Reprinted from
22 October 1971, Volume 174, pp. 371-378

SCIENCE

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Physical models of a simple system are limited by biological information and fluid dynamic theory.

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The interaction of the atmosphere and the land surface is of widespread interest because it affects the climate in which men live, practice agriculture and commerce, and enjoy nature. Several years ago, A. Leopold (*1*) urged society to develop a "land ethic" for a balanced plan to conserve and wisely use this interface where the air and land meet. In order to do this, we have to understand and quantitatively describe how it works.

Since a large part of the land is covered by plants, the mathematical analysis of the system is unusually complicated, simply by the many biological and physical interactions involved. Here we report the progress in our understanding of this system by describing a mathematical scheme that simulates a simple plant community—a cornfield. We believe it forms a basic framework that can eventually be adapted to analysis of more complex natural systems once certain unresolved problems are cleared up. We present field tests to pinpoint what these problems are and perform simulation experiments with hypothetical cases to answer some questions of interest.

Our article represents the culmination of more than a decade of extensive field study. Originally we aimed at answering agricultural problems of water conservation and crop production. While these problems are no less relevant today, we have discovered that our work can be applied to other important environmental problems.

Because both meteorological and plant processes derive their energy from solar radiation, we have treated crops as energy exchange systems. Most people are aware that photosynthesis uses energy from sunlight to fix carbon dioxide into organic materials. When carbon dioxide and oxygen in both photosynthesis and respiration are transferred across wet surfaces within leaves to the dry external atmosphere, water is unavoidably lost in evaporation (this process is called transpiration). However, many people are not aware that transpiration accounts for most of the energy transformed by plants from absorbed solar radiation. (In fact, almost 600 calories are required to evaporate a cubic centimeter of water.) Transpiration from leaves and direct evaporation from the soil surface also account for a large share of the water lost from the land; these processes convert tremendous amounts of energy that are directly controlled by plant and soil characteristics. For every inch of rainfall that is evaporated from an acre of land, 6×10^{10} calories are converted into latent heat. On the average, this amount of latent heat leaves an acre of land every 4 days during the summer in the eastern United States. This energy, in turn, drives the atmosphere's meteorological processes. Truly, the sun's work in a cornfield represents on a small scale the coupled meteorological and plant energy exchange processes responsible for the food we eat and the climate we live in.

If one were to make an accounting of the division of net radiation absorbed into the various energy sinks for the eastern United States in summertime, the proportions might be 1 to 5 percent to photosynthesis, 40 to 90 percent to evaporation (and transpiration), 10 to 60 percent to heat the air, and 5 to 10 percent to minor heat storage in the ground. The division of the energy balance rests largely upon water supply and transport through a soil-plant-atmosphere continuum.

Soil-Plant-Atmosphere Model (SPAM)

To deal with this continuum, a computer simulation model called SPAM was developed by D. W. Stewart (*2*) and tested under field conditions in Ellis Hollow, near Ithaca, New York (*3*). The logical sequence of SPAM is simple enough: (i) to define, on the scale of the leaf surface in a plant stand, how each leaf (and the soil surface) will respond to a given, immediate climate; (ii) to calculate from meteorology what that climate is; (iii) to calculate the specific leaf and soil responses to that climate; and (iv) to add up, leaf layer by leaf layer (and soil surface), the responses for the whole crop.

Figure 1 summarizes the essential components of the model and its predictions. We take up the predictions first, to stress what the model can and cannot do. SPAM can answer questions in two areas. Given the various leaf and community traits and the external climate, it can predict the microclimate in a community and at the leaf and soil surfaces. It can also predict the activity of the leaves and plant community in such processes as photosynthesis, respiration, evaporation, transpiration, and heat exchange.

Just how some predicted climatic properties can change vertically down through a plant community during midday are pictured in Fig. 1 (as "profiles" in the lower portion of the crop prediction box). From left to right are given profiles of wind, light, carbon dioxide, water vapor, and air temperature. These are predictions of steady-state mean values for, say, 1 hour. They quantitatively define living conditions for plants and other organisms in the different strata of the community.

In predicting community behavior, SPAM gives the vertical distributions of the activities of various community processes as source and sink intensities at any horizontal plane or as intensities of vertical fluxes in the air surrounding the plants. They can be defined for mass (water vapor and carbon dioxide), energy (radiation, latent and sensible heat, and photochemical energy equivalent), and momentum (wind shear). In Fig. 1 we depict, for example, the vertical exchange activity of carbon dioxide and water vapor in the top portion of the prediction box. On the left, one sees that carbon dioxide flows in both directions at midday. Carbon dioxide diffuses upward from respiration in the soil and

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from poorly lit bottom leaves, and it diffuses downward from the atmosphere to the well-lit, photosynthesizing upper portions of the leaf canopy. (By convention, flux upward is plus; downward, minus.) In the case of water vapor, daytime upflow steadily increases from the soil surface through the plant stand. (Flux densities are often stated in units per time per ground area.)

Source and sink activity are plus and minus, respectively. Thus, carbon dioxide given off by respiration in the base of the crop is a source, and photosynthesis in the upper portions of the canopy is a carbon dioxide sink. Water vapor caused by evaporation from the soil is a source at the base. In addition, transpiration from the leaf canopy provides a source of water vapor. (Source and sink intensities are often stated in units per time per volume.)

The prediction of evaporation has many applications to hydrology, forestry, agriculture, and water resource planning. In agriculture, water conservation aims at a more effective use of the water that is unavoidably lost by evaporation and transpiration. However, we have learned from big cities paved with concrete that evaporation and transpiration are needed for maintaining a comfortable climate (*4*). Thus, we do not want to stop evaporation, just make the most of it. To this end, SPAM has helped design new plant shapes and planting patterns.

