

Plant Growth

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Plant Processes

Many processes are involved in the growth of plants. Oxygen, carbon and hydrogen are all essential to plant life. These three elements form the building blocks of all organic compounds such as carbohydrates, lipids, proteins, and nucleic acids. Oxygen is obtained from water, gaseous oxygen (O_2), and carbon dioxide (CO_2) in the air. Hydrogen is obtained through water molecules. These three elements, oxygen, hydrogen and carbon make up approximately 96% of a plant's dry weight.

Nutrients, in the form of minerals, are also essential in plant development. Plants typically absorb these minerals through their root system. Nitrogen, potassium, calcium and magnesium are some examples of these nutrients. Nitrogen is involved in the synthesis of amino acids, proteins and nucleic acids. Potassium activates enzymes involved in the synthesis of protein and starch, photosynthesis and aerobic respiration. Calcium is involved in cell growth and division. Magnesium is essential in the formation of fats and sugars. It is also involved in the formation of amino acids and vitamins.

Photosynthesis and respiration are other important plant processes. Photosynthesis is the process by which plant cells make sugar from carbon dioxide and water in the presence of chlorophyll and light. Respiration deals with the process by which a plant secures oxygen from the air or water, distributes it, combines it with substances in the tissues, and gives off carbon dioxide.

Water uptake from the soil is indispensable for plant growth. Water is pulled upwards from the roots to the stems, and then into the leaves. Activities such as photosynthesis, cell division and cell enlargement all require water.

The following, taken from Thornley, (Mathematical Models in Plant Physiology) is a list of the many important plant processes and properties.

Plant Processes and Properties

Processes

light absorption, reflection
scattering, transmission
nutrient uptake
water uptake
within-plant transport of
gases, sugars, hormones,
growth factors, other
nutrients
photosynthesis
respiration
maintenance respiration
utilization of carbon
assimilates, other
nutrients
other aspects of metabolism
wastage, loss of material
storage
growth
development
germination
morphogenesis
reproduction
senescence
harvesting
post-harvest processes

Properties

size, weight, number, length,
area, volume
structure, internal structure,
external form, geometry,
position, pattern
composition, chemical concentrations
temperature
pressure
electrical and optical properties
absorptivity, conductivity,
reflectivity, scattering,
transmissivity
mechanical properties
elasticity, permeability

How is growth measured?

Size is typically the first characteristic that comes to mind when dealing with plant growth. Size can be measured in terms of length, area or volume.

Plant length can be somewhat difficult to measure. Plants typically possess an irregular shape, caused by branching of leaves and roots. Measuring the total weight of a plant might seem to be easier, but this can be misleading since plants contain much water, and this amount varies throughout the day. We might then try using dry weight as a measure of growth. Dry weight is the total plant weight minus its water weight. To find the dry weight, we simply weigh the plant after it has been dried.

We often use dry weight, length of branches, stems, roots, and area of leaves as a measure of plant growth. We can also use the number of leaves or roots as a measure of growth, since growth in plant size is usually accompanied with an increase in the number of organs.

Modelling Plant Growth

We consider a simplified model of growth based on plant dry weight. Before describing such a model, we need to list and explain a number of assumptions that will be made.

I. We assume that the plant is completely defined by its dry weight. We use the dry weight since it is a fairly convenient and simple growth metric. The total dry plant weight is denoted by W . The weight W varies with time t .

II. We shall also assume that plant growth occurs at the expense of a single substrate. A substrate is defined as being the base on which the plant develops. We will denote the amount of substrate by S . The assumption states that an increase in

plant growth leads to a decrease in the amount of substrate available for further plant growth. In an effort to simplify the model, we only consider the substrate as a means of food supply. All other processes that affect plant growth, such as photosynthesis and respiration, are ignored.

III. We will assume the conservation of mass principle holds. That is, we assume that matter cannot be created or destroyed.

IV. Our fourth assumption is that the rate of growth is linearly proportional to the amount of substrate S , and also to the dry weight W . Since we are only considering plant weight and substrate level, the rate of growth is then kWS , where k is a constant. We would then have

$$1. \quad \frac{dW}{dt} = kSW$$

That is, the rate of change in the plant's dry weight is directly proportional to the current dry weight, and the amount of substrate made available to the plant.

Now the amount of substrate S varies as the plant grows. Our second assumption states that an increase in W is matched by a decrease in S . If W and S are measured using the same units, and since the conservation of mass principle applies, we can say that there is no net loss of material when S is converted into W . We can therefore say

$$2. \quad dW = -dS$$

That is, an increase in plant weight is matched by a decrease in the level of substrate. Equation 2 can be expressed as $d(W + S) = 0$. If we integrate both sides with respect to t , we obtain:

$$3. \quad W + S = W_0 + S_0 = \text{constant},$$

where W_0 and S_0 are constants, representing the initial dry plant mass and amount of substrate, respectively.

