GROWTH ANALYSIS II

1) COLONY GROWTH

2) RELATIVE GROWTH RATES

3) NET ASSIMILATION RATE

4) CROP SPACING

GROWTH ANALYSIS II

1. Growth of Colonies

(a) Unrestricted Colony Growth

In unicellular organisms growth may consist simply of enlargement of the single cell, which after a time divides into two daughter-cells. Since each daughter-cell will, in due course, divide again, the number of cells will increase in geometric progression, so long as there is adequate nutriment and conditions remain favourable for growth.

Let n_o = initial no. of cells
n = number of cells after given time t.
x = number of generations occurring in time t.

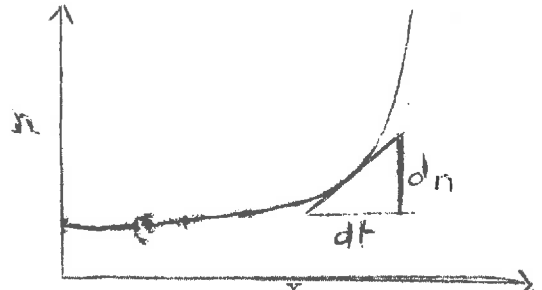
Then, at end of 1st generation $n = n_o \times 2$
" 2nd " $n = n_o \times 2 \times 2$
" xth " $n = n_o \times 2^x$

This means that the colony is growing at an ever-increasing rate or "exponentially".

Example Growth of colony of bacteria

Time (minutes)	No. bacteria	log no.
120	87	1.94
220	2876	3.46
290	36675	4.56
370	739200	5.87

If we plot the number of cells against time we get a curve of the following type:-



From the equation $n = n_o \times 2^x$ we can write:-

$$\log n = \log n_o + x \log 2.$$

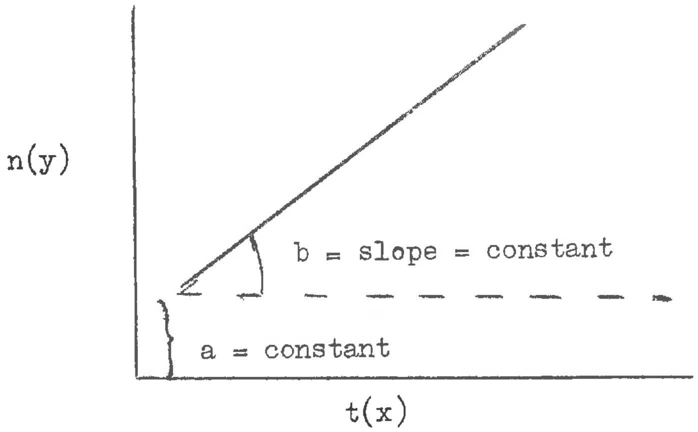
Since $x = \frac{t}{g}$ where g = the generation time, (or the time for one complete cellular life-cycle) we may write:-

$$\log n = \log n_o + \frac{t}{g} \log 2$$

Now $\frac{\log 2}{g}$ will be a constant (K)

$$\therefore \underline{\log n = \log n_o + kt.} \text{ ——(1)}$$

This equation is of the form $y = b + ax$, and hence if we plot the log of the number of cells against time, we get a straight line:-



This type of relationship has frequently been demonstrated for colonies of bacteria, yeast, *Lemna* etc.

The growth rate of the colony is given by the increase (dn) in the number of cells of the colony over a time interval (dt). This is clearly given by the slope $\left(\frac{dn}{dt}\right)$ of the curve at any time and it will be seen from the graph that the value of the slope increases progressively with time. If all cells are dividing at the same rate, clearly at any time t, the rate of growth of the colony is proportional to the number of cells present, i.e. $\frac{dn}{dt} \alpha N$. Thus, although the rate of cell-division (r) remains constant, the absolute growth-rate of the colony does not. The value of r is given by $\frac{dn}{dt}.\frac{1}{n}$, and this is known as the relative growth rate of the colony. Thus, for a colony showing this type of growth, the absolute growth rate increases with time, but the relative growth-rate remains constant.

Using elementary calculus we can deal with colony-growth in general terms to obtain the following relationship:

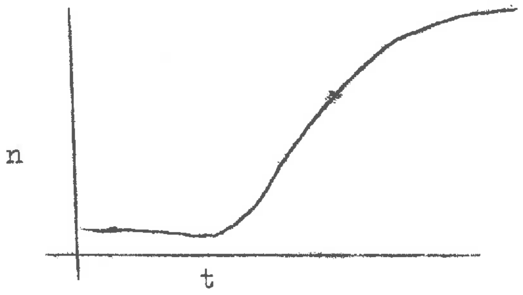
$$n = n_o e^{kt} \text{ ------------------------} (2)$$

where, e = exponential coefficient = 2.7182

In practice, unrestricted growth of a colony can never proceed indefinitely and some limiting factor, such as deficiency of nutrients, must always lead to a decline in growth-rate sooner or later.