By manipulating the submodels within SPAM, questions about the feasibility, desirability, and sensitivity of factor changes on the model's predictions can be tested. For example, one can determine whether changing the leaf angle of a crop has as much influence on net photosynthesis as changing the individual leaf's photosynthetic response to light. In predicting net photosynthesis, SPAM can help the plant breeder and agronomist select more desirable plant shapes and planting patterns.

With regard to carbon dioxide exchange, we need to stress that, while SPAM can predict net photosynthesis (net carbon dioxide uptake), it is not a model for plant growth or crop yield. Net photosynthesis is the major component of growth and yield, but it is only one of the many involved. Thus SPAM can form a submodel of a larger, more complex system. C. T. deWit is a leader in the development of complex models of plant growth (*5*). Ultimately, improved models of plant growth will answer questions of plant adaptation in changing ecological systems or questions of new crops or cropping sequence in established areas that are undergoing social and economic change.

Ideally, SPAM should be able to answer questions of plant community environment and behavior for systems of any size, shape, or external climate. At present it will give reasonable answers for systems that are (i) simple and uniform in structure, (ii) large enough in extent to avoid horizontal climate variation, and (iii) under steady-state or slowly changing conditions. Extensive, dense, and vigorous agricultural crops and forests approach the first two conditions. Clear or cloudy

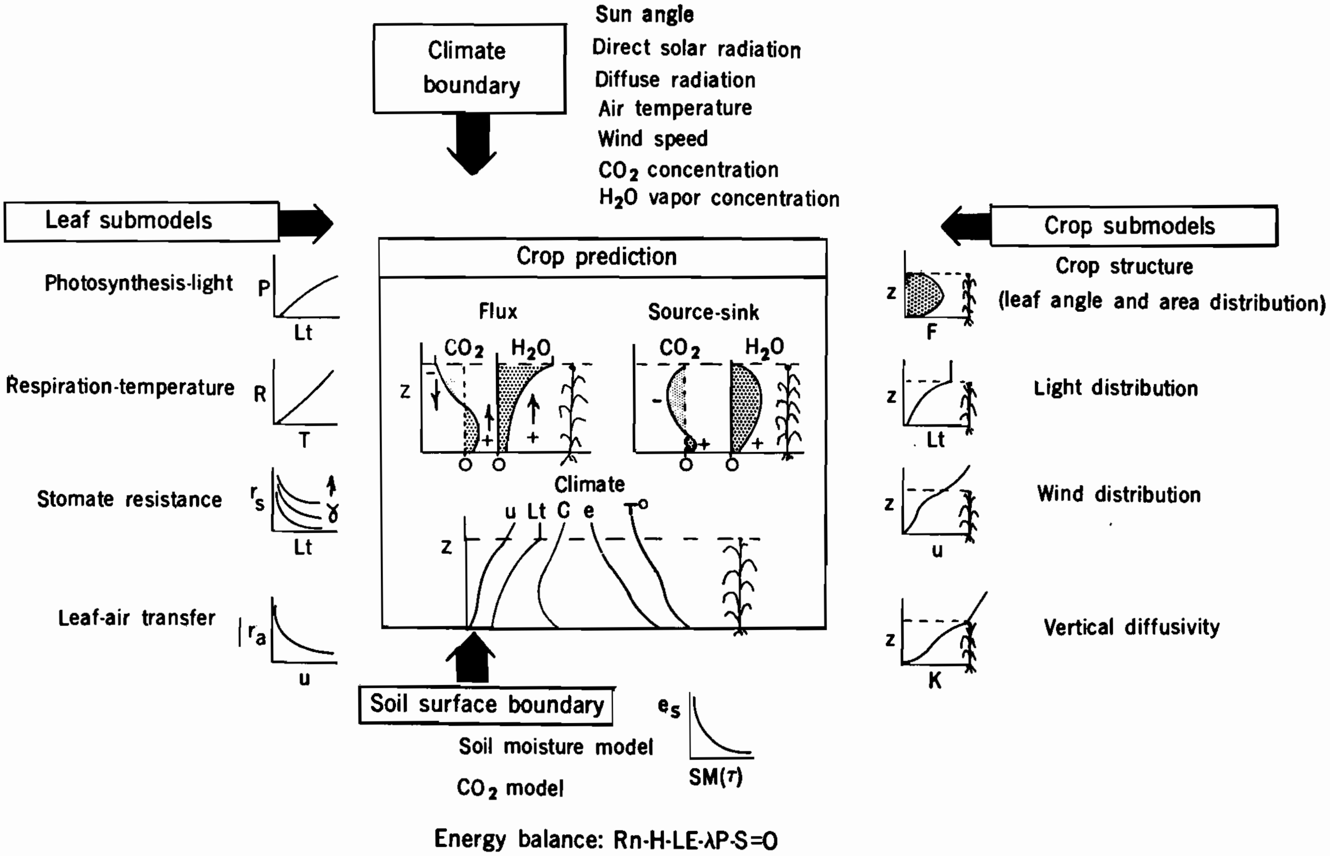

Fig. 1. Schematic summary of a mathematical soil-plant-atmosphere model (SPAM) giving required inputs, submodels, and representative daytime predictions of climate and community activity (that is, water vapor and carbon dioxide exchange). Abbreviations: height (*z*), wind (*u*), light (*Lt*), concentration of carbon dioxide (*C*), water vapor (*e*), air temperature (*T*°), surface vapor pressure (e_s), surface soil moisture or water potential [*SM* (τ)], photosynthesis (*P*), respiration (*R*), leaf temperature (*T*), stomate resistance (r_s), minimum stomate resistance at high light intensities (γ), gas diffusion resistance (r_a), leaf surface area (*F*), vertical diffusivity (*K*), net radiation (R_n), sensible heat (*H*), latent heat (*LE*), photochemical energy equivalent (λP), and soil heat storage (*S*).

days approach the third condition, except near sunrise and sunset. Despite present limitations, the basic framework of SPAM allows for future adaptation to more complex situations.