The maximum dry weight of the plant occurs when there is no substrate left, that is when $S = 0$. Equation 3 can be rewritten as:

$$4. \quad W + S = W_0 + S_0 = W_f,$$

where W_f is the maximum value of W . Note that the maximum value cannot exceed W_f , since S is never negative. S can be expressed as $S = W_f - W$, and substituting this into equation 1 yields

$$5. \quad \frac{dW}{dt} = k(W_f - W)W$$

basically the logistic law

Note that we have a differential equation in the variable W only; S has been eliminated through the substitution.

We can use separation of variables to solve the differential equation. Equation 5 can be rewritten as:

$$6. \quad \frac{dW}{(W_f - W)W} = k dt,$$

where $W = 0$ and $W_f = W$ are equilibrium solutions.

Integrating from W_0 to W and from 0 to t gives

$$7. \quad \int_{W_0}^W \frac{dW}{(W_f - W)W} = \int_0^t k dt = kt$$

We then use partial fraction decomposition:

$$\frac{1}{W(W_f - W)} = \frac{a}{W} + \frac{b}{W_f - W}$$

Now $a(W_f - W) + bW = 1$, thus $aW_f - aW + bW = 1$

Equating coefficients, we get $-aW + bW = 0$ and $aW_f = 1$.

Now $a = \frac{1}{W_f}$ and $\frac{-W}{W_f} + bW = 0$ implies that $b = \frac{1}{W_f}$.

$$8. \quad \int_{W_0}^W \frac{dW}{(W_f - W)W} = \int_{W_0}^W \frac{1}{W_f} \left(\frac{1}{W_f - W} + \frac{1}{W} \right) dW = kt$$

Integrating gives

$$9. \quad \int_{W_0}^W \frac{1}{W_f} \left(\frac{1}{W_f - W} \right) dW + \int_{W_0}^W \frac{1}{W_f} \left(\frac{1}{W} \right) dW$$

$$10. \quad = \frac{1}{W_f} (-\ln|W_f - W|) \Big|_{W_0}^W + \frac{1}{W_f} \ln|W| \Big|_{W_0}^W$$

Since $W \geq 0$ and $W_f - W \geq 0$, we have

$$11. \quad \frac{1}{W_f} \ln \left(\frac{1}{W_f - W} \right) \Big|_{W_0}^W + \frac{1}{W_f} \ln W \Big|_{W_0}^W$$

$$12. \quad = \frac{1}{W_f} \left[\ln \left(\frac{1}{W_f - W} \right) - \ln \left(\frac{1}{W_f - W_0} \right) + \ln W - \ln W_0 \right]$$

$$13. \quad = \frac{1}{W_f} \left[\ln \left(\frac{W_f - W_0}{W_f - W} \right) + \ln \left(\frac{W}{W_0} \right) \right] = kt = \ln \left[\left(\frac{W_f - W_0}{W_f - W} \right) \frac{W}{W_0} \right] = W_f kt$$

Taking exponentials, we have:

$$14. \quad \frac{(W_f - W_0) W}{(W_f - W) W_0} = e^{W_f kt}$$

$$15. \quad (W_f - W_0) W = (W_f - W) W_0 e^{W_f kt}$$

$$16. \quad W(W_f - W_0) = W_f W_0 e^{W_f k t} - W W_0 e^{W_f k t}$$

$$17. \quad W(W_f - W_0 + W_0 e^{W_f k t}) = W_0 W_f e^{W_f k t}$$

$$18. \quad W = \frac{W_0 W_f e^{W_f k t}}{W_f - W_0 + W_0 e^{W_f k t}}$$

$$19. \quad W = \frac{W_0 W_f}{(W_f - W_0) e^{-W_f k t} + W_0}$$

$$20. \quad W = \frac{W_f}{\left(\frac{W_f - W_0}{W_0} \right) e^{-W_f k t} + 1},$$

where W_f represents the maximum dry weight of the plant. We see that W is in the form of the logistic, or autocatalytic equation.

Applications of the logistic model

The logistic model has been used to model a variety of aspects of plant growth. Gregory (1921) modelled the growth of cucumber leaves using the logistic model. He measured the various diameters of cucumber leaves over a 16-day period and obtained growth curves similar to the logistic curve. Prescott (1922) modelled the number of flowers per plant of the egyptian cotton plant using the logistic model. He counted the average number of flowers per plant for a period of 110 days. The flowering curve was a logistic curve.

A number of other aspects of plant growth have been modelled using the logistic curve. More recently, Major (1980) modelled the effects of simulated frost injury on the growth and development of corn (*Zea mays*) over a three-year period, from 1975 to 1977. Each year, corn hybrids were sprayed with a substance called paraquat which simulated the effect of frost. The curves obtained when plotting the grain dry matter over a 100-day period yielded logistic curves.

Ferraris and Sinclair (1980) obtained logistic curves when studying the dry weight of elephant grass (*Pennisetum purpureum*) in the wet tropics of north Queensland, Australia.

Silisbury and Fukai (1977) examined the dry weight of shoots of the subterranean clover (*Woogenellup*) over a 6-month period, in Adelaide, Australia. The growth curves obtained were logistic curves.

To demonstrate these growth curves, we will examine the flowering records of cotton plants, collected by Prescott. Consider the following table.

