

CHAPTER 10

PLANT RESPONSE TO THE ENVIRONMENT

10.1. INTRODUCTION

As mentioned in the preceding chapter, it is very important to include a plant growth sub-model in the total model. However, plant growth, particularly under cover, is complex, and modelling it is not simple. This is one of the main reasons why most greenhouse models do not have or have only rather simple sub-models of plant growth. In the open field, the time courses of environmental conditions such as air temperature and carbon dioxide concentration are smoother than those in some greenhouses where the objective is to optimize the environment. Basic response curves, such as photosynthetic and respiratory responses to light and temperature conditions, have been studied for many years and are useful for modelling plant growth in open fields. In protected cultivation such as heated greenhouses with CO₂ enrichment facilities, some conditions can be changed drastically and positively.

Studies on dynamic modelling of plant response to the environment started some years ago (*e.g.*, Takakura and Jordan, 1970). In those models, the static response curves, which are used for open field conditions were applied. A so-called black-box technique to find optimum environmental conditions for certain plant responses, such as photosynthesis and respiration, has also been studied (*e.g.*, Takakura *et al.*, 1978). The series of studies by Takakura and Jordan (1975) showed that the main physiological responses, such as photosynthesis and respiration, change considerably according to the dynamic change of environmental conditions, and that static response curves cannot be applied when environmental conditions can change drastically. Later this technique was called the "speaking plant technique", which means that environment conditions are optimized on the basis of plant responses. However, it can be said that there are not yet reliable reports on dynamic responses of plants to the environment, and that response curves obtained under static conditions are used for environments under cover where changes occur smoothly.

10.2. PLANT PHOTOSYNTHESIS AND RESPIRATION

Plant stomata control the flows of water vapor and carbon dioxide to and from plant leaves. The mechanism that opens and closes stomata is an interesting topic in simulation as well as in plant physiology. It is known that physical environments such as light, temperature and carbon dioxide affect their movement. A comprehensive model of their movement in terms of resistance is shown in Fig. 10.1 (Takakura *et al.*, 1975).

The components involved in stomatal resistance are shown in the figure separately. Resistance in the cuticle is parallel to that in stomata, and other

resistances, such as boundary layer resistance on the leaf and internal resistance, are also connected serially. There are some experimental data which show that the stomatal resistance (**RS**) changes like an electrical switch based on the carbon dioxide level in the stomata (**CO2ST**). Another functional relationship found experimentally is that internal resistance (**RI**) is dependent on leaf temperature. Respiration (**RESP**), which takes place in the stomata, is a function of leaf temperature (**TP**) and is a well-known **Q10** function, which means that respiration doubles when temperature increases by 10°C. These functional relationships are expressed as:

$$\mathbf{RS} = \mathbf{AFGEN_RSTB}(\mathbf{CO2ST}) \quad (10.1)$$

$$\mathbf{RI} = \mathbf{AFGEN_RITB}(\mathbf{TP}) \quad (10.2)$$

$$\mathbf{RESP} = \mathbf{Q10}(\mathbf{TP}) \quad (10.3)$$

These expressions are different from mathematical ones, but are easily understood.

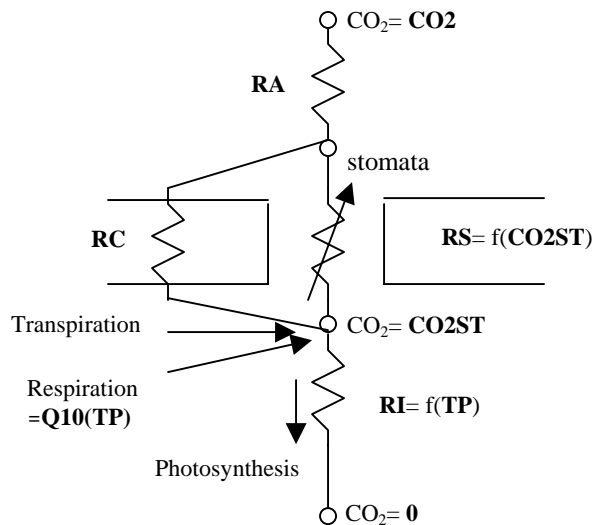


Figure 10.1. Basic structure of the model (after Takakura et al., 1975).

Another important relationship to be included is that of photosynthesis (**PHOTO**) and photosynthetically active radiation (**PAR**, W/m^2). The relationship is expressed by two straight lines. If light is limiting the process, photosynthesis is expressed as

$$\mathbf{PHOTO} = \mathbf{EFF} * \mathbf{PAR} \quad (10.4)$$

On the other hand, if light is sufficient and carbon dioxide is limiting, then the equation becomes

$$\text{PHOTO} = 68.4 * \text{CO2ST} / \text{RI} \quad (10.5)$$

where 68.4 is a unit conversion factor (from $\mu\text{l/l CO}_2 / \text{m/s}$ to $\text{kg CO}_2 / \text{ha/hr}$), **CO2ST** is CO_2 concentration in the stomata ($\mu\text{l/l}$), and **RI** is internal resistance (s/m). The unit of gas concentration is confusing. The unit 'ppm' is very popular but it does not indicate whether it is based on volume or weight. This is the reason why the unit 'vpm' is sometimes used to show clearly it is a volume basis. Then the effect of temperature on the volume and in the fixation of CO_2 must be taken into account; the concentration of CO_2 is often converted to photosynthesis products and expressed on a weight basis. In this sense, the unit ' $\mu\text{mol CO}_2 / \text{mol air}$ ' is introduced. This is weight basis, but the value remains the same for mol basis at a fixed temperature. In the present textbook, as far as CO_2 is concerned, the effect of temperature on the conversion factors from volume to weight or vice versa is not taken into account.

Applying Ohm's law to the flow of CO_2 from the atmosphere, where its concentration is **CO2**, to inside the stomata, we have

$$\text{PHOTO} - \text{RESP} = 68.4 * (\text{CO2} - \text{CO2ST}) / 1.6 / (\text{RA} + \text{RT}) \quad (10.6)$$

where **RESP** is respiration ($\text{kg CO}_2 / \text{ha/hr}$), **RA** is boundary layer resistance, and **RT** is the total resistance of stomata and cuticle. The value 1.6 is introduced because of the difference in the diffusivities of water vapor and CO_2 gas. Stomatal resistance to CO_2 flow is 1.6 times larger than that to water vapor.

10.3. ENERGY BALANCE OF A PLANT LEAF

Energy balance equations for plant leaves are needed to find leaf temperature. First, it is assumed that the net radiation (**QNET**) on a leaf is the sum of sensible (**QS**) and latent heat (**QL**),

$$\text{QNET} = \text{QS} + \text{QL} \quad (10.7)$$

Then, we need an approximation to relate the net radiation (**QNET**) and the photosynthetically active radiation (**PAR**), because **PAR** is the only variable to be defined as an energy source.