SPAM is a one-dimensional model with two boundaries. The top is a plane in the airstream, at 1 to 4 meters above the crop stand. The bottom is the soil surface. At the top, external climate is defined by solar radiation, wind, temperature, humidity, and carbon dioxide. At the soil surface, boundary conditions needed are flux densities of heat storage, carbon dioxide evolution, and surface soil moisture or water potential. From the latter, SPAM calculates in a submodel the apparent surface vapor pressure, the most important factor in forecasting evaporation from the soil and one of the most difficult to obtain. Along with inputs at the top and bottom boundaries, we need additional information about the leaves and the crop. These subcomponents of the model define the mathematical relationships required, but they vary widely in level of theoretical development.

Leaf submodels are on the left in Fig. 1. For photosynthetic response of individual leaves to incident light, P. Chartier's model (*6*) has been modified to incorporate a variable stomatal control mechanism. Response to carbon dioxide is included in the photosynthesis submodel. For response of respiration to leaf temperature, P. Waggoner's approach is used (*7*).

For a leaf submodel defining the relationship between stomatal resistance to gas diffusion and response to light, we use one described by P. J. C. Kuiper (*8*). Stomates, little valves on leaf surfaces, control the passage of water vapor, carbon dioxide, and oxygen between the wet inside surfaces and the dry outside air. With no water deficit, corn stomates usually open in daylight and close at night. However, as a water deficit develops, stomates partially close in daylight to protect against water loss. Carbon dioxide diffusion is therefore reduced too. R. W. Shawcroft (*9*) has modified Kuiper's model to include drought effects, which are represented in Fig. 1 by a family of hyperbolic curves. Gamma is essentially the minimum stomatal resistance at high light intensities, and it increases with increasing water deficit (for a wet leaf, stomatal resistance = 0). Gamma is an empirical innovation; lack of quantitative knowledge of this very complex relationship is perhaps the weakest biological link in SPAM. The status of stomates rigidly controls transpiration and photosynthesis, and thus the entire energy balance. We cannot overstate this fact.

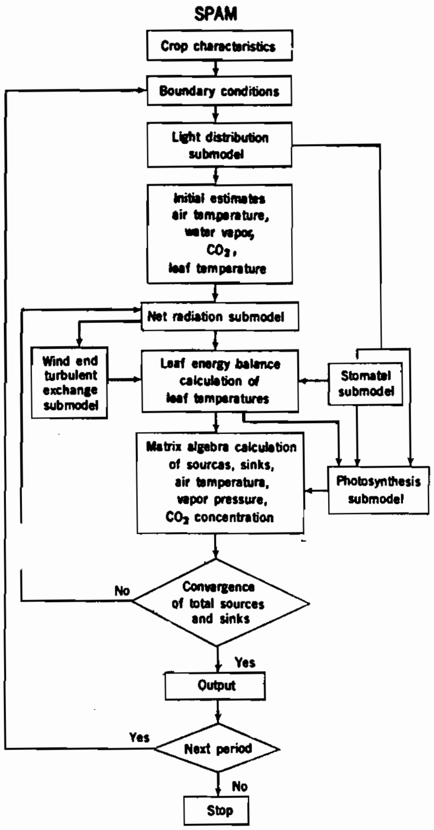

Fig. 2. The general procedure of SPAM, given as a flow diagram.

The final leaf submodel deals with the gas diffusion resistance through the thin film of still air on the surface of the leaf (leaf boundary layer). Pohlhausen's formula, as presented by B. Gebhart (*10*), has been modified to account for this resistance under natural turbulence in the field. Our experiments indicate that under conditions of turbulence in the field there will be an appreciable reduction in the resistance of the leaf boundary layer, with a given mean flow comparable to the classical relationships that have been established in the relatively smooth flow of air in a wind tunnel.

The crop structure and submodels are pictured on the right in Fig. 1. The submodels deal with meteorological processes after the structure, or architecture, has been defined. The quantitative description of crop structure is important and difficult. It is defined by the surface area of the leaves, how the leaves are distributed with respect to height, and the angle at which the leaves are displayed. Leaf size and leaf angle are required, while azimuthal angle is assumed to be random. An adequate definition can only be made for simple stands, where horizontal area distribution is random and vertical area distribution is adequately described by a tractable function. Regular clumping and regular distributions of gaps in vegetation present special problems to models that predict light distribution in the canopy.

To predict light relative to height in the stand, W. G. Duncan's model is used (*11*). With modifications, infrared portions of the solar spectrum are predicted as well. Thermal radiation is assessed from surface temperatures and hinges on a calculation of the energy balance. All three radiation regimes are needed to find the net absorbed radiation, which is necessary for calculating the energy balance of each layer.

