A Model of Photosynthesis for Desert Species

E. G. Brittain

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A MODEL OF PHOTOSYNTHESIS FOR DESERT SPECIES

E. G. Brittain
Australian National University
Canberra

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GENERAL INTRODUCTION

Several models of photosynthesis of varying resolution levels and to differing degrees of completion have been prepared.

At a meeting of experimental workers and modellers held in Logan on October 5, 1972, it appeared that there was a general desire for two classes of models, one suitable for plants which possess crassulacean acid metabolism and one for other plants. Within these two divisions, two levels of complexity were also desirable. I decided upon three levels of complexity, resulting in a plan for a potential of six models.

Data for plants with non-crassulacean acid metabolism (*Artemisia tridentata*) came to hand immediately after the meeting and these were used to prepare models for this class of plant. The first and second level models have been completed, debugged and given limited exercise. Their outputs are presented later. The third level model is coded and hopefully may be debugged and running also.

Data for *Ambrosia dumosa* have since arrived but there will not be time to utilize them. At a suitable place in the model descriptions it will be indicated where and how they should be utilized.

Data for plants with crassulacean acid metabolism have been received but the models in this area have been taken only to a preliminary stage. At the lowest level of complexity, a model has been coded and recorded on Fastrand, but it lacks driving data and so cannot be debugged at present. The second and third levels of complexity have been taken only to the box and arrow diagram stage. The data would permit further development of these models, but time does not.

The data used in devloping these models were collected and provided by M. M. Caldwell and E. De Puit (*Artemisia tridenta*); S. Bamberg (*Ambrosia dumosa*); and I. Ting (crassulacean acid metabolism plants).

Symbology used for these models is as follows:

Level	Non-CAM	Stage reached	CAM	Stage reached
First	PHOTO1	running	PHOTO2	coded
Second	PHOTO3	running	PHOTO4	planned
Third	PHOTO5	running?	PHOTO6	planned

SUBMODEL PHOTO1

First level of resolution, non-CAM plants.

INTRODUCTION AND SIMPLIFYING ASSUMPTIONS

This model considers photosynthesis as the net flow of carbon from the atmospheric pool into the plant (see PHOTO1 diagram). Respiration, the reverse direction flow, is not considered explicitly. The only factors considered to influence the net flow of carbon are irradiance, temperature, plant water potential, and phenological stage. The temperature used is air temperature.

VERBAL DESCRIPTION -- WORD MODEL

The driving variables consist of experimental data on the effects of irradiance, temperature and plant water potential at several phenological stages on the photosynthesis of *Artemisia tridentata* at Green Canyon (near Logan, Utah) in 1971. Radiation is supplied as daily totals of photosynthetically active radiation (global radiation, solar and scattered x 0.47) measured above the Natural Resources-Biology building at Utah State University in 1971.

There are two state variables, the atmospheric pool of CO_2 and the photosynthate. Since the first of these is

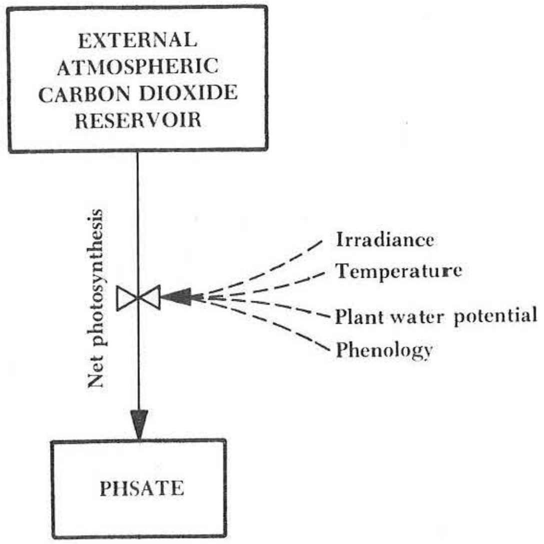


PHOTO1

effectively infinite in size and since variations in CO_2 concentration are not considered to influence the net flow, it is not explicitly modelled although it is conceptually necessary. The second state variable is contained within the calling routine VEGET where it is called PHSATE. Hence this subroutine effectively only calculates the rate of the net flow of carbon, PSRATE.

There is one process, net flow of carbon, and this is considered to be controlled by four information flows. These are irradiance, temperature, plant water potential, and phenological stage. The effect of each of these factors is scaled from 0 to 1.

The last of these, phenological stage, is provided for by supplying the driving data in sets, each set applying to one particular phenological stage. These stages are identified by the subscript (M) and the cycling through the values of (m), (8) is provided within VEGET. Thus no equation for the effect of phenology is provided.

The effect of irradiance is provided for by an equation which relates irradiance to rate of net photosynthesis, which is of the Michaelis-Menton form. The effect of temperature is obtained by interpolating linearly between data values, using the function subroutine AINT3. The effect of plant water potential is obtained in the same way. All three effects are expressed on the scale 0-1.