Let's assume **PAR** is half of the total solar radiation and make a radiation balance for plant leaves (also see section 5.2):

$$\text{QNET} = 2 * \text{PAR} * \text{ALP} + \text{QUL} * \text{EPSP} - 2 * \text{EPSP} * \text{SIG} * (\text{TP} + 273)^4 \quad (10.8)$$

where **ALP** is the absorptivity of the plant for solar radiation, **QUL** is the sum of

long wave radiation from the atmosphere and the ground, and it is assumed that **PAR** is constant. **EPSP** is emissivity and absorptivity of plant leaves for long wave radiation and **SIG** is the Stefan-Boltzmann constant.

Sensible heat itself is expressed as

$$QS = CA * (TP - TA) / RA \quad (10.9)$$

where **CA** is volumetric heat capacity of the air ($J/m^3/^\circ C$), **TP** is leaf temperature ($^\circ C$), and **TA** is ambient temperature. Then, it is clear that the heat transfer coefficient due to convection is **CA/RA**. On the other hand, the latent heat is expressed by using a very common expression in meteorology, that is, the psychrometric constant (**PSCH**, $mb/^\circ C$) as

$$QL = (PLS - PA) / (RA + RT) * CA / PSCH \quad (10.10)$$

Again, the saturated water vapor pressure at the leaf temperature is obtained from the saturation curve shown in Fig. 4.9. In this case, another simple approximated exponential curve is used and it is in a function form:

$$PLS = PSYCR(TP) \quad (10.11)$$

Eliminating **QNET**, **QS**, **QL**, and **PLS** from eqs. 10.7 to 10.10, and taking one **TP** term, which is first order, to the left-hand side of the equation, we have

$$TP = TA + (2 * PAR * ALP + QUL * EPSP - 2 * EPSP * SIG * (TP + 273)^4 - CA * (PSYCR(TP) - PA) / PSCH / (RA + RT)) * RA / CA \quad (10.12)$$

This is an implicit expression in terms of **TP** because the fourth order term and the function are still on the right hand side of the equation.

Therefore, the unknown variables in eqs. 10.1 through 10.6 and eq. 10.12 are **PHOTO**, **CO2ST**, **TP**, **RS**, **RI**, and **RESP**. Then, the total number of equations is six (eqs. 10.4 and 10.5 are counted as one), although eq. 10.12 is an implicit expression.

10.4. STOMATAL RESISTANCE OF PLANTS (CUC151)

Instead of **IMPL** function, available in **CSMP**, **MATLAB** provides function **fzero** to solve the implicit form of equations. This part of the program is as follows:

```
%CUC151.m
.....
y=fzero('findco2ver1',CO2ST);
.....
%findco2ver1.m
```

```

function y=findco2ver1(CO2ST)
...
RS = AFGEN_RSTB(CO2ST);
RT = RC*RS/(RC+RS);
TP = TA+(2*PAR*ALP+QUL*EPSP-2*EPSP*SIG*(TP+273)^4 ...
      - CA*(PSYCR(TP) - PA)/PSCH/(RA+RT))*RA/CA;
RI = AFGEN_RITB(TP);
PHOTO = MIN (EFF*PAR, 68.4*CO2ST/RI);
Q10 = 2.0^((LIMIT(0.,40.,TP) - TREF)*0.1);
RESP = 5.0*Q10;
CEND= CO2 - (PHOTO - RESP)*1.6*(RT+RA)/68.4;
y=CO2ST - CEND;

```

Fzero is a scalar non-linear zero finding function. $Y = \mathbf{fzero}(\text{FUN}, Y_0)$ tries to find a zero of FUN near Y_0 . FUN is usually an M-file. The value Y returned by **fzero** is near a point where FUN changes sign, or NaN if the search fails. **CEND** is the expression for **CO2ST** in an implicit form. If the difference of **CO2ST** and **CEND** is within an acceptable range, the implicit equation is solved. A more detailed description of the **fzero** function can be found at the end of this chapter.

The stomatal resistance **RS** is considered to change from its minimum value (**RSMN**) to its maximum value (**RSMX**) according to the aperture of the stomata; the aperture is controlled by the CO_2 concentration in the stomata (**CO2ST**), as shown in Fig. 10.2, and this is involved in the function **AFGEN_RSTB**. Internal resistance (**RI**) is also expressed by using **AFGEN_RITB**. The relationship between **RI** and **TP** can be approximated using a downward convex parabola. This indicated that **RI** has a minimum value at a certain temperature.

MIN is a function to find the minimum value among options listed in the parentheses and in this case **PHOTO** is set equal to the lower value of either **EFF*PAR** or $68.4 \cdot \text{CO2ST}/\text{RI}$. This approximation is called Blackman's expression (see Fig. 10.6). Another approximation can be made using hyperbolic curves.

Leaf resistance consists of the resistances of stomata and cuticles in parallel; therefore the total resistance (**RT**) is as shown in the program.

The function **LIMIT** is used to limit the third argument -- **TP** in this case. If **TP** is outside the range between 0 and 40, then **TP** is set to the nearer boundary.