Because gases and heat are diffused by the wind, SPAM has to calculate the distribution of wind speed and the vertical diffusivity of turbulence (Fig. 1). Vertical diffusivity is defined as an eddy diffusion coefficient. It is arrived at by assuming that transport of heat and water vapor can be expressed as diffusion equations of time-averaged flux, gradients, and a coefficient (diffusivity) in the energy balance, or as time-averaged flux of momentum, wind gradients, and coefficients (diffusivity) in the momentum balance theory used in SPAM. To calculate profiles of wind speed above the stand, we used W. C. Swinbank's method (*12*), which requires knowing traits of aerodynamic roughness of the stand, as well as components of its energy balance. Profiles of wind speed in the stand are predicted next. This prediction rests on distributing the wind drag on plant surfaces from the top of the stand downward, by means of A. Perrier's method (*13*). At this point, vertical diffusivity can be calculated by using a constant relationship between it and the predicted wind in the stand, much as I. R. Cowan has done (*14*).

Finally, the whole scheme must obey the energy balance, in which energy sources must equal energy sinks. In this case (see Fig. 1), the net absorbed radiation is the driving source. The sinks are sensible heat, latent heat, photochemical energy equivalent, and soil heat storage (*15*). In the computer program, the energy balance is solved for each leaf layer and soil surface as well as for the entire system.

It is obvious that solving the equation of any given part of SPAM is dependent on solving the equation of some other

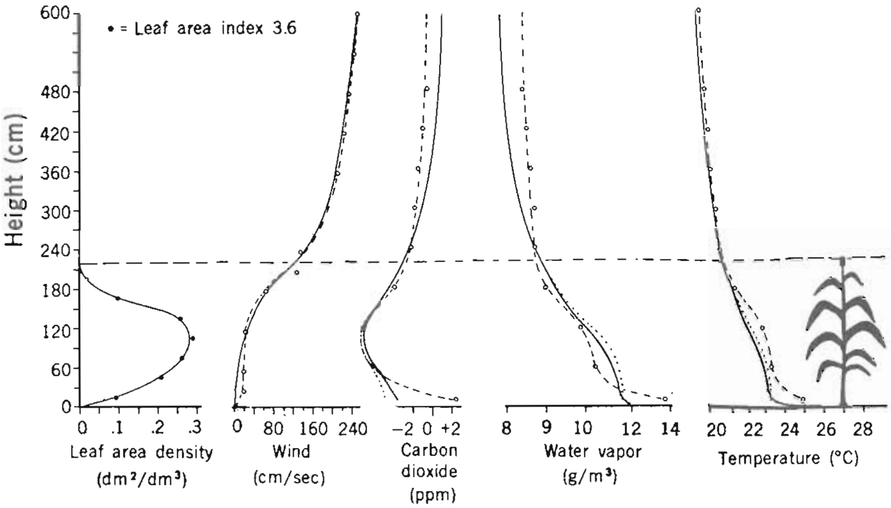

Fig. 3. Measured (circles and dashed lines) and predicted (solid and dotted lines) profiles of climate factors in and above a cornfield, with the field's vertical leaf area density shown. Profiles are half-hour mean values. (18 August 1968; 11:45 a.m. to 12.15 p.m., Eastern Standard Time.)

part. This interdependence requires the use of successive approximations, in order to solve all of the equations simultaneously. The converging solutions thus give final answers for the complete system. Figure 2 gives the general procedure as a flow diagram.

Testing SPAM

An experimental test of a mathematical model is an indispensable part of its proper development. We chose the best data we had to test SPAM for its weaknesses. On 18 August 1968, we obtained all the needed data in a 10-hectare cornfield in Ellis Hollow. Corn, *Zea mays* (Cornell M3), is an ideal crop for this purpose, since the leaves are randomly oriented and relatively uniformly distributed in size and display. We had planted the field in a hexagonal array like an orchard; thus all plants occupied an equal space, at six plants per square meter of land. The crop was fully grown and dense, with a leaf area index of 3.6 square meters per square meter of land. The corn was healthy, but under moderate stress because of a lack of water; otherwise, the weather on the test day was ideal for the growth of corn. Midday conditions are given in Fig. 3; also see Table 1.

R. B. Musgrave (*16*) obtained for us the needed measurements on the leaves for the photosynthesis submodel, while a team of several individuals took field measurements of climate profiles and vertical fluxes, for comparison with the model calculations. Figure 4 shows the equipment (in a field of soybeans) that was used to measure climate profiles in corn. All of the SPAM requirements, such as structure, optical and fluid dynamic properties, and stomate response, were measured on the same crop.

Theory versus test results are illustrated in Figs. 3, 5, and 6. Figure 3 compares predicted microclimate profiles as solid and dotted lines; the dashed lines were hand drawn through the data points we measured. Margin of error in data points is about equal to the diameters of the circles. All data are half-hour means, spanning the local noon. Leaf area density, on the left, and a plant drawn to scale, on the right, are given for reference. All profiles have been adjusted to data points at 240 centimeters, which is the best reference level within the boundary layer. SPAM underestimates temperature by about 0.5°C through most of the stand, and overestimates water vapor by about 0.5 gram per cubic meter. It comes close to the mark on wind and carbon dioxide, except near the soil. The serious spread between predicted and measured profiles for water vapor and carbon dioxide above the stand raises some questions, despite the accuracy of wind and temperature profiles. Questions of the quality of the data and the suitability of the site can be raised. However, we are fairly confident of our measurements. Downwind fetch over the crop to the sensors was about 200 to 250 meters, which is adequate for a boundary layer 2 to 3 meters over the stand. This leads us to question whether classical fluid dynamic theory for turbulent boundary flow is applicable to tall vegetation that is porous and flexible. We suspect that troubles may start within the canopy, since we cannot explain airflow there. In Fig. 3, one can see in the real wind profile a fairly constant wind velocity from the densest part of the stand almost down to the soil. This indicates that there was no wind drag on the vegetation in the bottom half of the stand—a physical impossibility. Evidently some aerodynamic mechanism adds entrained air at the base of the canopy. This phenomenon is even more striking in forests (*17*). To see if this would explain the other profile differences, we put measured wind data into SPAM and then repredicted the dotted lines in Fig. 3. Changes are slight.