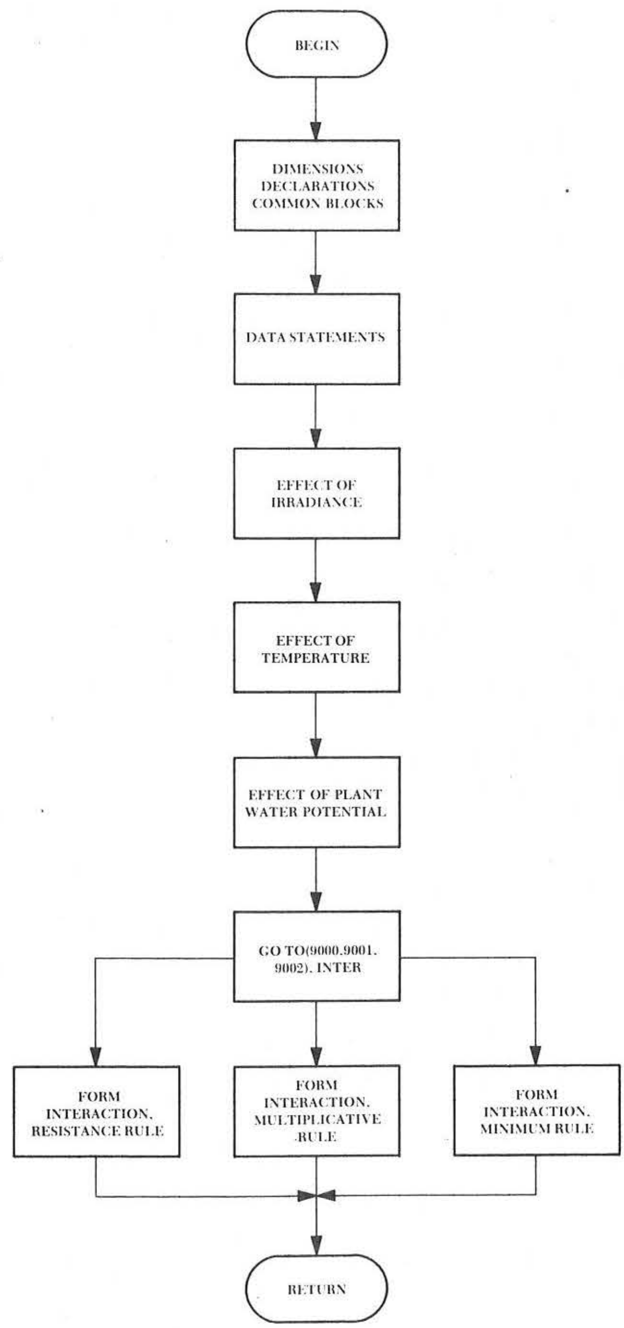
The interaction between these three controlling factors may be chosen from three possible alternatives. Which of these three alternatives is actually used depends on the value of INTER which is allotted in PHOTOSDATA.

When INTER = 1 the interaction is formed by regarding the three effects as conductances (in the electrical analogue sense). The overall conductance is given by taking the reciprocal of the sum of the reciprocal conductances, or the resistances. This overall conductance is then multiplied by the number of factors concerned (3) and by the maximum photosynthetic rate available in the data, expressed as g carbon/g protein carbon.

When INTER = 2 the interaction is formed by multiplying the three conductances together, i.e., the overall conductance is considered to be the product of the individual conductances. This product is then multiplied by the maximum photosynthetic rate as before.

When INTER = 3 the interaction is obtained by selecting the smallest of the three conductances and multiplying the maximum rate of photosynthesis available in the data by this. This applies the concept of limiting factors.

Since the available data are expressed in terms of rates per hour it was convenient to make all the calculations as rates per hour, multiplying the final rate by the photoperiod length in hours to obtain the daily rates. This has the advantage that it provides for the possibility of utilizing hourly values of irradiance, temperature and plant water potential if or when they should become available. This is done in other models of this series.



FLOW DIAGRAM

ALPHABETICAL LIST OF VARIABLE NAMES -- A USER-DEFINED FUNCTION FOR INTERPOLATING VALUES FROM A TABLE SUPPLIED

CURV = The curvature parameter for the photosynthesis irradiation curve, calories/cm^2/hr.
DAPHOT = The photoperiod, hours.
IDAY = The current time interval.
I = The counter for cohorts.
IRADF = The effect of irradiation on photosynthesis, 0-1.
IRRAD = The actual radiation (400-700) for the day, cal/cm^2.
IRRADM = The average radiation per hour for the day, cal/cm^2.
M = The counter for the phenological stage.
MNPHOT = Net photosynthesis calculated by the minimum rule, g C/g protein C/hr.
MTPHOT = Net photosynthesis calculated by the multiplicative rule, g C/g protein C/hr.
NFACT = The number of factors affecting the process.
NTPHOT = Net photosynthesis calculated by the resistance formula, g C/g protein C/hr.
PMAXI = The maximum rate of photosynthesis on the scale 0-1.
PMAXL = The maximum rate of photosynthesis available in the data, mg CO_2/dm $leaf^2$ (2 sides)/hr.
PMAXN = The maximum photosynthetic rate g CO_2/g protein C/day.
PSRATE = The photosynthetic rate, g C/g protein C/day.
PWPOT = The average plant water potential for the month, bars.
PWPOTF = The effect of plant water potential on photosynthesis, 0-1.
PWPX = The set of X values for the PWP data, bars.
PWPY = The corresponding set of Y values, 0-1.
TDAY = The average daytime temperature, °C.
TEMPF = The effect of temperature on photosynthesis, 0-1.
TEMPX = The set of X values for the effect of temperature on photosynthesis (DATA), °C.
TEMPY = The corresponding set of Y values, 0-1.

SUBMODEL PHOTO 2

First level of resolution, CAM plants.

INTRODUCTION AND SIMPLIFYING ASSUMPTIONS

In this model, only the net flow of carbon from the atmosphere into the plant is considered, where it is regarded as being a part of the organic acid pool. Thus it concerns itself only with CO_2 fixation, which in CAM plants is a "dark" process, and decarboxylations and subsequent photosynthesis of released CO_2 are regarded as internal rearrangements within the internal pool of carbon compounds. If this results in loss of CO_2, this loss will be accounted for by the use of net uptake.

The net uptake of CO_2 is modelled as being influenced by irradiance (which in this case means its effect on stomatal aperture, not on photosynthesis), temperature, plant water potential, and the size of the organic acid pool.

VERBAL DESCRIPTION -- WORD MODEL

The data from Dr. Ting arrived too late to be used. Hopefully it will be possible to replace that being used (which is not relevant, being carried over from PHOTO1) with Dr. Ting's data.