(b) Restricted Colony Growth

Under cultural conditions in a flask or test tube, for example, the food supply will ultimately be exhausted and growth will finally cease. Instead of the typical 'exponential' growth curve for cell-number, we get an s-shaped or sigmoid type of curve.

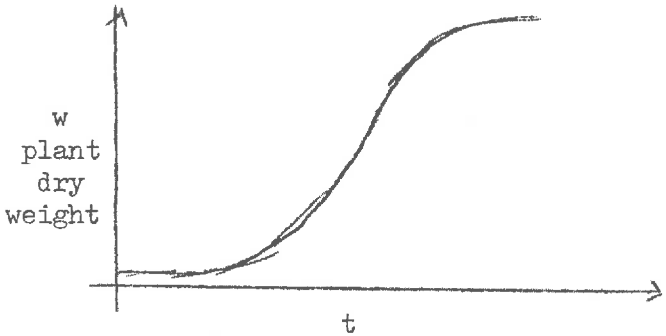


In addition to the exhaustion of some food factor, growth in such colonies may also be limited by some toxic substance which is itself the product of growth. The production of such substances often occurs with cultures of bacteria, fungi, Chlorella, etc.

2. Growth of Multicellular Organisms

(1) The Exponential Phase The sigmoid type of growth curve observed for colonies of unicellular organisms is characteristic also of the growth of individual multicellular plants. This is true not only for the whole plant, but also for individual organs, such as leaves or internodes.

This means that initially the organism is increasing in size (or weight) by geometrical progression or 'exponentially'.



V.H. Blackman (1919) showed that during this initial phase the growth of seedlings follows a 'Compound Interest Law' fairly colosely and is given by the equation

$$w = w_o e^{rt} \text{ - - - - - - - - - - - - } (3)$$

where w = Weight of plant after time t

w_o = initial " "

r = % age rate of increase

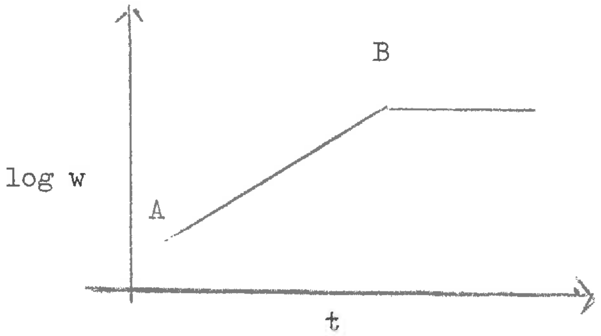
e = exponential coefficient (= 2.7182)

This equation is clearly exactly comparable with equation (2) above for xolony-growth and may be derived in a precisely similar manner.

From equation (3) we may write

$$\log w = \log w_o + rt \log e$$

This equation is again of the form $y = b + ax$. This means that we should obtain a straight line when we plot log-weight against t, (at least for the initial phase of growth, which we are now considering) and this has, in fact, been demonstrated in many cases. (see portion A-B of the following curve):



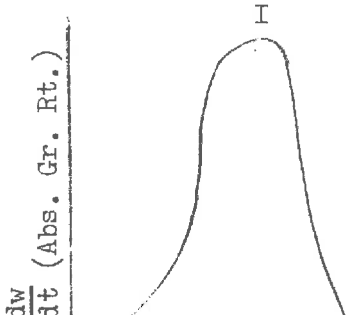
The final weight attained will clearly depend upon (i) the initial weight, (ii) the rate of 'interest'interest' (r); (iii) the time. The rate of interest represents the efficiency of the plant as a producer of new material and was called by Blackman the efficiency index of dry weight production. A small difference in the efficiency index between two plants will soon make a marked difference in the total yield, and the difference will increase with the lengthening of the period of growth.

It should be noted that the efficiency index is merely a different method of expressing the relative growth rate $\left(\frac{dw}{w.dt}\right)$ as described for colony-growth (see p.2). Whereas the efficiency index (or relative growth-rate) remains constant through the exponential growth phase, the absolute increments per unit time increase progressively. The absolute growth increment over a time interval dt is clearly $(W \times \frac{r}{100}).\ dt$. Thus, the absolute growth rate at any given time is proportional to the size of the plant at that time. The physiological basis of this latter conclusion is easily understood, for when photosynthesis has become active in a young seedling, the power of the plant to synthesize new material (and hence increase dry weight), is clearly dependent upon its leaf area. Hence, as the plant grows and increases its leaf-area, the rate at which new material is assimilated will increase proportionately,

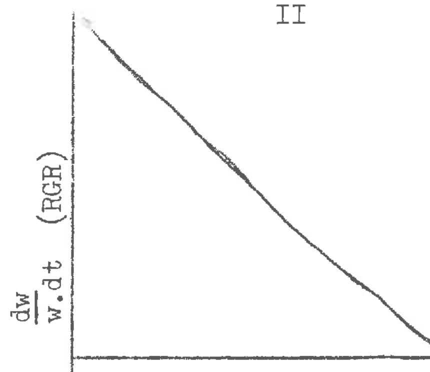
(2) Late phases of growth

Just as the growth rate $\left(\frac{dn}{dt}\right)$ of a bacterial colony ultimately falls off with time due to the exhaustion of nutrients or the accumulation of toxic products, so the growth rate of a multicellular organism decreases gradually, resulting in a sigmoid curve. The (absolute) growth rate $\frac{dw}{dt}$ is clearly given by the slope of the curve at any time t if we plot the changes in this growth rate with time we get a curve of the type I.