Next we looked to the vertical diffusivity for answers. The application of diffusion equations in both cases can be

Table 1. A daytime energy balance for a corn crop, 18 August 1968, Ellis Hollow, New York. (Total incident solar radiation is 696 calories per square centimeter; total net radiation, 453 calories per square centimeter.)

Cases	Latent heat (cal/cm²)	Sensible heat (cal/cm²)	Photo energy (cal/cm²)	Soil storage (cal/cm²)
	$SM(\tau)$ = −600 (Fig. 6a)*			
Case 1				
γ† = 0.97	350 (0.77)‡	57 (0.12)	15 (0.033)	33 (0.074)
γ = 0.52	200 (0.45)	204 (0.45)	9.4 (0.021)	33 (0.074)
	γ = 0.97 (Fig. 6b)			
Case 2				
$SM(\tau)$ = —600	350 (0.77)	57 (0.12)	15 (0.033)	33 (0.074)
$SM(\tau)$ = —8000	219 (0.50)	171 (0.39)	14.1 (0.032)	33 (0.075)
	$SM(\tau)$ = −8000 (Fig. 6c)			
Case 3				
γ = measured values §	147 (0.33)	252 (0.57)	11.1 (0.025)	33 (0.074)
Measured energy balance	186 (0.41) ±53	222 (0.49) ±53	12.3 (0.027) ±4.7	33 (0.073)

* $SM(\tau)$ is surface soil moisture or water potential, measured in bars. † γ is minimum stomatal resistance at high light intensities, measured in seconds per centimeter. ‡ Figures in parentheses are fractions of net radiation. § Measured γ are in Figs. 6c and 7.

questioned if vertical mass flow occurs in the canopy. The additional entrained air in the base of the canopy suggests that mass flow does occur; now turbulent diffusivity values arrived at by either method will not account for the two transport mechanisms. Fortunately, from an operational point of view, our lack of understanding and the incorrectness of the estimates of vertical diffusivity have little effect on outcome in a uniform crop. It is serious in a multistory forest, however (*17*).

Figure 5 compares the vertical diffusivity predicted by SPAM and values computed from measurements of energy balance (*18*). The latter's odd variation with height is dictated by the measured constant temperature and water vapor in midstand, as well as by the measured added airflow at the base. We have already shown, however, that the additional mean airflow at the base does not appreciably alter the other predicted profiles. Thus, unexplained traits of fluid dynamics are at work both in the midcanopy and at the bottom (*18, 19*).

At the base of the canopy, errors in the temperature and water vapor profiles are traceable to a relatively small error in predicting net radiation and to a large error in predicting soil surface moisture or water potential. Although we have measured soil moisture beneath the surface, we have not been able to predict soil surface moisture in Ellis Hollow. Over 50 percent of the soil surface is occupied by flat stones, which create an abnormally hot, dry surface in the daytime, despite adequate and measurable moisture below the surface.

Stones are only part of the problem, however. SPAM estimates vapor pressure at the soil surface from the water potential of the soil, in a range where vapor pressure is substantially less than saturation. In this situation, the vapor flux is influenced by the dynamic time and space distributions of the heat and water fields below the surface. We have not as yet incorporated enough theory into SPAM to be able to deal with this complexity. Error in estimating carbon dioxide evolution at the base of the canopy has little effect on outcome.

Despite inadequacies in theories of fluid dynamics and soil moisture, the prediction of the stand's climate is probably sufficient from a biological point of view.

Figure 6 shows the corn crop's behavior on the ideal day, comparing SPAM output fluxes from the entire stand to energy balance fluxes from real data. In Fig. 6, a and b, we present a sensitivity test for wet and dry soil surface and for partially closed and open stomates. We put into SPAM two fixed values for soil moisture and two fixed values for minimum stomatal resistance. Figure 6c has real minimum stomatal resistance values in SPAM, but a fixed input of soil moisture values for the day. Comparisons of a case in which there is no moisture stress, when corn stomates are wide open (minimum stomatal resistance = 0.97 second per centimeter), to a case in which there is mild moisture stress, when the stomates are partially closed (minimum stomatal resistance = 5.2 seconds per centimeter), are given in Table 1. When the stomates are partially closed, the latent heat flux is reduced for the day from 350 to 200 calories per square centimeter, or by 43 percent, and the sensible heat flux is increased from 57 to 204 calories per square centimeter per day. Net photosynthesis was reduced 37 percent. Reducing the soil surface moisture from a damp −600 bars to a dry −8000 bars reduced latent heat flux 38 percent and net photosynthesis 6 percent. Sensible heat flux increased from 57 to 171 calories per square centimeter per day.