The program as it stands is to be regarded as a sketch or illustration of an idea, which may need to be changed to fit the data which are actually to be used. In it, the effect of irradiation (IRADF) is read from a table of supplied data by

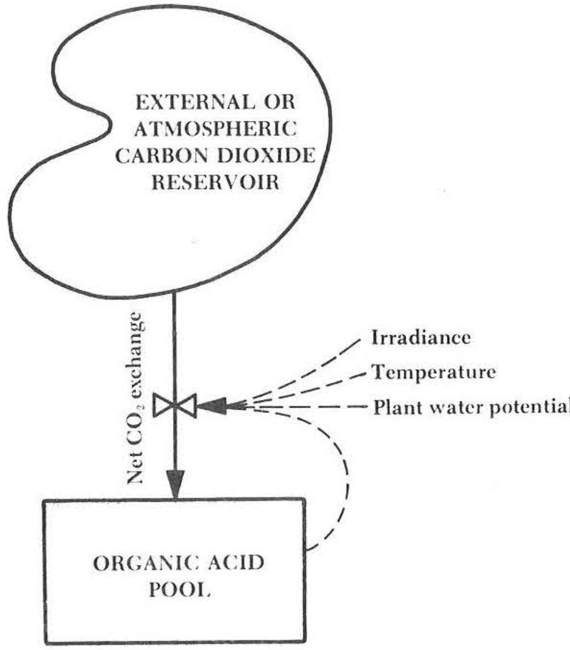


PHOTO2

the interpolation routine, AINT3. So are the effects of temperature (TEMPF) and of plant water potential (PWPOTF). The effect of the organic acid pool size (ORAGCF) is modelled as a descending curve from the maximum value (1) at zero pool size to minimum (0) at a pool size of 1.0 g C/g protein C(value of BBB). The curve is a generalized Poisson density function, the parameters of which may be varied to match the curve to data if it becomes available. However, such data may be hard to obtain and the curve may need to be shaped on theoretical grounds. The organic acid pool is accumulated and used as a parameter in the equation. The four factors are combined as in the other models of the series by means of a choice of three interaction mechanisms, the resistance formula, the multiplicative rule and the minimum rule.

ALPHABETICAL LIST OF VARIABLE NAMES

AAA = The photosynthate level at which photosynthesis is maximal.

AINT3 = A user-defined function for interpolating values from a table supplied.

FXMAXL = The maximum rate of fixation available in data.

FXMAXN = The maximum rate of fixation g CO_2/g protein C/day.

DAPHOT = The photoperiod, hours.

I = The counter for cohorts.

IDAY = The current time interval.

INTER = The integer label used in VEGET to select the interaction which is to be used: 1 = resistance formula; 2 = multiplicative rule; 3 = minimum rule.

IRADF = The effect of irradiation on photosynthesis, 0-1, leaf.

IRRAD = The actual radiation (400-700) for the day, cal/cm^2.

IRRADM = The average radiation per hr for the day, cal/cm^2.

M = The counter for the phenological stage.

MNFIX = Net fixation calculated by the minimum rule, g C/g protein C/hr.

MTFIX = Net fixation calculated by the multiplicative rule, g C/g protein C/hr.

NFACTP = The number of factors influencing photosynthesis.

PWPOT = The average plant water potential for the month, bars.

PWPOTF = The effect of plant water potential on photosynthesis, 0-1.

PWPX = The set of X values for the PWP data, bars.

PWPY = The corresponding set of Y values, 0-1.

RSFIX = Net fixation calculated by the resistance formula, g C/g protein C/hr.

TDAY = The average daytime temperature, °C.

TEMPF = The effect of temperature on photosynthesis, 0-1, respiration.

TEMPX = The set of X values for the effect of temperature on photosynthesis (data) °C.

TEMPY = The corresponding set of Y values, 0-1.

ZZZ = An intermediate variable defined in the context of use.

SUBMODEL PHOTO3

Second level of resolution, non-CAM plants.

INTRODUCTION AND SIMPLIFYING ASSUMPTIONS

This model considers influx of carbon dioxide into the leaf as well as efflux from it, gross photosynthesis and dark respiration (see PHOTO3 diagram). Photorespiration is assumed to be present and net photosynthesis is obtained as the algebraic sum of gross photosynthesis and dark respiration. The temperature used is air temperature.

VERBAL DESCRIPTION -- WORD MODEL

The driving variables consist of experimental data on the effects of irradiance, temperature and plant water potential at several phenological stages on the photosynthesis of *Artemisia tridentata* at Green Canyon in 1971. Radiation is supplied as daily totals of photosynthetically active radiation (global radiation, solar and scattered x 0.47) measured above the Natural Resources-Biology building at

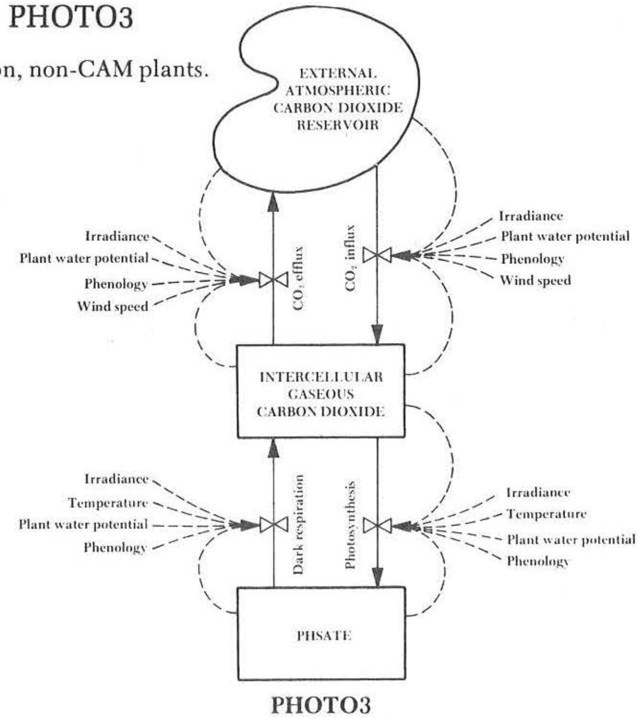


PHOTO3

USU in 1971. Wind speed used is that supplied by EXOGEN as DWINAV.