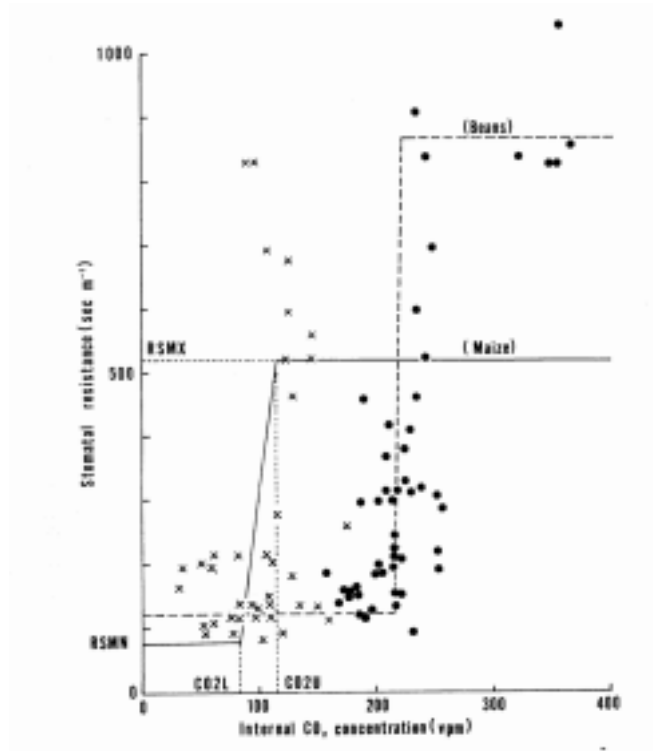


Figure 10. 2. Simplified relationship between stomatal resistance (s/m) and internal CO_2 concentration (vpm) with experimental data (after Takakura et al., 1975).

```

% Behavior model of stomata opening                                CUC151.m
% Changes of RS and PHOTO by CO2
% Enter 'cuc151' or 'cuc151(1)' in Command Window for Figs. 1 and 2,
% enter 'cuc151(2)' for Figs. 3, 4 and 5.
% Subprogram: findco2ver1.m
%
function cuc151(action)
if nargin==0,action=1;end;
switch action
case 1
    global rt photo co2 ra par
    global rs resp tp
    par1=[50 100 500];      %par: light level, in W/m2
    co2mat=0:20:1000;
    clc
    for k=1:length(par1)
    par=par1(k);  co2st=300;
    for j=1:51
        co2=co2mat(j);
%-----
        y=fzero('findco2ver1',co2st); % core of this program
%-----
    end
    clc

```

```

        fprintf('\nPAR=%3.0f CO2=%5.0f\n ',par,co2);
        rtl(k,j)=rt;          photol(k,j)=photo;
    end
end
cuc151_fig1=findobj('tag','fig1'); close(cuc151_fig1);
cuc151_fig2=findobj('tag','fig2'); close(cuc151_fig2);
figure('tag','fig1','name','CUC151: 1.Photosynthesis','menubar', ...
    'none','NumberTitle','off','Position',[100,150,520,380]);
cuc151_fig1=plot(co2mat,photol(1,:),'r*-',co2mat,photol(2,:),...
    'b^-',co2mat,photol(3,:),'ko-');
set(cuc151_fig1,'linewidth',1);
axis([0 1000 0 100]);
xlabel('CO_2 in the air (ul/l)');
ylabel('Photosynthesis (kgCO_2/ha/hr)');
legend('PAR=50W/m^2','PAR=100','PAR=500',2);
grid on;
figure('tag','fig2','name','CUC151: 2.Stomatal Resistance',...
    'menubar','none','NumberTitle','off','Position',[140,120,520,380]);
cuc151_fig2=plot(co2mat,rtl(1,:),'r*-',co2mat,rtl(2,:),...
    'b^-',co2mat,rtl(3,:),'ko-');
set(cuc151_fig2,'linewidth',1);
axis([0 1000 0 600]);
xlabel('CO_2 in the air (ul/l)');
ylabel('Total Resistance of Stomata & Cuticle (s/m)');
legend('PAR=50W/m^2','PAR=100','PAR=500',4);
grid on;
case 2
    global rt photo co2 ra par
    global rs resp tp
    co2=350;
    par1=0:10:500;
    clc
    for k=1:length(par1)
        par=par1(k); co2st=300;
%-----
        y=fzero('findco2ver1',co2st);
        % find root for eqs. listed in findco2ver1.m
%-----
        clc
        fprintf('\nPAR=%3.0f PHOTO=%3.0f RS=%4.1f TP=%3.1f resp=%4.2f\n'...
            ,par,photo,rs,tp,resp);
        rs1(k)=rs;      rtl(k)=rt;
        photol(k)=photo;  respl(k)=resp;          tpl(k)=tp;
    end
    cuc151_fig3=findobj('tag','fig3');close(cuc151_fig3);
    figure('tag','fig3','name','CUC151: 3.Given Constant CO2','menubar', ...
        'none','NumberTitle','off','Position',[100,150,520,380]);
    plot(par1,respl,par1,tpl)
    axis([0 500 0 100]);
    hold on;
    plotyy(par1,photol,par1,rs1);
    tit=(['Given Tair=30 degree C & CO2=' num2str(co2)]);
    title(tit);
    xlabel('PAR (W/m^2)');
    ylabel('Photosynthesis (kgCO_2/ha/hr), RESP, TP(^oC)');
    text(200,60,'Photosynthesis');
    text(10,85,'Stomatal resistance');
    text(200,27,'Leaf temperature');
    text(200,32,'Air temperature=30');
    text(300,12,'Respiration');
    text(540, 15, 'Stomatal Resistance,(RS) in s/m', 'Rotation', 90);

```

```

line([0 500],[30 30],'color',[1 0 0],'linestyle',':');
hold off
cuc151_fig4=findobj('tag','fig4');close(cuc151_fig4);
figure('tag','fig4','name','CUC151: 4. Net Photosynthesis', ...
    'menubar','none','NumberTitle','off','Position',[120,130,520,380]);
plot(par1,photo1,'r*-',par1,resp1,'b^-',par1,photo1-resp1,'ko-')
xlabel('PAR (W/m^2)');
ylabel('CO_2 released or absorbed (kgCO_2/ha/hr)');
legend('Photosynthesis','Respiration','Net Photosynthesis',4);
%
cuc151_fig5=findobj('tag','fig5');close(cuc151_fig5);
figure('tag','fig5','name','CUC151: 5. RS and RT','menubar', ...
    'none','NumberTitle','off','Position',[120,130,520,380]);
plot(par1,rs1,'r*-',par1,rt1,'k^-','linewidth',2);
xlabel('PAR (W/m^2)'); ylabel('Resistance, (s/m)');
title('Given RC is 4000 s/m');
legend('Stomatal resistance','Total resistance (Stomata + Cuticle)');
End

```

Figure 10.3a. Main program to simulate stomatal resistance (CUC151).

```

% findco2ver1.m
function y=findco2ver1(co2st)
global rt photo co2 ra par
global rs resp tp
aa=0; bb=0;
eff=0.62; % eff: slope of the photosynthesis curve at PAR=0,
% leaf light utilization efficiency, in umol CO2/umole photon
tref=20; % reference temperature, in degree C
ta=30; % Air temperature, in degree C
alp=0.8; % Absorptivity of plant leaf for solar radiation
epsp=0.95; % Emissivity/Absorptivity of plant leaf for long wave rad.
sig=5.67; % Stefan-Boltzman constant
rh=0.75; % Relative Humidity is 75%
ta=30; % ta: air temperature (degree C)
qul=150; % qul: longwave rad. for the atmosphere and the ground (W/m2)
ra=10; % ra: diffusion resistance in laminar layer (s/m)
rc=4000; % rc: cuticle resistance
ca=1164; % ca: volumetric heat capacity of air at constant pressure
psch=0.67; % psch: psychrometric constant (mb/C)
tp=ta;
%----- co2st=IMPL(300,0.01,cend)-----
rs=afgen_rstb(co2st);
rt=rc*rs/(rc+rs); % total resistance for water vapor of leaves (s/m)
tp4=((273.16+tp)/100)^4;
aa=(2*par*alp+qul*epsp-2*epsp*sig*(tp4))*ra/ca;
bb=ca*((psycr(tp)-rh*psycr(ta))/psch/(ra+rt))*ra/ca;
tp=ta+aa-bb; ri=afgen_ritb(tp);
photo=min(eff*par,68.4*co2st/ri);
tp=limit(0,40,tp); Q10=2^((tp-tref)*0.1); resp=5*Q10;
cend=co2-(photo-resp)*1.6*(rt+ra)/68.4;
y=co2st-cend;
%-----
function vapres_value=psycr(temp)
vapres_value=6.11*exp(17.4*temp/(239+temp));
% Saturated vapor pressure as a function of air temperature, in mb
%-----
function rs_value=afgen_rstb(co2st)
% rstb_x=[0 80 120 1000];
% rstb_y=[74.4 74.4 521 521];