Flowering Records of Cotton Plants

Dates of Sowing, 1920

<u>Days</u>	<u>Flowers per plant</u>
15	0.3
20	1.2
25	2.3

30	3.7
35	6.2
40	9.4
45	14.2
50	19.2
55	24.2
60	28.7
65	32.3
70	35.2
75	36.5
80	37.3
85	37.8
90	38.2
95	38.3
100	38.3
105	38.4
110	38.4

We will plot the above values and compare it with the least-squares approximation of the logistic equation. We will see that the data closely follows the logistic form.


```
In[5]:=
```

```
n = 20
```

```
Out[5]=
```

```
20
```

```
In[6]:=
```

```
days = {15,20,25,30,35,40,45,50,55,60,65,70,75,80,85,90,95,100,105,110}
```

```
Out[6]=
```

```
{15, 20, 25, 30, 35, 40, 45, 50, 55, 60, 65, 70, 75, 80, 85,  
90, 95, 100, 105, 110}
```

```
In[7]:=
```

```
flowers = {.3,1.2,2.3,3.7,6.2,9.4,14.2,19.2,24.4,28.7,32.3,35.2,36.5,37
```

```
Out[7]=
```

```
{0.3, 1.2, 2.3, 3.7, 6.2, 9.4, 14.2, 19.2, 24.4, 28.7, 32.3,  
35.2, 36.5, 37.3, 37.8, 38.2, 38.3, 38.3, 38.4, 38.4}
```

```
In[8]:=
```

```
max = 38.5 We assume that the maximum # of flowers  
per plant is 38.5
```

```
In[17]:=
```

```
f[X_] = Log[(max - X)/(X max)]
```

```
Out[17]=
```

```
Log[ $\frac{0.026974 (38.5 - X)}{X}$ ]
```

```
In[18]:=
```

```
c = Map[f, flowers]
```

```
Out[18]=
```

```
{1.19615, -0.213986, -0.894508, -1.40937, -2.00014,  
-2.52063, -3.11342, -3.64546, -4.19907, -4.72517,  
-5.30118, -6.01778, -6.55482, -7.08733, -7.63964,  
-8.49747, -8.90555, -8.90555, -9.6013, -9.6013}
```

```
In[20]:=
```

```
d1 = Sum[days[[i]],{i,1,n}]
```

```
Out[20]=
```

```
1250
```

```
In[21]:=
```

```
d2 = Sum[(days[[i]])^2, {i,1,n}]
```

```
Out[21]=
```

```
94750
```

```

In[22]:=
  c1 = Sum[c[[i]], {i,1,n}]
Out[22]=
  -99.6375
In[27]:=
  dc = Sum[days[[i]] c[[i]], {i,1,n}]
Out[27]=
  -8098.07
In[28]:=
  A = {{-d2,d1,tc},{-d1,n,c1}}
Out[28]=
  {{-94750, 1250, -8098.07}, {-1250, 20, -99.6375}}
In[29]:=
  MatrixForm[A]
Out[29]//MatrixForm=


|        |      |          |
|--------|------|----------|
| -94750 | 1250 | -8098.07 |
| -1250  | 20   | -99.6375 |


In[30]:=
  B = RowReduce[A]
Out[30]=
  {{1., 0, 0.112525}, {0, 1., 2.05092}}
In[31]:=
  R = N[B, 10]
Out[31]=
  {{1., 0, 0.1125247686}, {0, 1., 2.050921583}}
In[32]:=
  MatrixForm[R]
Out[32]//MatrixForm=


|    |    |              |
|----|----|--------------|
| 1. | 0  | 0.1125247686 |
| 0  | 1. | 2.050921583  |


In[41]:=
  g[X_] = -R[[1,3]]*X +R[[2,3]]
Out[41]=
  2.050921583 - 0.112525 X

```


In[42]:=

Y = Table[g[days[[i]]], {i,1,n}]

Out[42]=

{0.36305, -0.199574, -0.762198, -1.32482, -1.88745,
-2.45007, -3.01269, -3.57532, -4.13794, -4.70056,
-5.26319, -5.82581, -6.38844, -6.95106, -7.51368,
-8.07631, -8.63893, -9.20156, -9.76418, -10.3268}

In[45]:=

residual = Sum[(c[[i]]-Y[[i]])^2, {i,1,n}]

Out[45]=

1.74538

← we found the residual sum of squares.

In[46]:=

h[X_] = 1/((Exp[X] max + 1) / max)

Out[46]=

$$\frac{38.5}{1 + 38.5 E^X}$$

In[47]:=

s = Map[h,Y]

Out[47]=

{0.683209, 1.18336, 2.02999, 3.42672, 5.63595, 8.90776,
13.3097, 18.5252, 23.8494, 28.5191, 32.0999, 34.5728,
36.1599, 37.131, 37.708, 38.0447, 38.2393, 38.351, 38.415,
38.4515}