There are three state variables; the atmospheric pool of CO_2, intercellular gaseous CO_2 and the photosynthate. Since the first of these is effectively infinite in size, its magnitude is not monitored but is regarded as a constant. The third state variable is contained within the calling routine VEGET where it is called PHSATE. It is therefore not updated in this subroutine.

Carbon dioxide efflux and influx are both controlled by the same information flows, internal and external CO_2 concentrations, irradiance, plant water potential, wind speed, and phenological state. These controls are all assumed to act via the same mechanisms for efflux and influx, the only difference being the difference of direction of the flow. All controls are scaled from 0-1.

The effect of phenological stage is provided for by supplying the driving data in sets, each set applying to one particular phenological stage. These stages are identified by the subscript (M), and the cycling through the values of (M), (8) is provided within VEGET. Thus no equation for the effect of phenology is provided.

The effect of irradiance is provided as a linear increase of CO_2 flow as irradiance increases from 0 to 5 calories/cm^2/hr, the flow varying from 0 to 1 in this range. At levels of irradiance above this the rate of flow is set equal to 1. This amounts to assuming that stomatal resistance decreases linearly with irradiance from 0 to 5 calories/cm^2/hr at which level it is nonlimiting. This is, of course, a simplification of the probable state of affairs and is a point at which refinement might be introduced if the necessary data became available.

The effect of wind speed is handled as a linear increase of flow of carbon dioxide from 0.01 to 1 as the wind speed increases from 1 km/hr to 20 km/hr. Below 1 km/hr, wind speed is considered to be without effect but this does not prevent passage of CO_2 as would be implied by use of the factor 0. Instead, the factor 0.01 is employed as an estimate of the rate of passage of CO_2 to or from the bulk air by diffusion alone. Between wind speeds of 20 km/hr and 40 km/hr no change in rate of CO_2 passage occurs, but above this speed, a step function is employed to reduce passage of CO_2 drastically, simulating stomatal closure. The use of the factor 0.000001 simulates cuticular diffusion under these conditions.

Since no data are available for the effect of plant water potential on carbon dioxide efflux and influx, a simple linear relationship is assumed, with a negative slope from the value of 1 at 0 plant water potential to 0 at plant water potential of -30 bars.

The effects of external and internal concentrations of gaseous CO_2 are handled by calculating the differential and using the Ohm's law analogy, the resistance used being the reciprocal of the effect of irradiation, which is equivalent to stomatal aperture.

Dark respiration is regarded as being controlled by irradiance (photorespiration), temperature, plant water potential, photosynthate level, and phenological status. Phenological status is handled by the method already described.

Photorespiration has been assumed to be related to irradiance by a Michaelis-Menton curve, plateauing at 30 calories/cm^2/hr and reaching half the maximum rate at 6 calories/cm^2/hr.

The effects of temperature and of plant water potential are documented in the data provided by Caldwell and DePuit. Use is therefore made of the interpolation routine to read suitable values for these factors from the data.

The effect of photosynthate level on dark respiration has also been assumed to follow Michaelis-Menton kinetics with a maximum rate at 1.0 g C/g protein C and half the maximum rate at 0.02 g C/g protein C.

Photosynthesis is controlled in this model by irradiance, temperature, plant water potential, phenology, intercellular gaseous CO_2 concentration, and level of photosynthate.

The effect of irradiance is a hyperbolic curve with half the maximum rate being reached at 10.0 calories/cm^2 for phenological stages 1 and 3 to 8, 16.6 calories /cm^2 at phenological stage 2 (data of Caldwell and De Puit).

The effects of temperature and of plant water potential are read from data tables by means of the interpolation routine.

The effect of photosynthate level is modelled as a curve which falls from 1 at 0 photosynthate, to 0 at a photosynthate level of 1.0 g C/g protein carbon, following the curve of a generalized Poisson density function.

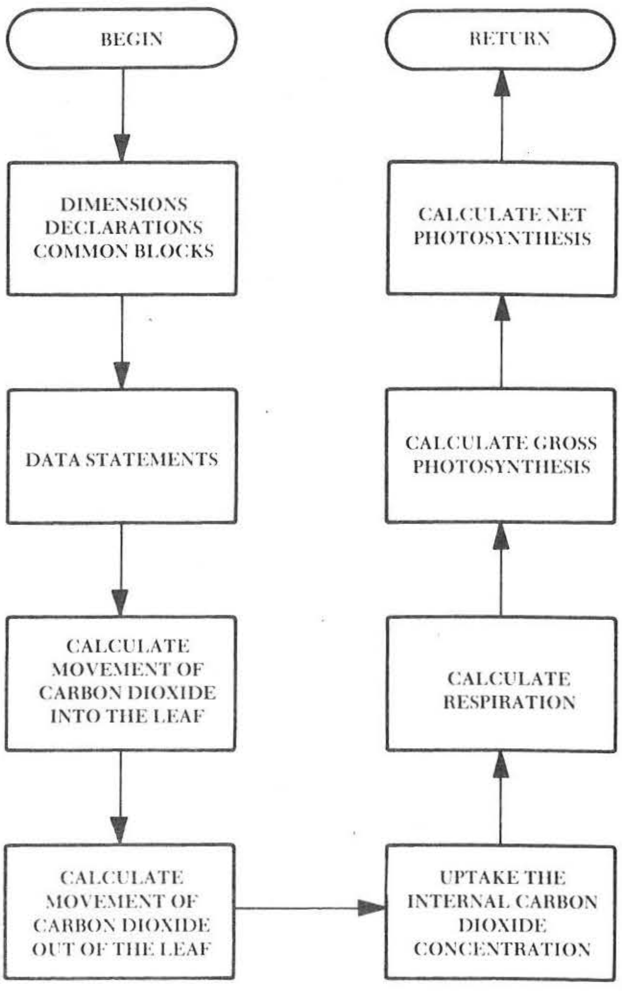
The effect of internal CO_2 concentration is handled as a hyperbolic function with half the maximum rate being reached at 6×10^{-7} g C/g protein C.