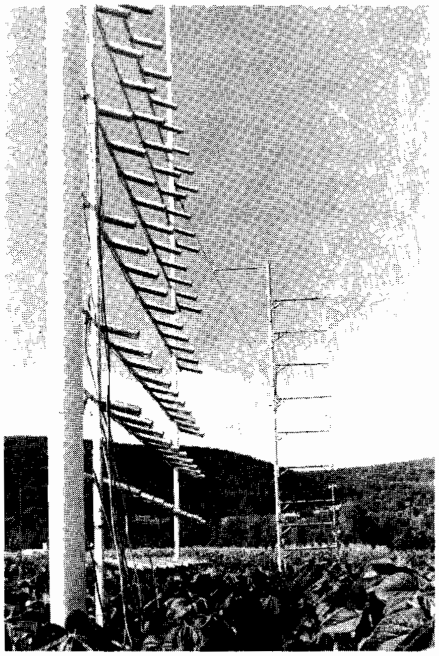

Fig. 4. Equipment used to measure air temperature, water vapor, carbon dioxide concentration, and wind speed at various heights in and above uniform agricultural crops (soybeans shown here). Measurements are used to calculate items (photosynthesis, transpiration, and sensible heat exchange) in the energy balance, where the source is solar radiation.

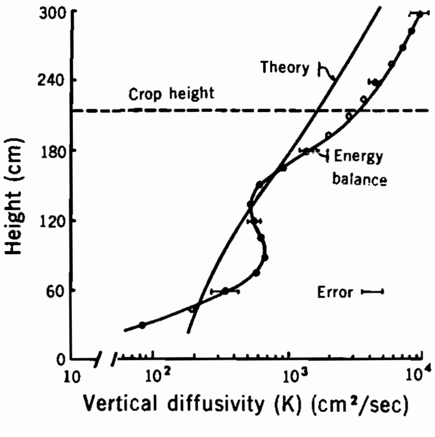

Fig. 5. Measured energy balance profiles of vertical diffusivity (*K*) (circles and solid line) and model prediction (solid line) from momentum balance. (18 August 1968; 11:45 a.m. to 12:15 p.m., Eastern Standard Time.)

It is obvious from Table 1 that both soil surface wetness and stomate status greatly influence the diversion of the sun's energy into latent or sensible heat. Again, we cannot overstress the importance of these factors.

Stomates also control net photosynthesis, but soil surface moisture has only a small influence here—through the effect of temperature on respiration.

Putting in SPAM the real stomate resistance values for the day yields a prediction of net photosynthesis that agrees with the energy balance measurement. (This gives us confidence that SPAM is working well.) However, we have more difficulty in predicting latent and sensible heat because soil surface moisture is difficult to predict. By putting a fixed dry soil surface of −8000 bars into SPAM, we get, in the morning, latent and sensible heat fluxes that are close to the mark (*20*). In the afternoon, however, SPAM underestimates latent heat flux, a fact that indicates a wetter effective surface or a lesser water potential, such as −1200 bars. This makes sense because the soil is heated in the afternoon, thus raising effective vapor pressure.

In the long run, the prediction of stomate status under a deficit of moisture is probably far more difficult than is the prediction of soil moisture. Figure 7 shows the complex trend in stomatal resistance, during the test day of moderate stress. We know from experience that, with no stress, stomatal resistance would approximately follow the prediction curve (solid line). Since the leaves had undergone previous stress, they exhibited a sluggishness in early morning (not opening completely until 0.14 light