In[49]:=

```
Do[Print[days[[i]]. " " ,flowers[[i]]. " " , s[[i]]], {i,1,n}]
```

15	0.3	0.683209
20	1.2	1.18336
25	2.3	2.02999
30	3.7	3.42672
35	6.2	5.63595
40	9.4	8.90776
45	14.2	13.3097
50	19.2	18.5252
55	24.4	23.8494
60	28.7	28.5191
65	32.3	32.0999
70	35.2	34.5728
75	36.5	36.1599
80	37.3	37.131
85	37.8	37.708
90	38.2	38.0447
95	38.3	38.2393
100	38.3	38.351
105	38.4	38.415
110	38.4	38.4515

In[50]:=

```
data = Table[{days[[i]], flowers[[i]]}, {i,1,n}]
```

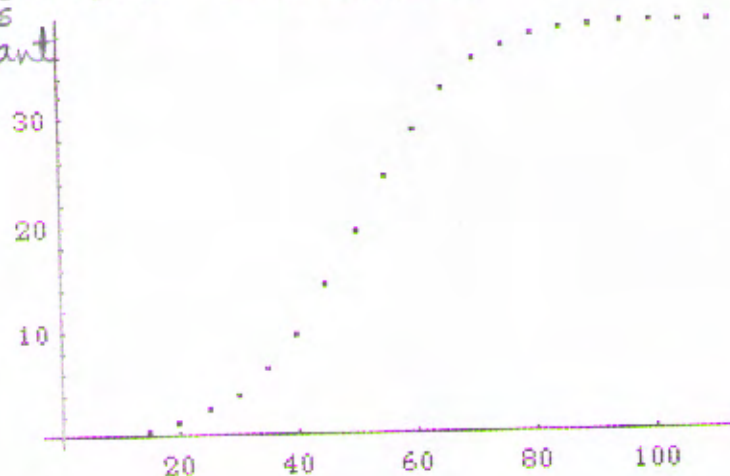
Out[50]=

```
{{15, 0.3}, {20, 1.2}, {25, 2.3}, {30, 3.7}, {35, 6.2},  
 {40, 9.4}, {45, 14.2}, {50, 19.2}, {55, 24.4}, {60, 28.7},  
 {65, 32.3}, {70, 35.2}, {75, 36.5}, {80, 37.3},  
 {85, 37.8}, {90, 38.2}, {95, 38.3}, {100, 38.3},  
 {105, 38.4}, {110, 38.4}}
```


In[54]:=

pointplot = ListPlot[data]

flowers
per plant



We plot the
data collected
from Prescott

Out[54]=

-Graphics-

In[72]:=

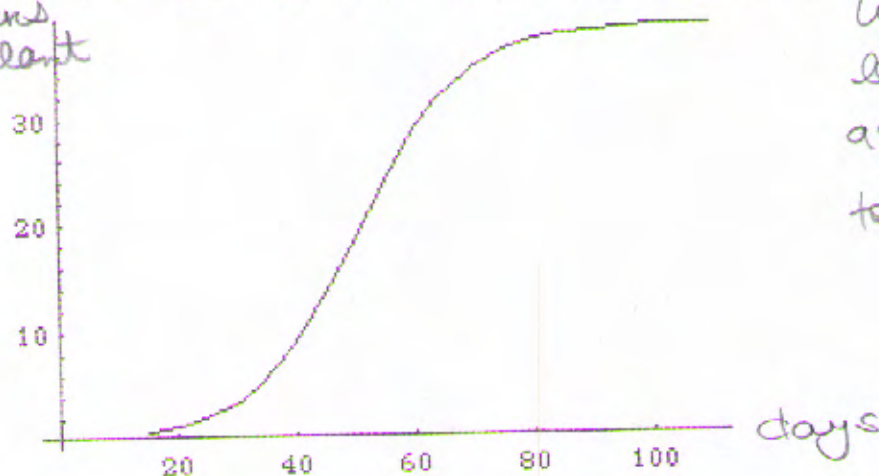
data2 = Table[{days[[i]], s[[i]]}, {i, 1, n}]

Out[72]=

```
{{15, 0.683209}, {20, 1.18336}, {25, 2.02999},
 {30, 3.42672}, {35, 5.63595}, {40, 8.90776},
 {45, 13.3097}, {50, 18.5252}, {55, 23.8494},
 {60, 28.5191}, {65, 32.0999}, {70, 34.5728},
 {75, 36.1599}, {80, 37.131}, {85, 37.708}, {90, 38.0447},
 {95, 38.2393}, {100, 38.351}, {105, 38.415},
 {110, 38.4515}}
```