In all cases, the interaction between the various controlling factors may be chosen (by means of the value allotted to INTER in PHOTOSDATA) from the resistance rule, the multiplicative rule or the minimum rule. Reference should be made to the documentation of PHOTO1 for details.

The relationship between net and gross photosynthesis has been handled in the following way. The data for photosynthesis are always for net photosynthesis. However, data for dark respiration are also available. Therefore, gross photosynthesis has been calculated as net photosynthesis plus dark respiration for the duration of the photoperiod. The net photosynthetic rate which is provided as final output is then calculated as the gross photosynthesis minus the dark respiration for the whole 24 hr.

ALPHABETICAL LIST OF VARIABLE NAMES

AAA = The photosynthate level at which photosynthesis is maximal.
AINT3 = A user-defined function for interpolating values from a table supplied.
BBB = The level of photosynthate in the leaves at which photosynthesis is reduced to zero.
CCC = See DDD



FLOW DIAGRAM

CO2IRT = Rate of movement of CO_2 into leaf, g C/g protein C/hr.
CO2ORT = Rate of movement of CO_2 out of the leaf, g C/g protein C/hr.
CURV = The curvature parameter for the photosynthesis/irradiation curve.
DAPHOT = The photoperiod, hours.
DCO2 = The differential CO_2 concentration inside/outside the leaf.
DCO2F = The effect of CO_2 differential on movement of CO_2 into or out of the leaf.
DDD = Shape parameters for the curve of photosynthesis/photosynthate.
I = The counter for cohorts.
ICO2PF = The effect of internal CO_2 concentration on photosynthesis, 0-1.
IDAY = The current time interval.
INCO2 = Amount of CO_2 inside the leaf air spaces, g C/g protein C.
INCO2C = Concentration of CO_2 in leaf intercellular spaces, g C/ml.
INTER = The integer label used in VEGET to select the interaction which is to be used: 1 = resistance formula; 2 = multiplicative rule; 3 = minimum rule.
IRADF = The effect of irradiation on photosynthesis, 0-1.
IRADIF = Effect of irradiation on rate of movement of CO_2 into the leaf.
IRADOF = The effect of irradiation on movement of CO_2 out of the leaf.
IRRAD = The actual radiation (400-700) for the day, cal/cm^2.
IRRADM = The average radiation per hour for the day, cal/cm^2.
M = The counter for the phenological stage.
MNCO2I = Rate of movement of CO_2 into leaf calculated using the minimum rule.
MNCO2O = Rate of movement of CO_2 out of leaf calculated using the minimum rule.
MNPHOT = Net photosynthesis calculated by the minimum rule, g C/g protein C/hr.
MTPHOT = Net photosynthesis calculated by the multiplicative rule, g C/g protein C/hr.
MNRESP = Respiration calculated by the minimum rule.
MTCO2I = Rate of movement of CO_2 into leaf calculated using the multiplicative rule.
MTCO2O = Rate of movement of CO_2 out of leaf calculated using the multiplicative rule.
MTRESP = Respiration calculated by the multiplicative rule.
NEWPHL = New photosynthate in the leaf, g C/g protein C.
NFACTI = The number of factors influencing movement of CO_2 into a leaf.
NFACTO = The number of factors affecting movement of CO_2 out of the leaf.

NFACTP = The number of factors influencing photosynthesis.
NFACTR = The number of factors influencing respiration.
OUTCO2 = The external air CO_2 concentration, g/mg.
PMAXI = The maximum rate of photosynthesis on the scale 0-1.
PMAXL = The maximum rate of photosynthesis available in the data, mg CO_2/dm^2 leaf (2 sides/hr.
PMAXN = The maximum photosynthetic rate g CO_2/g protein C/day.
PSATPF = The effect of concentration of photosynthate in the leaf on photosynthesis, 0-1.
PSAIRF = The effect of photosynthate level on respiration.
PSRATE = The photosynthetic rate, g C/g protein C/day.
PWPIF = Effect of plant water potential on rate of movement of CO_2 into the leaf.
PWPOT = The average plant water potential for the month, bars.
PWPOTF = The effect of plant water potential on photosynthesis, 0-1.
PWPRF = The effect of plant water potential on respiration.
PWPX = The set of X values for the PWP data, bars.
PWPY = The corresponding set of Y values, 0-1.
RMAXI = Maximum rate of respiration, 0-1.
RMAXL = Maximum rate of respiration in the data, mg CO_2/mg leaf/hr.
RMAXN = Maximum rate of respiration, g C/g protein C/day.
RSCO2I = Rate of movement of CO_2 into the leaf calculated by the resistance formula.
RESCO2O = Rate of movement of CO_2 out of the leaf calculated by the resistance formula.
RSPHOT = Net photosynthesis calculated by the resistance formula, g C/g protein C/hr.
RSRATE = Dark respiration rate, g C/g protein C/day.
RSRESP = Respiration calculated by the resistance formula.
TDAY = The average daytime temperature, °C.
TEMPF = The effect of temperature on photosynthesis, 0-1.
TEMPRF = The effect of temperature on respiration.
TEMPRX = The data table of X values.
TEMPRY = The data table of Y values for the effect of temperature on respiration.
TEMPX = The set of X values for the effect of temperature on photosynthesis (data), °C.
TEMPY = The corresponding set of Y values, 0-1.
WINDAV = The average wind velocity for the day, km/hr.
WINDIF = Effect of wind on rate of movement of CO_2 into the leaf.
WINDOF = The effect of wind on movement of CO_2 out of the leaf.
ZZZ = An intermediate variable defined in the context of use.