```



```

% rs=interp1(rstb_x,rstb_y,co2st,'linear');
% Another approach
if co2st<=80,
    rs_value=74.4;
elseif co2st>=120,
    rs_value=521;
else
    rs_value=74.4+(521-74.4)*(co2st-80)/(120-80);
end
%-----
function tp_value=limit(min,max,tp)
if tp<min,
    tp_value=min;
elseif tp>max,
    tp_value=max;
else
    tp_value=tp;
end
%-----
function ri_value=afgen_ritb(tp)
    ritb_x=[12 17 22 27 32 37 42]; % all in degree C
    ritb_y=[250 170 130 110 100 120 160];
    if tp<=12,
        ri_value=250;
    elseif tp>42,
        ri_value=160;
    else
        ri_value=interp1(ritb_x,ritb_y,tp,'*linear');
        % when intervals on ritb_x, are the same, *linear can be used
    end
end

```

Figure 10.3b. Subprogram to simulate stomatal resistance (**findco2verl.m**).

The main and subprograms are shown in Figs. 10.3a and 10.3b, respectively. In total, five functions were included in the subprogram (Fig. 10.3b) including **FINDCO2VERL**, **PSYCR**, **AFGEN_RSTB**, **LIMIT**, and **AFGEN_RITB**.

The function **PSYCR** is used to calculate saturated vapor pressure as a function of air temperature. A simpler and rougher expression than the one introduced in section 4.5 is used. In the present simulation the independent variable is **CO2**.

RS changes linearly according to **CO2ST** between its minimum (74.4) and maximum values (521) as shown in function **AFGEN_RSTB**. **RI** values can also be found in function **AFGEN_RITB**. In between minimum and maximum values, **RI** can be derived using function **interp1(X, Y, XI, method)**. All the interpolation methods require that the vector **X** be monotonic. **X** can be non-uniformly spaced. When **X** is equally spaced and monotonic, the methods **'*linear'**, **'*cubic'** or **'*nearest'** can be used for faster interpolation.

Two figures as shown in Fig. 10.4a and 10.4b can be generated after entering 'cuc151' or 'cuc151(1)' in the Command Window. Fig. 10.4a shows the photosynthesis in relation to external CO₂ concentration. Fig. 10.4b shows the stomatal resistances change due to the changes of CO₂ concentration in the air. Three different curves are given for different light levels. It is not indicated in this figure, but a shift in the transition range of internal CO₂ concentration from lower to

higher -- from 80 to 200 $\mu\text{l/l}$, for example -- causes the **RS** level to be steadily lower at a high light level.

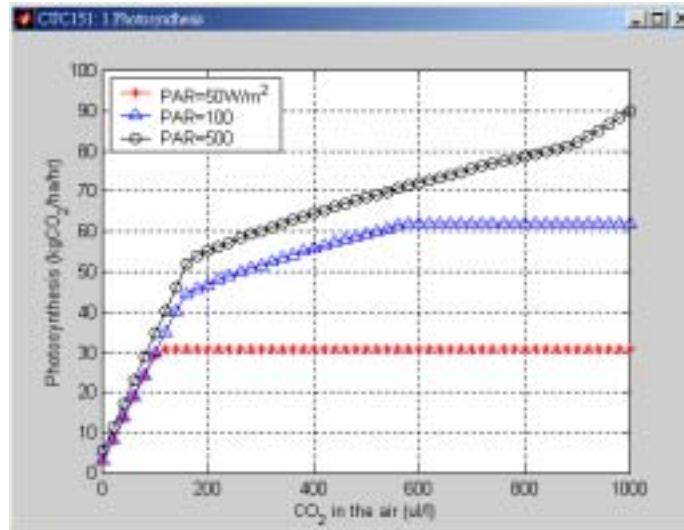


Figure 10.4a. Photosynthesis in relation to external CO_2 concentration: (First output figure after entering `cuc151(1)` in Command Window).

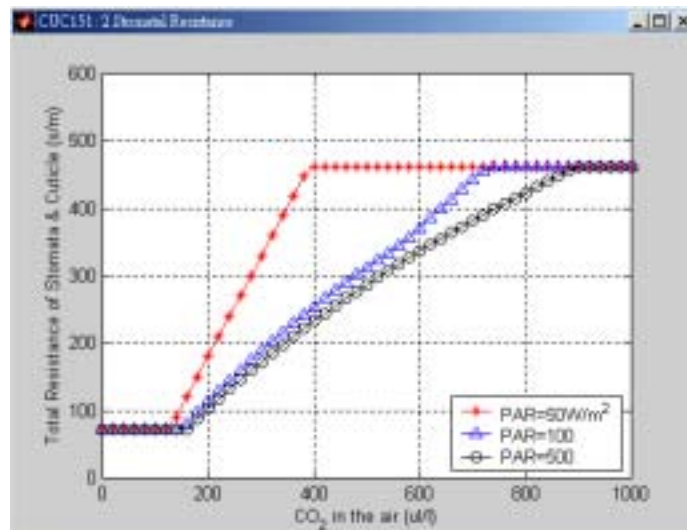


Figure 10.4b. Stomatal resistance in relation to external CO_2 concentration: (Second output figure after entering `cuc151(1)` in Command Window).

Three more figures can be generated after entering 'cuc151(2)' in the Command Window. Fig. 10.5a shows photosynthesis, stomatal resistance, respiration and leaf temperature under various PAR.

Gaastra (1959) reported the stomatal response of turnips to light intensity. The rapid change of stomatal resistance under lower light intensity and the shift of the occurrence of its drastic change to higher CO₂ range due to high light intensity are in good agreement with the simulated results (see Takakura et al., 1975).