In[73]:=

curve = ListPlot[data2, PlotJoined -> True]

flowers
per plant

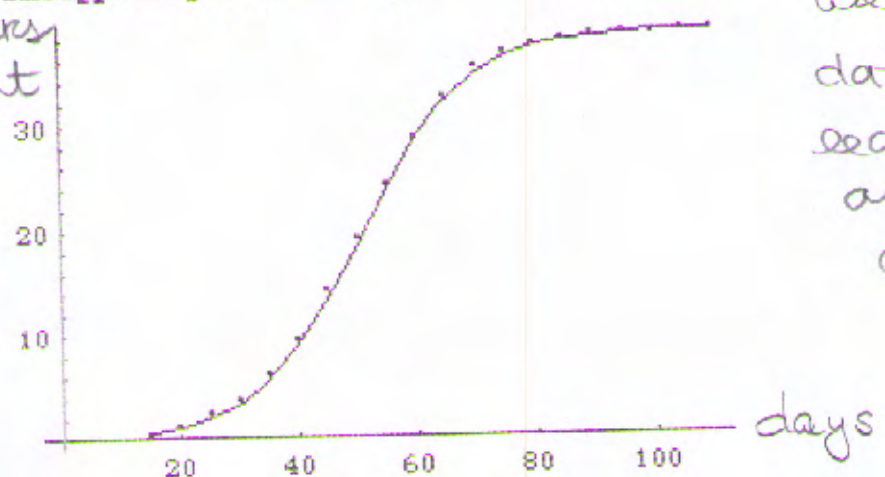
We plot the
least-squares
approximation
to the logistic
equation.

Out[73]=

-Graphics-

In[74]:=

Show[pointplot, curve]

flowers
per plant

We see that the
data and the
least-squares
analysis
correspond well.

Out[74]=

-Graphics-

A second model

The first model has a number of limitations. It doesn't take into account many of the various processes that can affect plant growth. These processes include respiration, the process by which plants remove waste products generated in the manufacture and conversion of nutrients, and nutrient assimilation, the absorption of nutrients from the soil through the root system. The model also doesn't account for changes in temperature, pressure and other environmental factors. The first model also doesn't differentiate between the different parts of the plant, and their individual requirements for growth.

In an effort to improve upon the first model, we will consider the effects of nutrient assimilation and respiration. We will also divide the plants into 3 parts: the roots, storage organ and leaves. Their individual requirements for nutrients will also be considered. Leaf death plays a role in decreasing the weight of the plant, and this will also be considered in the new model.

The following assumptions made in the model are as follows:

Each part of the plant, the roots, storage organ and leaves place a demand on the available supply of nutrients. The size (dry weight) of each component gives a reasonable measure for the component's demand. That is, each component absorbs a quantity of available nutrients directly proportional to its current dry weight.

The process of respiration applies to all parts of the plant, since all plant parts produce waste products. The rate of respiration is determined by how much the plant takes in (nutrient assimilation) and the size of the plant part. Thus, each plant part removes waste by an amount directly proportional to the amount of nutrients absorbed, and by an amount proportional to its current size.

Finally, we consider the loss of dry weight due to the death of leaves. This of course, only happens to one of the three components of the plants, the leaves.

If we assume that conservation of mass applies in this system, then the total nutrients available are taken up by the various plant components. We can express this as

$$1. \quad \Delta N = \Delta N_l + \Delta N_s + \Delta N_r,$$

where ΔN represents the total amount of nutrients available during the time interval Δt , and ΔN_l , ΔN_s , ΔN_r represent the amounts of nutrient supplied to the leaves, storage organs and roots respectively during the time interval Δt .

We now want to find expressions for ΔN_l , ΔN_s and ΔN_r . Recall our assumption that each component demands an amount of the total supply of nutrients linearly proportional to the component's current size (dry weight). We can therefore write

$$2. \quad \Delta N_l = A_l l \Delta N$$

$$\Delta N_s = A_s s \Delta N$$

$$\Delta N_r = A_r r \Delta N,$$

where l , s and r represent the dry weights of the leaves, storage organs, and roots, respectively. The values A_l , A_s and A_r represent the nutrient assimilation rates, or the demand strengths for each component.

$$\text{Now } \Delta N = \Delta N_l + \Delta N_s + \Delta N_r$$

$$3. \quad = A_l l \Delta N + A_s s \Delta N + A_r r \Delta N$$

$$= (A_l l + A_s s + A_r r) \Delta N, \quad \text{and} \quad A_l l + A_s s + A_r r = 1.$$

Note that the A 's cannot be constant values, since the values of l , s and r vary with time.

The dry weight of the whole plant is represented by W . The change in plant weight, ΔW , can be represented as

$$4. \quad \Delta W = \Delta N - \Delta R - \Delta D_l.$$

That is, the change in plant weight equals the change in the nutrient level minus the dry weight loss due to respiration, and ΔD_l , the loss of dry weight due to the death of leaves.

Now the dry weight is equal to the sum of the weights of the individual components, so we can write

$$5. \quad \Delta W = \Delta l + \Delta s + \Delta r.$$

Each component can be expressed as:

$$6. \quad \Delta l = \Delta N_l - \Delta R_l - \Delta D_l$$

$$\Delta s = \Delta N_s - \Delta R_s$$

$$\Delta r = \Delta N_r - \Delta R_r$$

That is, the dry weight of leaves equals the weight of the nutrients absorbed minus the dry weight loss through leaf respiration minus the dry weight loss attributable to leaf death. The dry weight of the storage organ and the root are expressed as the weight of nutrients absorbed minus the weight loss during respiration.