SUBMODEL PHOTO5

Third level of resolution, non-CAM plants.

INTRODUCTION AND SIMPLIFYING ASSUMPTIONS

This model is developed from PHOTO 3 and is similar to it in many respects. However, the temperature of the photosynthetic organs is here simulated and, by the means of an internal loop, the simulation is run on an hourly basis. A by-product of the simulation of photosynthetic organ temperature is the estimation of transpiration rate. This might be of use elsewhere in the model.

VERBAL DESCRIPTION -- WORD MODEL

The driving variables consist of experimental data on the effects of irradiance, temperature and plant water potential at several phenological stages, on the photosynthesis of *Artemisia tridentata* at Green Canyon in 1971. Radiation is supplied as hourly totals of global radiation (solar and scattered) measured above the Natural Resources-Biology

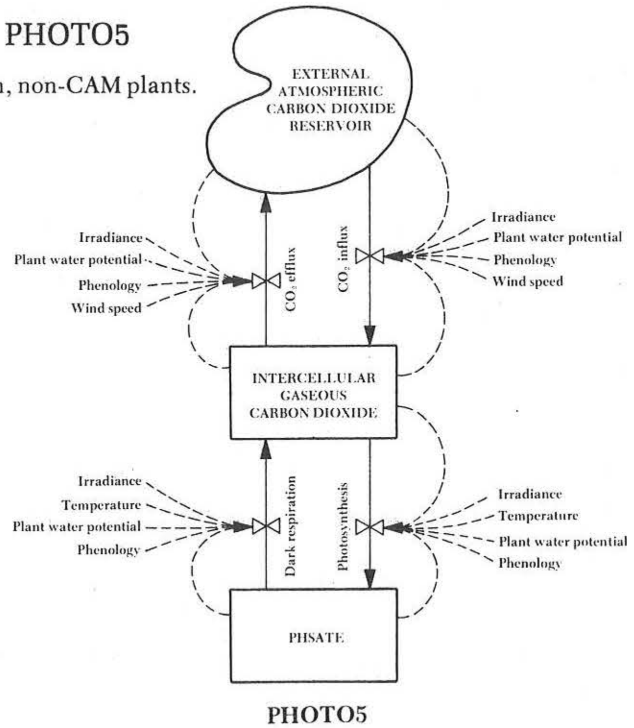
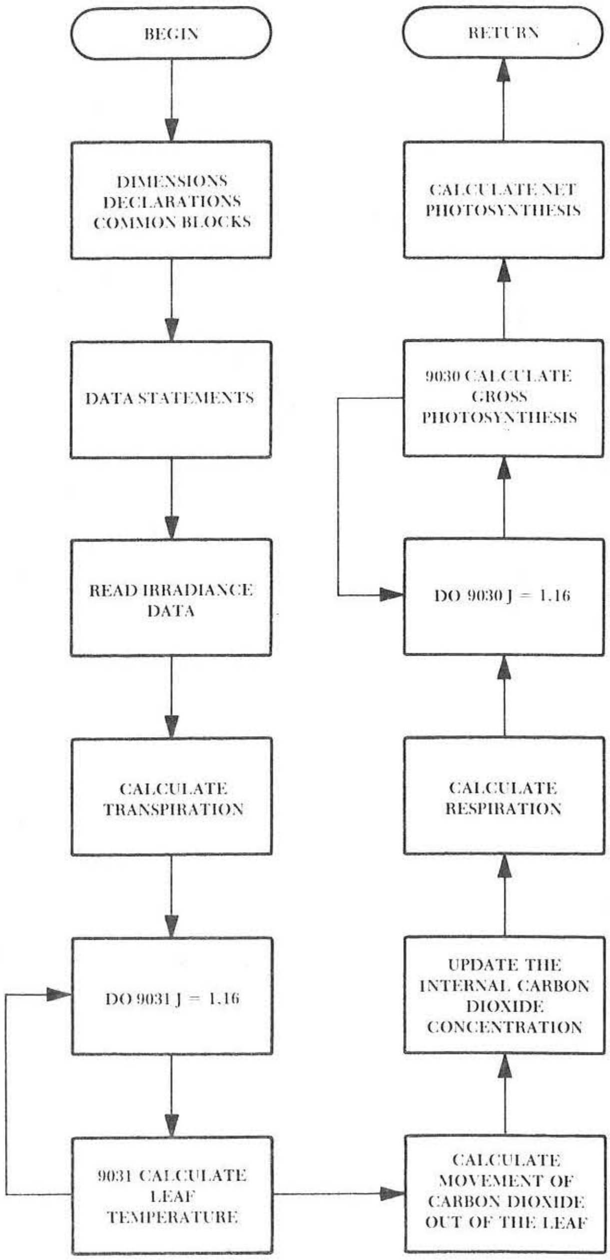


PHOTO5

building at USU in 1971. These data are stored in PHOTOSDATA and ready by this subroutine. Wind speed is that supplied by EXOGEN as DWINAV.

Data for emissivity of the leaf and of its surroundings, average leaf thickness and leaf area index are needed, as is the volumetric soil moisture. Since these are not immediately available, estimates of them have been made so that progress can be made, but attention should be given to these.