The response curves of photosynthesis in Fig. 10.4b are not consistent according to the change of light levels. When light level is low, the photosynthetic response is very similar to that of light change, that is, Blackman's curve. When PAR is 100 W/m², the sharp edge from the CO₂ limiting range to the saturated range is smoothed compared to the curve for PAR of 50 W/m². The shape of the curve is strange when PAR is 500 W/m². Sharper increase in photosynthetic CO₂ uptake appears after the stomata are completely closed due to the upper limit of resistance. This phenomenon has not been experimentally verified yet. The experimental data are mostly scattered around these curves, but this kind of phenomenon cannot be substantiated if we do not know the theory. This is one of the definite reasons why simulation is one of the two wheels of a cart; the other wheel is field experiments.

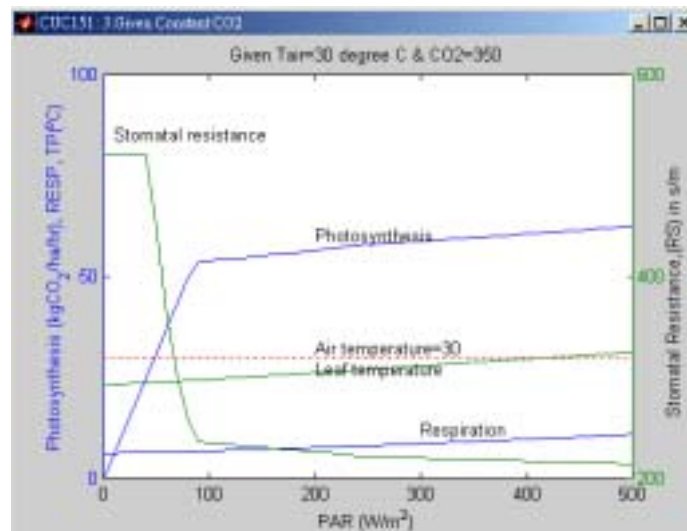


Figure 10.5a. Simulated results of photosynthesis, stomatal resistance, respiration and leaf temperature under various PAR: (First figure after entering cuc151(2)) (after Jordan, 1992).

In Fig. 10.5a, it is clearly shown that the original shape of Blackman's curve for photosynthesis is modified to a hyperbolic type to some extent due to the small change of stomatal resistance. When light level is low, stomata are closed. It is often said that photosynthesis is light-dependent when light is the limiting, but it can be explained by the fact that stomata are closed at low light level. Actually stomata are the limiting factor. Leaf temperature is lower than the air temperature but leaf

temperature monotonously increases with light increase. The same tendency occurs in leaf respiration.

Fig. 10.5b shows photosynthesis, net photosynthesis and respiration, and Fig.10.5c shows stomatal resistance and total resistance (stomatal and cuticle).

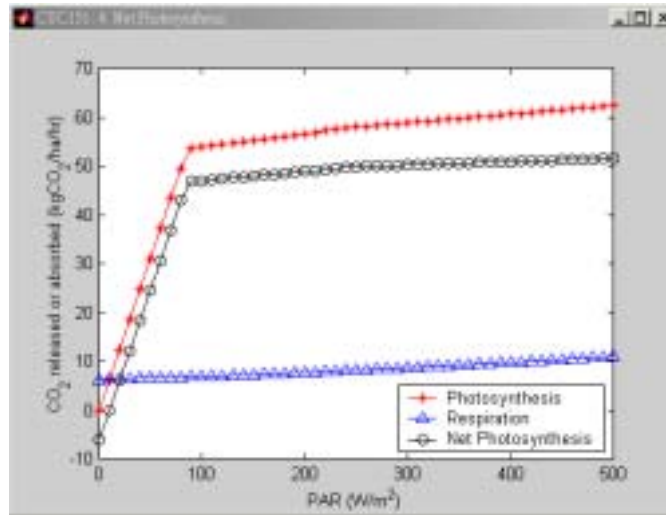


Figure 10.5b. Simulated results of (net) photosynthesis and respiration under various PAR: (Second figure after entering cuc151(2) in Command Window).

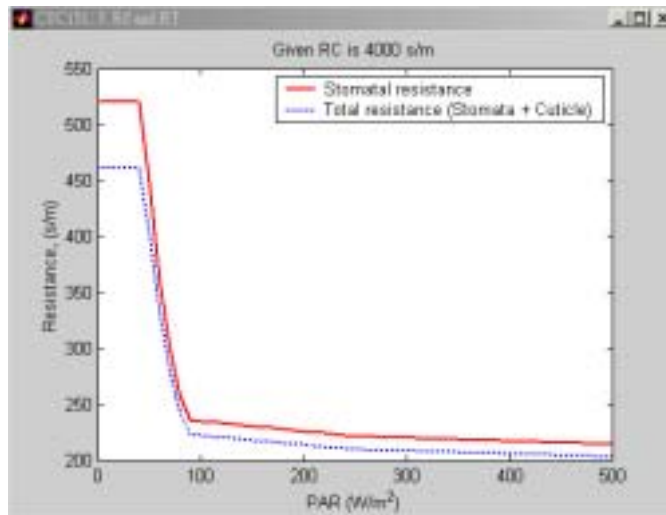


Figure 10.5c. Simulated results of stomatal resistance due to PAR change: (Third output figure after entering cuc151(2) in Command Window).

10.5. PLANT GROWTH MODEL

10.5.1. General concept of plant growth and yield models

Plant growth is an example of a set of non-linear dynamic systems and has been studied for many years. Plant vegetative growth, development, and production phases have been studied by the Dutch group led by de Wit (*e.g.*, 1972; 1974). Continuous research efforts have been conducted in this area, and the same methodology has been expanded from open-field crops to greenhouses (Jones *et al.*, 1991; Jones, 1991). In general, plant growth which is continuously changing can be expressed as systems of differential equations such as the system of equations in section 3.3.2.

The transition from vegetative to reproductive stages in crops can also be modelled in a similar way. For example, introducing the rate of development (**DVS**), which is assumed to be a function of temperature (**TEMP**) and daylength (**DAYL**),

$$d\mathbf{DVS}(t) / dt = f(\mathbf{TEMP}, \mathbf{DAYL}) \quad (10.13)$$

If **DVS** is assumed to be a function of temperature alone, the following expression could be used (Horie, 1987):

$$d\mathbf{DVS}(t)/dt = 1.0 - \exp(-\mathbf{KD} * (\mathbf{TEMP} - \mathbf{TCD})) \quad \text{when } \mathbf{TEMP} \geq \mathbf{TCD} \quad (10.14)$$

$$= 0 \quad \text{when } \mathbf{TEMP} < \mathbf{TCD} \quad (10.15)$$

where **TEMP** is daily temperature, **TCD** is a minimum temperature for development, and **KD** is a parameter. Then, **DVS** is 1.0 at flowering and is between 0 and 1 during the vegetative phase.