We had assumed as part of our assumptions that the rate of respiration in a given time interval Δt depended on the amount of nutrient assimilated by each component as well as the individual size of each component. We can therefore express each of the partial respiratory dry weight losses as:

$$\Delta R_l = \alpha_l \Delta N_l + m_l l \Delta t$$

$$7. \quad \Delta R_s = \alpha_s \Delta N_s + m_s s \Delta t$$

$$\Delta R_r = \alpha_r \Delta N_r + m_r r \Delta t,$$

where the α 's may be constants and the m values represent respiration rates ^{per} unit mass.

Since we now have expressions for the partial respiration dry weight losses, we can substitute these expressions into equations 6 to obtain

$$\Delta l = \Delta N_l - \alpha_l \Delta N_l - m_l l \Delta t - \Delta D_l$$

8.
$$\Delta s = \Delta N_s - \alpha_s \Delta N_s - m_s s \Delta t$$

$$\Delta r = \Delta N_r - \alpha_r \Delta N_r - m_r r \Delta t$$

If we let $\Delta t \rightarrow 0$, we can express the above as a system of differential equations

9.
$$\frac{dl}{dt} = \beta_l \frac{dN_l}{dt} - m_l l - \frac{dD_l}{dt}$$

$$\frac{ds}{dt} = \beta_s \frac{dN_s}{dt} - m_s s$$

$$\frac{dr}{dt} = \beta_r \frac{dN_r}{dt} - m_r r,$$

where $\beta_l = 1 - \alpha_l$, $\beta_r = 1 - \alpha_r$ and $\beta_s = 1 - \alpha_s$.

We see that this set of equations describe the rate of increase in dry weight of the individual components in terms of the available nutrients.

Consider equation 2. We can rewrite these expressions as differential equations by letting $\Delta t \rightarrow 0$. We have

10.
$$\frac{dN}{dt} = \frac{dN_l}{dt} \frac{1}{A_l l} = \frac{dN_s}{dt} \frac{1}{A_s s} = \frac{dN_r}{dt} \frac{1}{A_r r}$$

We can rewrite equations 9 in terms of the nutrient supply terms and substitute

them into equation 10 to obtain

$$11. \quad \frac{1}{\beta_l A_l l} \left[\frac{dl}{dt} + m_l l + \frac{dD_l}{dt} \right] = \frac{1}{\beta_s A_s s} \left[\frac{ds}{dt} + m_s s \right] = \frac{1}{\beta_r A_r r} \left[\frac{dr}{dt} + m_r r \right]$$

Before proceeding, we need to make some assumptions regarding the A , β

values, as well as the value $\frac{dD_l}{dt}$. We know that the A values, the relative demand strengths for the individual components are not constant values. However, it is possible that the ratio of the rates of assimilation is constant. That is, we assume the ratio of the rates of assimilation for leaves to the rate of assimilation of the storage organs is constant. β_l and β_s depend on the chemical composition of the leaves and storage organs. These values depend mostly on the protein contents of the respective tissues. Although the fraction of plant tissue which is protein tends to decline as plants grow, it has been shown by Greenwood that the ratio of protein fractions for two types of tissue may remain approximately constant, at least for the leaves and storage organ. Therefore, $\frac{\beta_l}{\beta_s}$ may not vary much during growth, and we can consider their ratio to be constant.

We now consider the term $\frac{dD_l}{dt}$. We will approximate this term by the average death rate for leaves, $d_l l$, in order to simplify the model.

Consider the expressions involving the leaves and the storage organ in equation 11. If we make all the above assumptions, we have

$$12. \quad \frac{1}{l} \left(\frac{dl}{dt} + m_l l + d_l l \right) = \frac{\mu \beta_l}{\beta_s s} \left(\frac{ds}{dt} + m_s s \right), \text{ where } \mu = \frac{A_l}{A_s}.$$

$$13. \quad \left(\frac{1}{l} \frac{dl}{dt} + m_l + d_l \right) = \frac{\mu \beta_l}{\beta_s} \left[\frac{1}{s} \frac{ds}{dt} + m_s \right]$$

We can now integrate with respect to t (from t_0 to t)

14. $\int_{l_0}^l \frac{1}{l} \frac{dl}{dt} = \int_{s_0}^s \gamma \frac{1}{s} \frac{ds}{dt} + \int_{t_0}^t (m_s \gamma - m_l - d_l) dt$, where $\gamma = \frac{\mu \beta_l}{\beta_s}$ and l_0, s_0 are the initial dry weights of the leaves and storage organs, respectively. Now $l \geq l_0$ and $s \geq s_0$, so we have

15. $\ln(l - l_0) = \gamma \ln(s - s_0) + (\gamma m_s - m_l - d_l)(t - t_0)$

This can be expressed as $\ln l = a + \gamma \ln s - bt$,

where $a = \ln l_0 - \gamma \ln s_0 + t_0(\gamma m_s - m_l - d_l)$

$$= \ln l_0 - \gamma \ln s_0 + bt_0$$

and $b = -\gamma m_s + m_l + d_l$.

We now have a formula relating the dry weights of the leaves and storage organs. Note that this formula could also be expressed as

16. $l = e^{a + \ln s^\gamma - bt} = e^a s^\gamma e^{-bt} = K s^\gamma e^{-bt}$, where $K = e^a$ and a, b, γ are constants.