FLOW DIAGRAM

In order to calculate leaf or other photosynthetic organ temperatures it is necessary to know, among other things, the evaporative heat loss. This makes it necessary to first calculate transpiration. This is done here by means of Thornwaite's equation for evapotranspiration. Depending on the value of the evapotranspiration so calculated, a set of values for the parameters in an arctangent function are calculated and used to predict transpiration. The arctangent function itself is contained in the function subroutine ATANF.

The program then proceeds to the calculation of leaf temperature. The temperature of the photosynthetic organ TORG is initially set equal to air temperature. A loop is then entered in which first the initial heat content of the organ is calculated. Then the evaporative heat loss, the sensible heat loss, the long wave-length radiation from the leaf, and the radiation input are summed to obtain the heat gain of the organ. The heat content is obtained from the initial heat content plus the heat gain. Thence the temperature of the organ can be obtained from the heat content, the specific heat and the thickness of the organ. This loop is repeated for the 16 hr of the maximum photoperiod. The organ temperature so obtained is used elsewhere in the model in place of TDAY which is used in PHOTO1 and PHOTO3.

Although the effect of irradiance on photosynthesis is essentially the same in this model as in PHOTO3, in this case it is calculated from the hourly data for irradiation in another DO LOOP incremented for each of the 16 hr of the maximum photoperiod, which should improve the resolution of this section of the model significantly. Included in this DO LOOP is the calculation of new photosynthate, which is utilized as a modifying factor of the rate of photosynthesis. This should thus vary in its effect during the photoperiod in a realistic manner.

The remaining functions are identical with those used in PHOTO3, to which reference may be made.

ALPHABETICAL LIST OF VARIABLE NAMES

AAA = The photosynthate level at which photosynthesis is maximal.

AINT3 = A user-defined function for interpolating values from a table supplied.

ALAI = The leaf area index for the area being considered.

BBB = The level of photosynthate in the leaves at which photosynthesis is reduced to zero.

BLRES = Boundary layer resistance, sec/cm.

CCC = See DDD

CO2IRI = Rate of movement of CO_2 into leaf, g C/g protein C/hr.

CO2ORT = Rate of movement of CO_2 out of the leaf, g C/g protein C/hr.

CURV = The curvature parameter for the photosynthesis/irradiation curve.
CCURV = The curvature parameter for the curve relating CO_2 concentration to photsynthetic rate, g C/g protein C.
DAPHOT = The photoperiod, hours.
DCO2 = The differential CO_2 concentration inside/outside the leaf.
DCO2F = The effect of CO_2 differential on movement of CO_2 into or out of the leaf.
DDD = Shape parameters for the curve of photosynthesis/photosynthate.
DPHS = Daily photosynthesis g C/g protein C/day.
DPL = Diffusion path length, mm.
EHL = Evaporative heat loss, calories.
EMISL = The emmissivity of the leaf (=1.0).
EMISW = Emissivity of the surroundings of the leaf -- assumed = 1.0.
EVAPT = Evapotranspiration, mm.
HCORG = The heat content of the photosynthetic organs, calories.
HCORGI = The initial heat content of the organ, calories.
HGORG = The heat gain of the photosynthetic organs, calories.
HPHS = Hourly photosynthesis g C/g protein C/hr.
I = The counter for cohorts.
ICO2PF = The effect of internal CO_2 concentration on photosynthesis, 0-1.
IDAY = The current time interval.
INCO2 = Amount of CO_2 inside the leaf air spaces, g C/g protein C.
INCO2C = Concentration of CO_2 in leaf intercellular spaces, g C/ml.
INTER = The integer label used in VEGET to select the interaction which is to be used: 1 = resistance formula; 2 = multiplicative rule; 3 = minimum rule.
IRADF = The effect of irradiation on photosynthesis, 0-1.
IRADIF = Effect of irradiation on rate of movement of CO_2 into the leaf.
IRADOF = The effect of irradiation on movement of CO_2 out of the leaf.
IRRAD = The actual radiation (400-700) for the day, cal/cm^2.
IRRADA = The irradiance absorbed by the photosynthetic organs.
IRRADI = The irradiance incident on photosynthetic organs, cal/cm^2.
IRRADM = The average radiation per hour for the day, cal/cm^2.
LWR = Long-wave radiation from the leaf, calories.
M = The counter for the phenological stage.
MNCO2I = Rate of movement of CO_2 into leaf calculated using the minimum rule.
MNCO2O = Rate of the movement of CO_2 out of leaf calculated using the minimum rule.
MNPHOT = Net photosynthesis calculated by the minimum rule, g C/g protein C/hr.
MTPHOT = Net photosynthesis calculated by the multiplicative rule, g C/g protein C/hr.
MNRESP = Respiration calculated by the minimum rule.
MTCO2I = Rate of movement of CO_2 into leaf calculated using the multiplicative rule.
MNCO2O = Rate of movement of CO_2 out of leaf calculated using the multiplicative rule.
MTRESP = Respiration calculated by the multiplicative rule.
NEWPHL = New photosynthate in the leaf, g C/g protein C.
NFACII = The number of factors influencing movement of CO_2 into a leaf.
NFACTO = The number of factors affecting movement of CO_2 out of a leaf.
NFACTP = The number of factors influencing photosynthesis.
NFACTR = The number of factors influencing respiration.
OTCN = The thickness of the photosynthetic organ, mm.
OUTCO2 = The external air CO_2 concentration, g/ml.

SUBMODELS PHOTO4 AND PHOTO6

Levels 2 and 3, CAM plants.

At this stage there is no point in presenting more than the box and arrow diagram which was planned for use in these models. The general outline which is present in PHOTO3 and PHOTO5 will be applicable, and it is expected that it may be found advantageous, as in those models, to make a distinction between PHOTO4 which should run on a daily time step and PHOTO6 with an hourly time step. The variable names used in PHOTO2 will be found applicable, although no doubt others will also be needed.