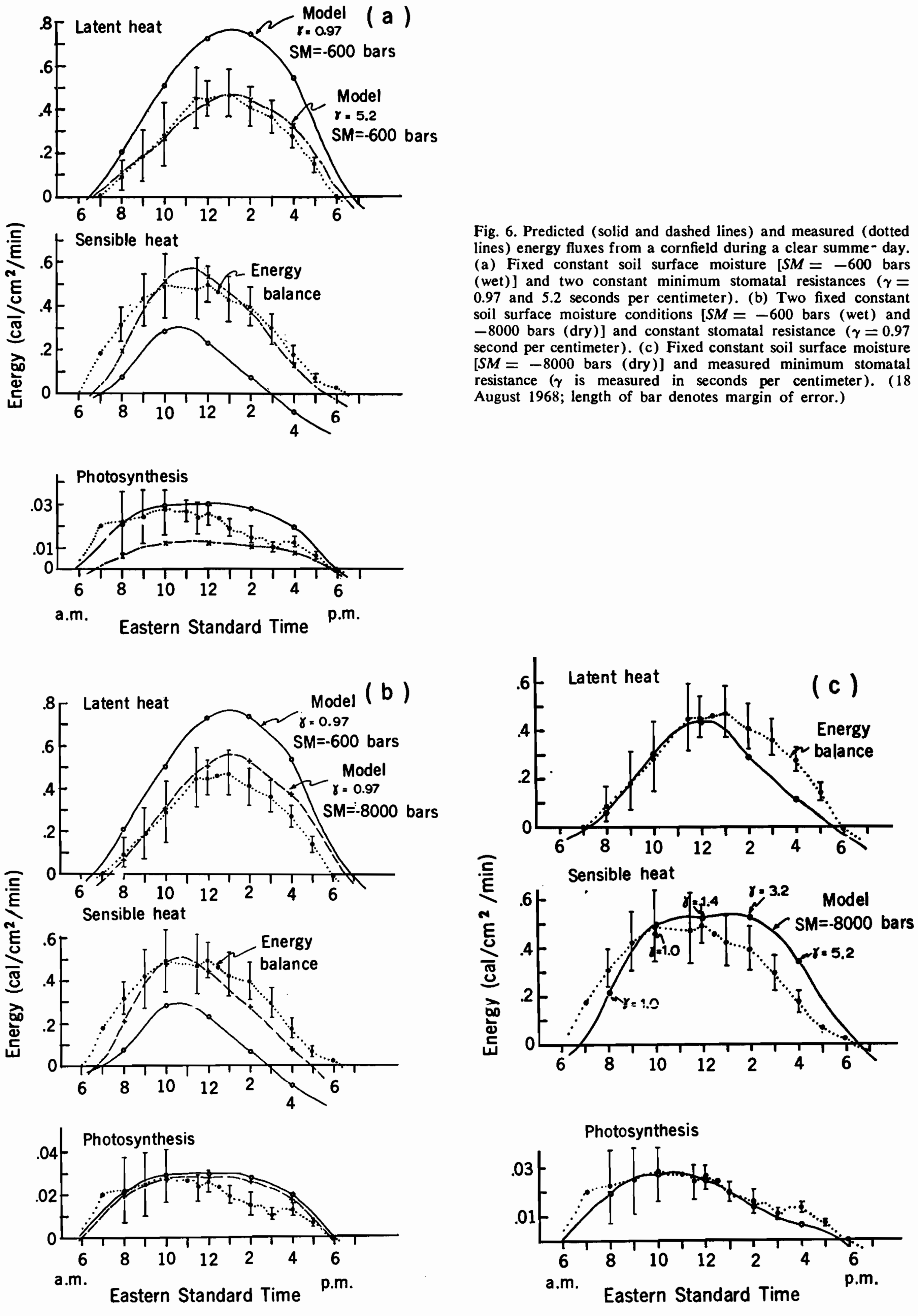

Fig. 6. Predicted (solid and dashed lines) and measured (dotted lines) energy fluxes from a cornfield during a clear summer day. (a) Fixed constant soil surface moisture [*SM* = −600 bars (wet)] and two constant minimum stomatal resistances ($\gamma = 0.97$ and 5.2 seconds per centimeter). (b) Two fixed constant soil surface moisture conditions [*SM* = −600 bars (wet) and −8000 bars (dry)] and constant stomatal resistance ($\gamma = 0.97$ second per centimeter). (c) Fixed constant soil surface moisture [*SM* = −8000 bars (dry)] and measured minimum stomatal resistance (γ is measured in seconds per centimeter). (18 August 1968; length of bar denotes margin of error.)

unit at 8 a.m., Eastern Standard Time), despite ample water. Shortly after noon, the stomates closed because of a shortage of water. They regained some water later in the afternoon and reopened at 0.08 light unit at 5 p.m. At sundown they closed. All of these observations indicate that stomates have more than one complex feedback system to control opening and closing. Indeed, we know that light, water, leaf temperature, and carbon dioxide are involved, as well as aging and hormonal control (*21*).

Can we rely on SPAM's predictions in Fig. 6, knowing that we do not understand the fluid dynamics of canopy flow and that errors can be hidden by our assuming values for soil surface moisture? We can hazard a cautious "yes," based upon three arguments: (i) predictions of net photosynthesis are fairly accurate, where here we know SPAM is relatively insensitive to soil surface wetness; (ii) latent and sensible heat, which are sensitive to soil surface wetness, respond diurnally in a consistent manner; and (iii) the predictions are what one would expect, judging from previous experiments (*22*).

Adding Carbon Dioxide to the Plant Community

Two important questions have been raised about the plant community's response to increased concentrations of carbon dioxide: one is agricultural, the other geophysical. In intense light, the photosynthesis of individual leaves is increased by adding carbon dioxide to the atmosphere. The successful addition of carbon dioxide to plants in greenhouses has raised the question of whether it is feasible to fertilize out-of-doors crops with carbon dioxide. Man has long known that animal manures benefit crops, but generally these benefits have been attributed to the added mineral nutrients and the physical conditioning of the soil rather than to the resulting evolution of carbon dioxide. The possibility of cheap sources of carbon dioxide, either from sewage disposal and feed lot wastes or from industrial byproducts and natural underground reservoirs, has stimulated interest in using it for agriculture. From a geophysical point of view, an increase in global net photosynthesis, caused by the increase of atmospheric carbon dioxide from fossil fuel burning, may affect long-term changes in climate (*23*). Increasing net photosynthesis should lessen the present rate of increase of atmospheric carbon dioxide (*24*). Quantitative knowledge of the phenomenon could help project long-term effects.

With reasonable confidence in SPAM's predictions of net photosynthesis, our colleagues have experimented with the model to gauge the effects of additional carbon dioxide on the net photosynthesis of four hypothetical plant communities that differ in density and leaf angle (*25*). The simulations were not concerned with whether carbon dioxide causes stomates to close and consequently to conserve water (*26*).

Results were obtained by adding carbon dioxide from the soil at a normal rate under field conditions (10 kilograms per hectare per hour). This rate was increased to a maximum of 450 kilograms per hectare per hour, which would be possible only by releasing carbon dioxide from a grid system of pipes. Even at this high rate of release, the concentrations of carbon dioxide in the air around the upper, active parts of the crop canopies was increased by only about 50 parts per million in the open canopies (leaf area index = 4) and 150 parts per million in the dense canopies (leaf area index = 10) (the average carbon dioxide content of the atmosphere is about 320 parts per million). Adding large amounts [for example, 30 metric tons (dry weight) per hectare per year] of animal manure or solid wastes from sewage disposal systems to crops would only double the normal carbon dioxide release rates. This would scarcely affect concentrations of carbon dioxide in the actively photosynthesizing parts of a plant community.

From the simulations, we draw the following general conclusions:

1) Carbon dioxide fertilization in tremendous quantities can, at best, increase midday photosynthesis 45 percent; on a daily basis this would probably amount to no more than 10 to 20 percent. Adding large amounts of decaying organic matter would have almost no direct effect because atmospheric mixing is so vigorous a diffusion process. SPAM showed that, under the highest rate of release, 60 to 80 percent of the added carbon dioxide was lost to the atmosphere. On the other hand, under normal soil flux densities, the atmosphere supplied 80 to 90 percent of the crop needs.