To demonstrate this model, consider the following data for harvests of carrots in 1978, derived from Barnes.

The following data lists the values of the natural logarithms of the dry leaf weight and dry storage organ weight for various times after emergence.

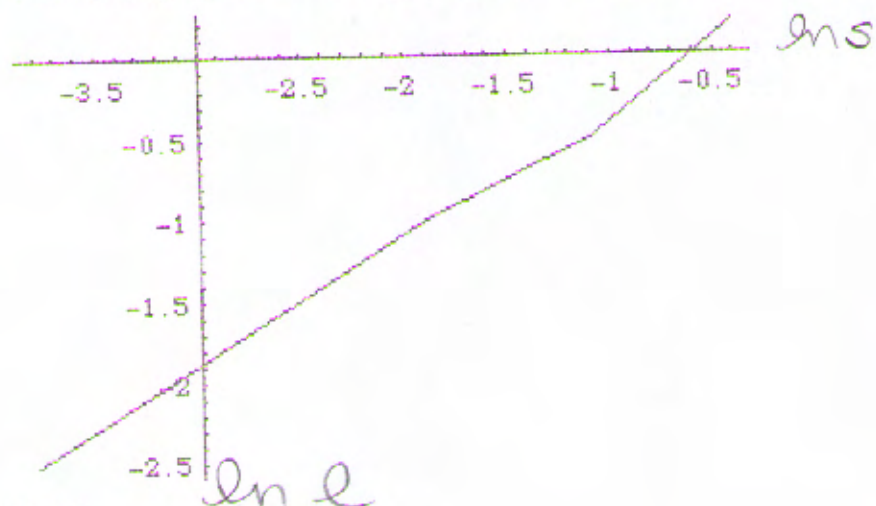
Grouped carrot data

Time from emergence (days)									
35		63		91		119		140	
ln s	ln l	ln s	ln l	ln s	ln l	ln s	ln l	ln s	ln l
-3.8	-2.5	-1.9	-1.3	-1.7	-1.4	-1.3	-1.4	-0.6	-1.2
-1.9	-1.0	-0.2	-0.1	0.7	0.4	1.0	0.1	1.3	0.3
-1.1	-0.5	0.6	0.6	1.4	0.9	1.7	0.8	2.0	0.8
-0.4	0.2	1.2	1.1	2.3	1.6	2.7	1.6	2.8	1.4

integrated

In[78]:=

ListPlot[{{-3.8,-2.5},{-1.9,-1.0},{-1.1,-0.5},{-0.4,0.2}}, PlotJoined -

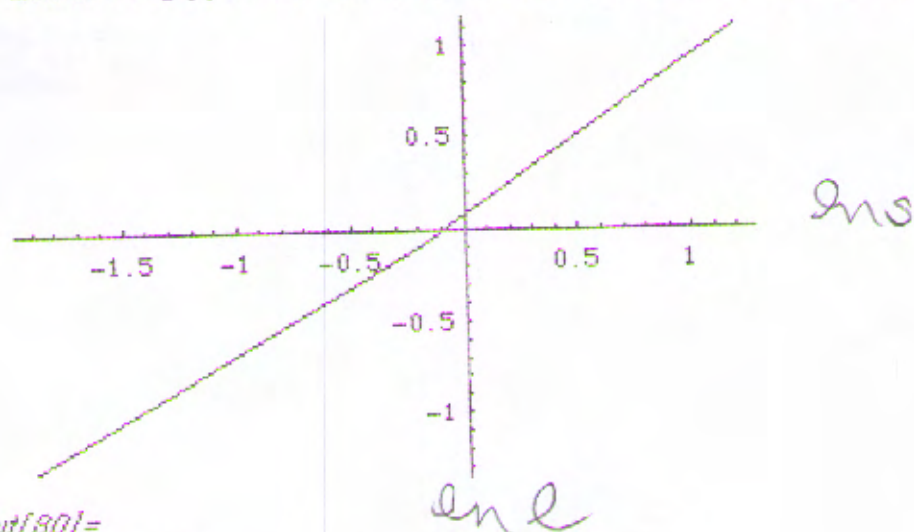


Out[78]=

-Graphics-

In[80]:=

ListPlot[{{-1.9,-1.3},{-0.2,-0.1},{0.6,0.6},{1.2,1.1}}, PlotJoined -> T

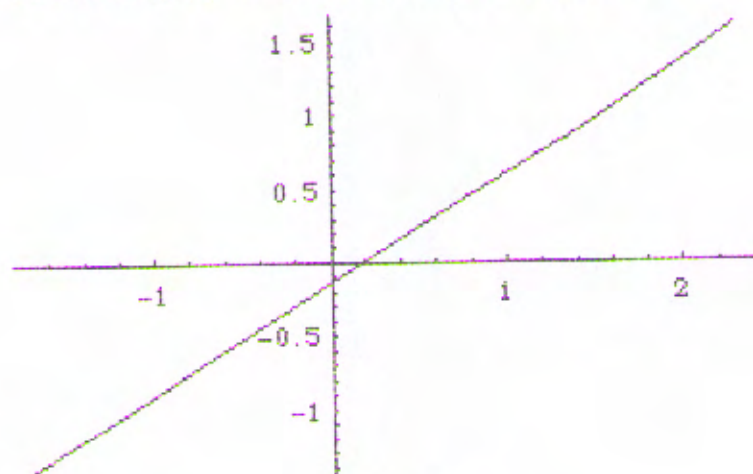


Out[80]=

-Graphics-

```
In[81]:=
```

```
ListPlot[{{-1.7,-1.4},{0.7,0.4},{1.4,0.9},{2.3,1.6}}, PlotJoined -> Tr
```