10.5.2. Dry matter production model (CUC160)

Plant models, in general, cover a long period of time from seedling to harvest, so the time period for most plant models is several months. Each reaction is described by a differential equation. The main consideration is to attain agreement between the model and experimental data over the entire period of time. The main purpose of the present plant modelling is not to see hourly changes, although hourly changes can be seen through the same model. A simple model offered by Jones (1991) is considered.

The basic equation in Jones' model describes the change in dry matter production which is related to photosynthesis and respiration by the expression

$$d\mathbf{WGT} / dt = \mathbf{E} * (\mathbf{PHOTO} - \mathbf{RESP} * \mathbf{WGT}) \quad (10.16)$$

where $dWGT/dt$ is the rate of dry matter production of the plant ($g \text{ tissue}/m^2/hr$), **WGT** is total plant dry weight (g/m^2), **E** is conversion efficiency of CH_2O to plant tissue ($g \text{ tissue}/g \text{ } CH_2O$), and **PHOTO** is canopy gross photosynthesis rate ($g \text{ } CH_2O/m^2/hr$).

Gross photosynthesis is expressed by the well-known formula

$$\mathbf{PHOTO} = \frac{\mathbf{P_{MAX}} * \mathbf{EFF} * \mathbf{PAR}}{\mathbf{P_{MAX}} + \mathbf{EFF} * \mathbf{PAR}} \quad (10.17)$$

where **P_{MAX}** is the maximum rate of photosynthesis to be attained and is a function of CO_2 concentration and leaf temperature, **EFF** is the slope of the photosynthesis curve where **PAR** is zero, and **PAR** is the photosynthetically active radiation on a leaf. Thus, a typical expression for **P_{MAX}** is the product of **PHI*CO₂** and **PTM** where **PHI*CO₂** is the amount of CO_2 flow, **PTM** is a function of leaf temperature, and **PHI** is leaf conductance to CO_2 transfer. Eq. 10.17 is another form of Blackman's expression, which was shown in the preceding section. A general curves resulting from these equations and a **MATLAB** program are shown in Figs. 10.6a and 10.6b.

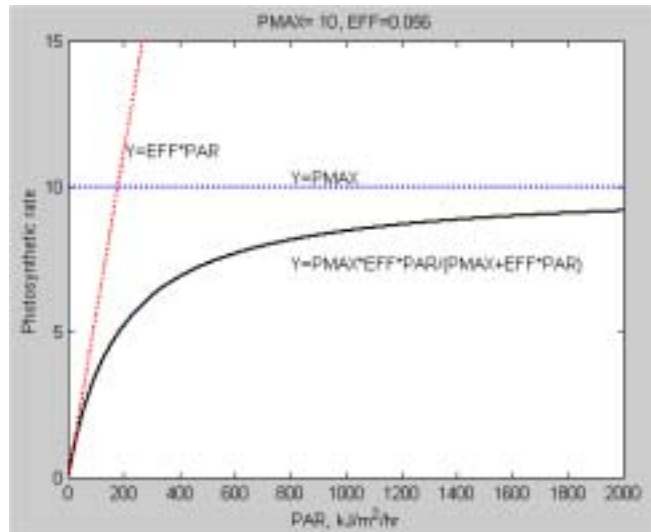


Figure 10.6a. Program output showing Blackman's expression (CUC155.m).

```
% Blackman's Expression CUC155.m
par0=2000; % (kJ/m2/hr)
EFF=0.056; % slope
P_MAX=10; % Max. photosynthetic rate at CO2 and Light saturation points
t=1:1:par0;
for par=1:par0;
    photo(par)=P_MAX*EFF*par/(P_MAX+EFF*par);    photo2(par)=EFF*par;
```

```

end
hl=findobj('tag','Blackman');close(hl);
figure('tag','Blackman','Resize','on','MenuBar','none',...
    'Name','CUC155: Blackman's Expression',...
    'NumberTitle','off','Position',[160,80,520,420]);
plot(t,photo,'k-',t,photo2,'r:','linewidth',2);
line([0 par0],[PMAX PMAX],'linestyle',':','linewidth',2);
axis([-inf inf 0 PMAX*1.5]);
titleline=['PMAx= ' num2str(PMAX) ', EFF=' num2str(EFF)];
title (titleline);
xlabel('PAR, kJ/m^2/hr'); ylabel('Photosynthetic rate');
text(800,PMAX*1.03,'Y=PMAX'); text(205,EFF*200,'Y=EFF*PAR');
text(800,0.9*PMAX*EFF*800/(PMAX+EFF*800),'Y=PMAX*EFF*PAR/(PMAX+EFF*PAR)');

```

Figure 10 6b. Program to illustrate Blackman's expression (CUC155.m).

Light penetration in the plant canopy has been analyzed for many years. One of the typical representations for downward light at a certain level in a plant canopy is derived from Lambert-Beer's law as,

$$\text{PAR} = \text{PAR0} * f(L) = \text{PAR0} * \exp(-K * L) \quad (10.18)$$

where **PAR0** is the **PAR** at the top of the canopy, **K** is the extinction coefficient of the canopy, and **L** is the leaf area index from the top to the chosen level in the canopy. The absorbed fraction of light, **dPAR**, is the product of leaf fraction, **dL**, and **PAR** which is not transmitted. **LT** is the light transmission coefficient of leaves. The equation for **dPAR** is

$$-d\text{PAR} = dL * (1 - \text{LT}) * \text{PAR} \quad (10.19)$$

Then,

$$\begin{aligned} \text{PAR} &= -\frac{1}{1 - \text{LT}} * \frac{d\text{PAR}}{dL} = -\frac{\text{PAR0}}{1 - \text{LT}} * \frac{df(L)}{dL} \\ &= \frac{\text{PAR0}}{1 - \text{LT}} * K * \exp(-K * L) \end{aligned} \quad (10.20)$$

Combining eqs. 10.17 and 10.20, and integrating over the entire leaf area of the canopy gives the rate of canopy net photosynthesis per unit ground area as

$$\begin{aligned} \text{PHOTO} &= \mathbf{D} / \mathbf{K} * \mathbf{PHI} * \mathbf{CO2} * \mathbf{PTM} * \log((\mathbf{EFF} * \mathbf{K} * \\ &\quad \mathbf{PAR0} + (1 - \text{LT}) * \mathbf{PHI} * \mathbf{CO2} * \mathbf{PTM}) / (\mathbf{EFF} * \mathbf{K} \\ &\quad * \mathbf{PAR0} * \exp(-\mathbf{K} * \mathbf{LAI}) + (1 - \text{LT}) * \mathbf{PHI} * \mathbf{CO2} * \\ &\quad \mathbf{PTM})) \end{aligned} \quad (10.21)$$

where **D** is the coefficient to convert photosynthesis calculations from the unit $\mu\text{mol CO}_2/\text{m}^2/\text{s}$ to the unit $\text{g CH}_2\text{O}/\text{m}^2/\text{hr}$, **PHI** is leaf conductance to CO_2 flow ($\text{mol air}/\text{m}^2/\text{s}$), **CO2** is CO_2 concentration of the air ($\mu\text{mol CO}_2/\text{mol air}$), **PTM** is a

dimensionless function of temperature, **EFF** is leaf light utilization efficiency ($\mu\text{mol CO}_2/\mu\text{mol photon}$), **K** is the canopy light extinction coefficient, **PAR0** is light flux density at the top of the canopy ($\mu\text{mol photon}/\text{m}^2/\text{s}$), and **LAI** is the canopy leaf area index ($\text{m}^2 \text{ leaf}/\text{m}^2 \text{ ground}$).