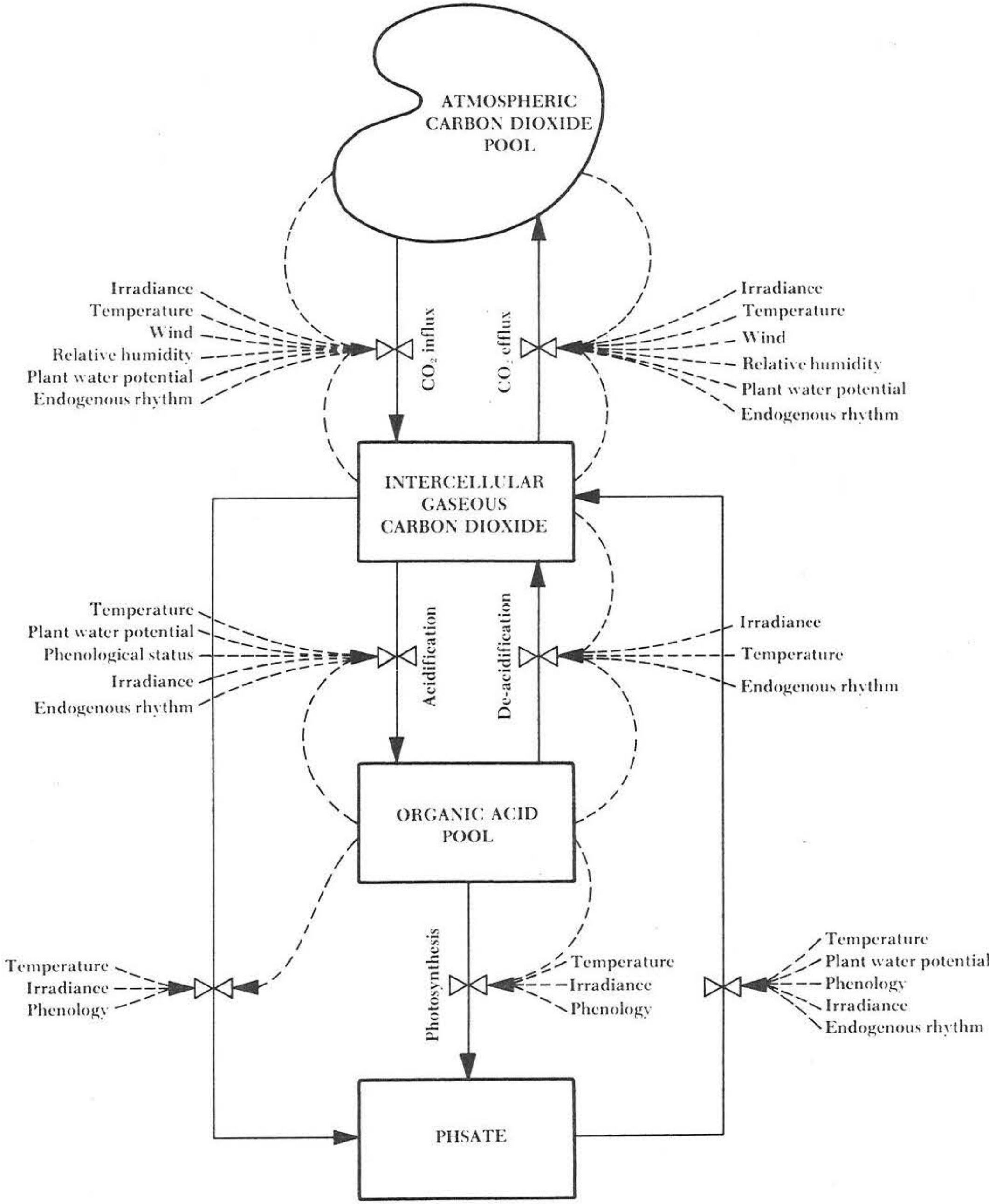
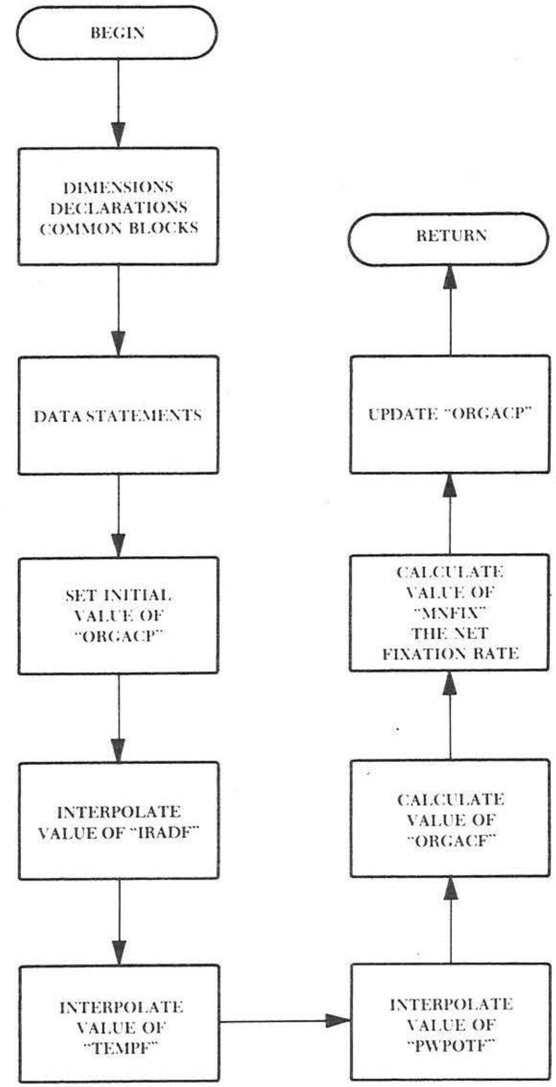


PHOTO4 AND PHOTO6



FLOW DIAGRAM