If the reported increase (0.7 part per million per year) of atmospheric carbon dioxide from burning fossil fuels continues unabated for 100 years, we estimate that plant communities, under the best of conditions, will be photosynthesizing at a rate about 10 to 20 percent higher than today's.

2) Wind has a significant influence

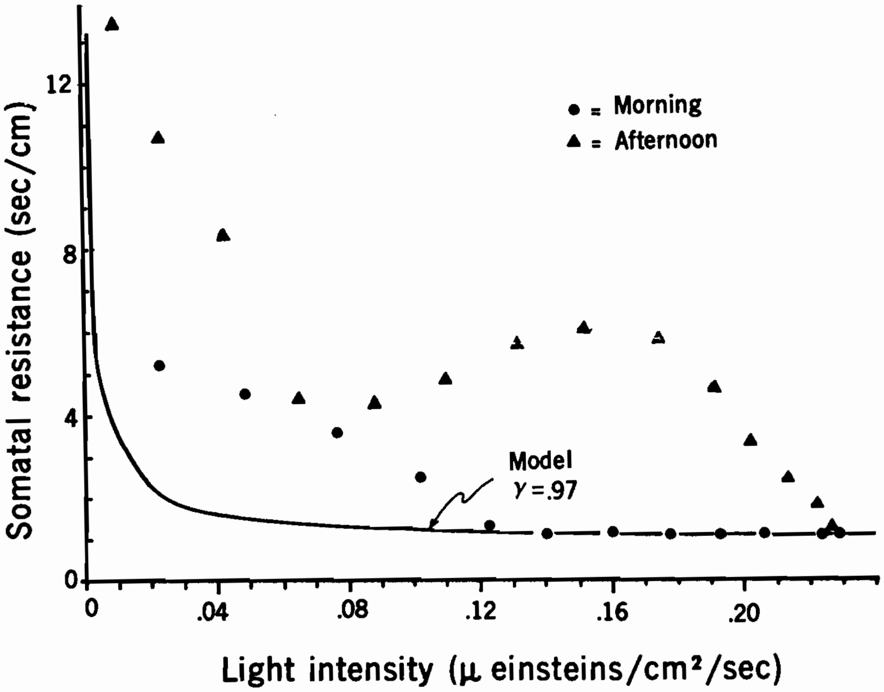

Fig. 7. Stomate light response of corn leaves under mild water stress (data points). Resistance to gas diffusion through stomates is r_s (measured in seconds per centimeter). Solid line is prediction curve for the no-stress case, when corn stomates are wide open under bright sunlight [γ minimum stomatal resistance) = 0.97]. Wet leaf r_s = 0 second per centimeter (18 August 1968).

on carbon dioxide supply to plant surfaces, especially in dense vegetation. Thus, designing plant communities to enhance airflow has merit for carbon dioxide supply as well as for heat dissipation.

3) Structure of the community had the greatest effect in the computer experiment. This points out both the danger and the strength of computer modeling experiments. The danger lies in ignoring the specifications and restrictions of one's experiment in extrapolating answers to the real world. The strength of the model lies in its capability for evaluating the significance of isolated, individual parameters under "controlled conditions" that would be logistically impossible to achieve in nature. The answers from SPAM about leaf angle response were probably reasonable for the imaginary plant stands used and the conditions set. It would be wrong to conclude, for example, that a real crop with all of its leaves tipped up 80° from the horizontal would do 40 to 60 percent better than one with all of its leaves tipped up 40°. The interplay between sun angle and leaf angle throughout the day and the season and the variation with latitude, as well as with other geometric features, rule against any simple blueprint (*27*). In all likelihood, no one structure can be "ideal"; rather, it will vary with climate, crop, latitude, and time of year. From an engineering point of view, it would be increasingly difficult, as leaf angle increases, to realize uniform distribution of leaves; that is, 80° leaves would "cluster" around the stem, thus shading one another.

Summary

After extensive field experiments, we developed SPAM, a comprehensive mathematical model that simulates energy and material exchange in the plant-air layer at the earth's interface. The model is based upon the conservation of energy, where the sun is the driving force. Our understanding and deficiencies were gauged initially by testing model predictions against actual experience with a relatively simple system—a cornfield. Climatic predictions are physically and biologically good enough for many applications, but they reveal inadequacies in our understanding of the fluid dynamics of airflow within the plant stand. Our present inability to measure or predict the degree of wetness of the soil surface hampers correct prediction of evaporation. Probably the most difficult problem to resolve is that of predicting how stomates open and close under drought stress, thus affecting both evaporation and photosynthesis in leaves. Along with resolution of these problems, the basic framework of the model can be adapted to more complex systems in nature, where variability is much greater than in an agricultural crop. The model in its present form can be used, with caution, as a powerful tool to help man order his priorities of plant community traits for whatever outcome he desires, be it food production, nature and water conservation, climate modification, or esthetic enjoyment.

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28. We thank the many people who have contributed in the team effort over the years, especially George Drake, Michael Johnson, L. H. Allen, Jr., and Winton Covey. Professors R. B. Musgrave and C. B. Tanner have also contributed much through their cooperation and stimulating discussions. Cornell University Agronomy Department Series Paper No. 931. This article is a contribution of the Northeast Branch Soil and Water Conservation Research Division, Agricultural Research Service, U.S. Department of Agriculture, in cooperation with the New York Agricultural Experiment Station at Cornell University, Ithaca.