The function **PTM** expresses the effect of leaf temperature (**TP**) on the maximum rate of photosynthesis for a single leaf,

$$\text{PTM} = 1 - ((\text{TPH} - \text{TP}) / (\text{TPH} - \text{TPL}))^2 \quad (10.22)$$

where **TPH** is the temperature at which leaf photosynthesis is maximum, and **TPL** is the temperature below which leaf photosynthesis is zero.

The leaf area index is

$$\text{LAI} = \text{NP} * \text{DELTA} / \text{BETA} * \log(1 + \exp(\text{BETA} * (\text{NL} - \text{NB}))) \quad (10.23)$$

where **LAI** is leaf area index ($\text{m}^2 \text{ leaf}/\text{m}^2 \text{ ground}$), **NP** is plant density (number of plants/ m^2), **NL** is leaf number, and **DELTA**, **BETA** and **NB** are empirical coefficients.

Maintenance respiration is a function of leaf temperature and is expressed as

$$\text{RESP} = \text{RESP25} * \exp(0.0693 * (\text{TP} - 25)) \quad (10.24)$$

where **RESP** is the maintenance respiration rate ($\text{g CH}_2\text{O}/\text{g tissue}/\text{hr}$), and **RESP25** is the respiration rate at 25°C ($\text{g CH}_2\text{O}/\text{g tissue}/\text{hr}$).

The state variable for number of leaves on a vegetable plant (**NL**) is assumed to be a function of temperature:

$$d\text{NL} / dt = \text{RESP} * \text{AFGEN_RTP}(\text{TP}) \quad (10.25)$$

where **AFGEN_RTP(TP)** is a function of leaf temperature (**TP**) as shown in Fig. 10.7.

Two differential equations, eqs. 10.16 and 10.25, and four functional relationships (eqs. 10.21 - 10.24) connect the unknown variables. There are six unknown variables, **WGT**, **PHOTO**, **RESP**, **PTM**, **LAI**, and **NL**, and three inputs (boundary conditions), **PAR0**, **CO2**, and **TP**. All other terms are parameters or constants that should be specified by the programmer. The complete listing of the model is in Fig. 10.8, and the result of a two-day run is shown in Fig. 10.9.

This model can easily be combined with any of the greenhouse models such as those described in Chapter 6.

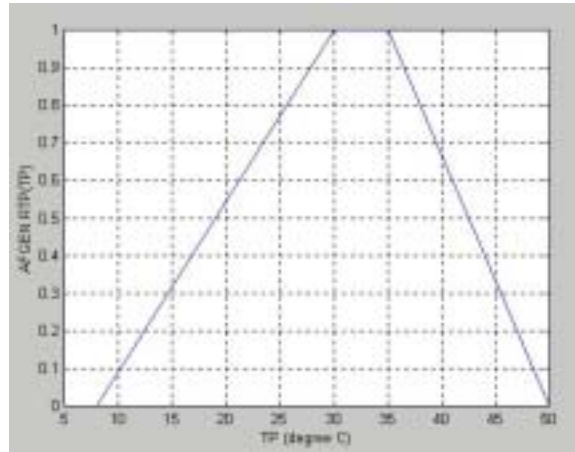


Figure 10.7. Effect of temperature on number of leaves (after Jones, 1991).

```

% Plant Growth Model                                     CUC160.m
% also requires function: soil160.m
%
clear all;clc
t0=0;tfinal=48;
y0=[0; 0]; % initial condition of WGT and NL
[t,y]=ode15s('soil160',[t0 tfinal],y0);
hl=findobj('tag','Plant Growth'); close(hl);
figure('tag','Plant Growth','Resize','on','MenuBar','none',...
    'Name','CUC160: Example of plant dry weight increase',...
    'NumberTitle','off','Position',[160,80,520,420]);
subplot(1,2,1); plot(t,y(:,1)*1000);
xlabel('Time (hr)'); ylabel('Drymatter Production (mg tissue/m^2/hr)');
axis([0, 50, 0, 54]);
set(gca,'ytick',[18 36 54]); grid on;
subplot(1,2,2); plot(t,y(:,2));
xlabel('Time (hr)'); ylabel('Leaf Number');
axis([0, 50, 0, 0.005]);
set(gca,'ytick',[0.001 0.002 0.003 0.004 0.005]); grid on;
fprintf('\n\n');
disp('Thank you for using'); disp(' ');
disp('CUC160: a plant growth model. '); disp(' ');

```

Figure 10.8a. Main program of plant dry weight increase model (CUC160).

```

% Subprogram for model CUC160                             soil160.m
% Also requires functions TABS.m and SOLAR.m (refer to Chapter 4)
function dy = soil160(t,y)
RP=500; % RP: Solar radiation amp (kJ/m2/hr)
OMEGA=2.0*pi/24.0; % Time (hr)
clk=mod(t,24); % time (24 hr basis)
T0=10.0; TU=5.0; TBL=10.0; % Temp (C)
TP = T0 + TU*sin(OMEGA*(clk-8)); % Temp (C)
PAR0= SOLAR(RP,OMEGA,clk); % calling function SOLAR()
% PAR0: Light flux density at the top of the canopy (umol photon/m2/s)