Ins

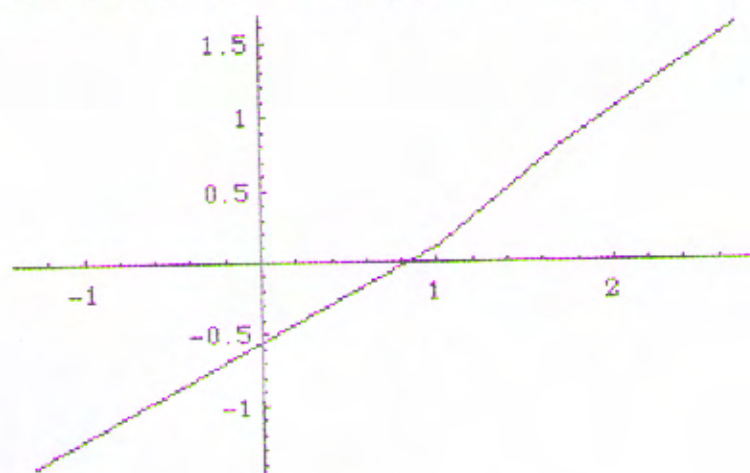
```
Out[81]=
```

```
-Graphics-
```

Inl

```
In[82]:=
```

```
ListPlot[{{-1.3,-1.4},{1.0,0.1},{1.7,0.8},{2.7,1.6}}, PlotJoined -> Tru
```



Ins

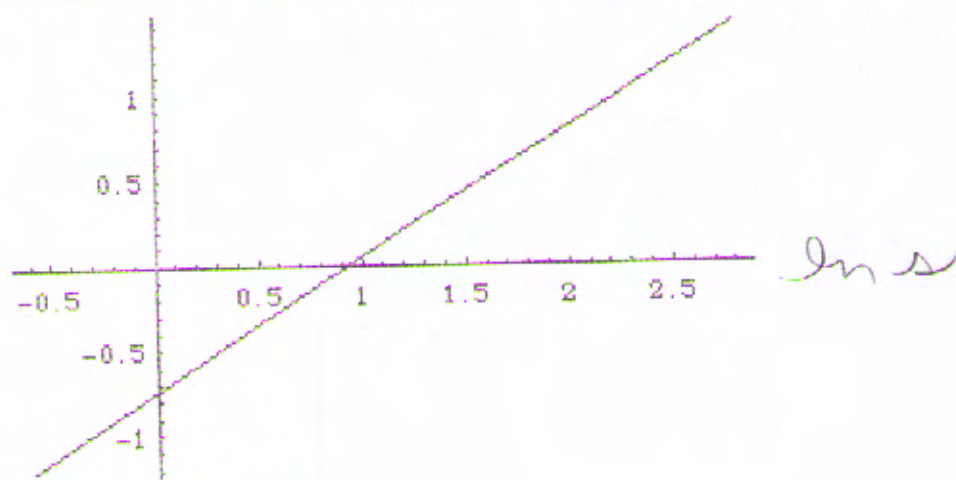
```
Out[82]=
```

```
-Graphics-
```

Inl

```
In[83]:=
```

```
ListPlot[{{-0.6,-1.2},{1.3,0.3},{2.0,0.8},{2.8,1.4}}, PlotJoined->True
```



```
Out[83]=  $\ln l$   
-Graphics-
```

We see that the relationship between $\ln s$ and $\ln l$ is approximately linear, thus supporting the model.

If we plot this data, for various values of t , we should see a linear relationship between $\ln s$ and $\ln l$.

Conclusion

Although the two models presented describe the given data quite well, there are situations where the models are inadequate. Although the second model addresses the need to incorporate such factors as assimilation rates, respiration rates and leaf death, a number of other factors have not been dealt with. For example, the effects of photosynthesis, temperature and pressure on plant growth are not included in the models.

Many other models have been developed that address these and other issues. Mechanistic models of leaf photosynthesis have been proposed by Setlik, Acock, Thornley and Wilson. Variations of the model that take into account light flux density and light and dark respiration have also been constructed.

There are also models that incorporate geographical partitioning of the plant. These models are concerned with the distribution of material between the different parts of a plant, such as leaves, stems, roots, fruit, stem, etc. Other models make use of chemical partitioning, dealing with the distribution of carbon (or some other compound) over different substances such as carbohydrates, organic acids, etc.

In short, there exists many different types of models of plant growth. Referring back to the table of plant processes and properties, we see that many different types of models could be constructed, each focusing on different processes affecting plant life.

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