosoma* spp., and seven minor root and tuber crops), food legumes (black gram, broad bean, chickpea, cowpea, common bean, lentil, moth bean, mung bean, pea, pigeon pea, soybean, and winged bean), vegetables, peanut, citrus, subtropical and tropical fruit trees (avocado, mango, fig, guava, lychee, olive, papaya, persimmon, cashew, macadamia, pistachio, kiwi, passion fruit, and eight miscellaneous fruit trees), coconut, oil palm, date palm, arecanut, coffee, cocoa, tea, banana, plantain, abaca, cotton, jute, sugarcane, tobacco, pineapple and spices (black pepper, cardamom, ginger, turmeric and nine other minor species).

The chapters are organized so as to provide the reader with information dealing with the most important as well as the lesser nematode pathogens of each crop, covering symptoms, biology, races, survival and dissemination, other hosts, environmental factors affecting parasitism, disease complexes, economic importance, population damage, threshold levels, control measures and diagnosis. Most chapters also include black-and-white photos of symptoms. Only those chapters dealing with subtropical and tropical fruit trees, banana, plantain and abaca have a different format than the one outlined here. Since most of the authors are specialists in these crops, subject matter is usually well covered, updated and with a good, although sometimes incomplete, list of references at the end of each chapter. All of this information is invaluable for any nematologist, crop protection specialist, or agronomist.

The last chapter is entitled "Effects of tropical climates on the distribution and post-parasite relationship of plant parasitic nematodes;" one wonders about the lack of information dealing with the host-parasite relationship, why the section "crop loss assessment in the tropical regions" was not mentioned in the title, and where those places where it rains continuously all growing season, as attested in Fig. 5, really are. This chapter must be considered of lesser quality than the others. There are good color photographs showing symptoms of damage caused by nematodes on different crops, as well as two appendices, the first dealing with nematicides and the second with nematode genera and species cited in the text, and their corresponding authorities. Finally, there is a subject matter index, which, at least in the reviewed copy, was missing eight pages (from letters A to M).

There are some dubious statements, some typographical errors, and important information seems to be missing in certain chapters. After reading the book, a Spanish-speaking nematologist may feel that certain literature dealing with plant nematodes in the American tropics has been ignored. The Preface states that "this text... is the first volume addressing tropical nematology to be published in more than 20 years," which completely ignores the book, in Spanish, authored by Dr. Jesse Roman in 1978: "Fitonematología Tropical." The book also lacks a chapter dealing with plant-parasitic and subtropical areas of the world.

In spite of its shortcomings, the book is to be considered a must in any nematological laboratory or library. We must commend the editors, the authors and CAB International's Institute of Parasitology for the good job they have done on this book.

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