```

```

CO2=350+50*sin(OMEGA*(clk+6));
% CO2: CO2 concentration of the air (umol CO2/mol air, ppm, ul/l)
E=0.7; % conversion efficiency of CH2O to plant tissue (g tissue/g CH2O)
% WGT: total plant dry weight (g/m2)
% PHOTO: canopy gross photosynthesis rate (g CH2O/m2/hr)
D=0.108; % coefficient to convert photosynthesis calculations
          % from umol CO2/m2/s to g CH2O/m2/hr
K=0.58; % canopy light extinction coefficient
PHI=0.0664; % leaf conductance to CO2 (umol CO2/umol air m2/sec)
EFF=0.056; % leaf light utilization efficiency (umol CO2/umol photon)
LT=0.002; % light transmission coefficient of leaves
NP=4; % plant density, (Number of plants/m2)
DELTA=0.074;BETA=0.38;NB=13.3; % empirical coefficient
TPH=30; % Temperature at which leaf photosynthesis is maximum
TPL=5; % Temperature below which leaf photosynthesis is zero
PTM=1-((TPH-TP)/(TPH-TPL))^2; % dimensionless function of temperature
WGT=y(1); % y(1) is dry weight increase (WGT)
NL=y(2); % y(2) is number of leaves (NL)
LAI=NP*DELTA/BETA*log(1+exp(BETA*(NL-NB)));
% LAI: canopy leaf area index (m2 leaf/m2 ground)
PHOTO=D/K*PHI*CO2*PTM*log((EFF*K*PAR0+(1-LT)*PHI*CO2...
*PTM)/(EFF*K*PAR0*exp(-K*LAI)+(1-LT)*PHI*CO2*PTM));
% Growth and maintenance respiration
RESP25=0.0006; % respiration rate at 25 degree C (g CH2O/g tissue/hr)
RESP=RESP25*exp(0.0693*(TP-25));
% RESP: maintenance respiration rate (g CH2O/g tissue/hr)
WGT=E*(PHOTO-RESP*WGT); % dry weight increase
RTP= AFGEN_RTP(TP); % function AFGEN_RTP
NL=RESP*RTP; % NL: leaf number increase
dy=[WGT; NL];
%-----
function RTP= AFGEN_RTP (TP)
%TP= [8 12 30 35 50];
%RTP=[0 0.55 1 1 0];
if TP<=8 | TP>=50,RTP=0;
elseif TP<=12, RTP=(TP-8)/(12-8)*0.55;
elseif TP<=30,RTP=0.55+(TP-12)/(30-12)*(1-0.55);
elseif TP<=35,RTP=1;
elseif TP<50,RTP=1-(TP-35)/(50-35)*1;
end

```

Figure 10.8b. Subprogram of plant dry weight increase model (Soil160).

It is apparent that the plant weight increase is continuous, but the present model is too rough to express its hourly change. Leaf number is also expressed as a continuous function, but it is in reality discrete. Therefore, the outputs shown in Fig 10.9 are hypothetical. However, for a longer range of time, that is, for the whole growth period, it would give reasonable results. If daily changes of weather can be supplied, longer term of prediction can be attained.

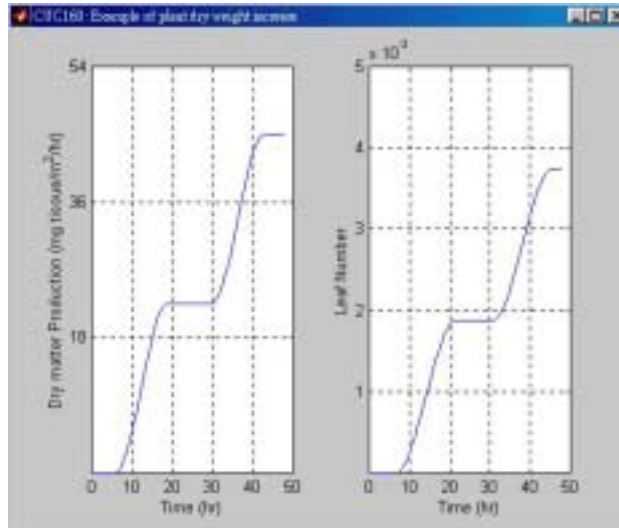


Figure 10.9. Simulated results of dry weight increase and number of leaves produced over time (Output figure after entering cuc160 in command window).

MATLAB FUNCTIONS USED

Fzero If $f(x)$ is a function of a single variable and is coded in an M-file function with the name **fname**, and if **k0** is a guess for a root of this function, then **fzero** will attempt to find the actual root of the function to a tolerance, **tol**. The implementation is **kroot** = **fzero('fname', k0, tol)**. If the third item in the argument list, **tol**, is omitted, a tolerance equal to **eps**, the machine accuracy, is used. If there is a nonzero fourth item in the list, intermediate steps in the calculation will be printed. The algorithm searches for a change in sign of the function and uses quadratic interpolation near the root.

PROBLEMS

1. Derive the conversion factor 68.4 from the unit $\mu\text{l/l m/s}$ to the unit $\text{kgCO}_2/\text{ha/hr}$.
2. At a fixed temperature, verify that CO_2 concentration in the air of 350 ppm is equal to $350 \mu\text{mol CO}_2/\text{mol air}$.
3. Derive eq. 10.12 from eqs. 10.7- 10.11.

4. Show the relationship between **KM** in eq. 4.14 and **PSCH** in eq. 10.10.
5. Explain why **RS** cannot be solved explicitly.
6. Change the transient region of CO₂ from 80 – 120 μl/l to 200 – 240 μl/l in function **AFGEN_RSTB** in the program **Soil151** and rerun the program.
7. Change the programs **CUC151** and **Soil151** in order to obtain the result shown in Fig. 10.6.
8. Use **MATLAB** to solve the following equation: $x = \tan(x) - 1.0$
9. Write a program to calculate wet-bulb temperature (**TOW**) given dry-bulb temperature (**TO**) and humidity ratio (**WO**) by using the **fzero** function of **MATLAB**. Then, from dry-bulb and wet-bulb temperatures, find humidity ratio and dew point temperature. Note: Use the following equations:

$$\mathbf{WWS} = \mathbf{FWS}(\mathbf{TOW}), \text{ and}$$

$$\mathbf{TOW} = \mathbf{TO} - (2501.0 - 2.38*\mathbf{TOW})*\mathbf{WWS} + (2501.0 + 1.805*\mathbf{TO} - 4.186*\mathbf{TOW})*\mathbf{WO}$$
 where **FWS** is a function to calculate the saturated humidity ratio in Fig. 4.9c.
10. Derive eq. 10.21, using the formula $\int_0^x \frac{f'(x)}{f(x)} dx = \log f(x)$
11. Plot **PHOTO** by using eq. 10.17 as a function of **PAR** with **CO2** as a parameter and the remaining terms as constants.
12. Explain why the unit of **PHI** is mol air/m²/s.
13. The equation **PMAX** = **PHI***(**CO2** - 0.0) shows that the maximum CO₂ flow is the product of CO₂ flow conductance and CO₂ gradient. Find **PMAX** (g CO₂/m²/hr) if outside CO₂ concentration is 350 μmol/mol. The conversion factor at 0°C can be used.
14. Compare the respiration function in this chapter with the function **RESP** = **Q10(TP)** shown in the section 10.2.
15. Plot **LAI** as a function of **NL** by using eq. 10.23 with all values shown in the model in Fig. 10.8.