I



II



This clearly attains a maximum (corresponding to the point of inflexion of the s-shaped growth curve) and then falls away to zero. If, on the other hand, we plot the relative growth rate $\left(\frac{dw}{w.dt}\right)$ against time, we frequently get a curve of type II. It is seen that the relative growth rate falls more or less uniformly over the whole period of growth.

The reason for the fall in the relative growth rate throughout the period of growth is not fully understood and various hypotheses have been suggested. The deficiency of some nutritive factor is clearly not the cause, as it is in colonies of unicellular organisms under artificial conditions. It has been suggested, however, that the reason for the departure from 'exponential' growth in a normal plant is that part of the plant material formed during growth gives rise to mecanical, vascular and other tissues which do not directly contribute to further synthesis of new material. The leaves which are the organs most directly concerned in the synthesis of new material thus constitute a diminishing fraction of the total plant weight i.e. the ratio: $\frac{\text{leaf area (L)}}{\text{total dry weight (W)}}$ (known as the Leaf/Weight ratio) gradually falls.

Now the relative growth rate = $\frac{dw}{dt} \cdot \frac{1}{w}$

Multiplying numerator and denominator by L, we get

$$\frac{dw}{L} \cdot \frac{L}{W} \cdot \frac{1}{dt}$$

Now $\frac{dw}{L} \cdot \frac{1}{dt}$ is the photosynthetic rate or Net Assimilation Rate(NAR),

which usually does not change appreciably with the age of the plant. Hence, it has been suggested that the fall in the relative growth rate must primarily be due to the fall in value of $\frac{L}{W}$, the leaf-weight ratio, for the reasons already indicated.

Allometric Growth

It was the first clearly demonstrated by J.S. Huxley that a simple mathematical relation exists between the sizes of different organs of animals, e.g. between chela-size and body-size in crabs, between antler size and body size in deer, etc. This relation is of the form

$$y = b\,x^{k} \text{ - - - - - - - - } (4)$$

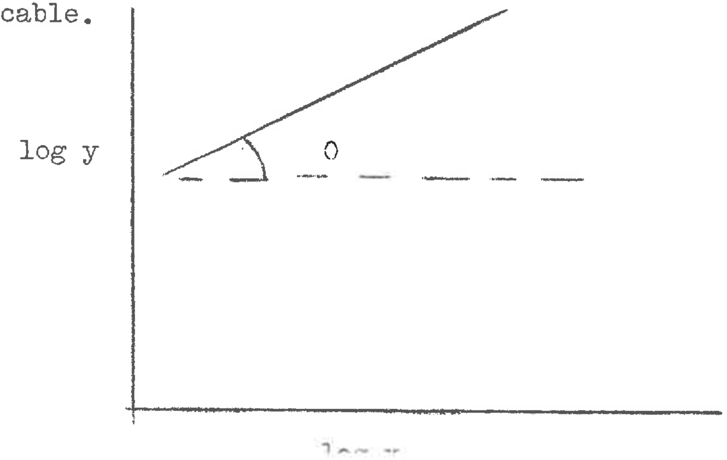
where x and y are the dimensions (or weights) of the organs and b and k are constants. This is known as the 'Allometric' growth relationship.

A similar relationship has been shown to exist between the relative sizes of various organs in plants, e.g. between weight of shoot and root, between lamina diameter and petiole length, length and width in Cucurbita fruits, between leaf length and leaf breadth in may species etc.

From equation (4) we can write:-

$$\text{Log } y = k.\ \log x + \log b \text{ - - - - } (5)$$

Now equation (5) is of the form y = ax + b, so that if we plot log y against log x, we should get a straight line, where this law is applicable.



It is clear that the value of "k" is given by the slope of the line ($\tan\theta$) while log b is given by the value of log y for log x = o.

Let us consider the implications of this law. Firstly, if we differentiate equation (5), we can re-write it in the form :-

$$\frac{dy}{y} = k.\frac{dx}{x}$$

or

$$\frac{dy}{y.dt} = k.\frac{dx}{x.dt}$$

Now $\frac{y}{y.dt}$ and $\frac{x}{x.dt}$ are the relative growth rates of the two plant parts and hence we see that there is a constant relation between these two rates. If k = 1, the two dimensions are increasing at the same <u>relative</u> growth rate. If K 1, the y is increasing relatively slower than x, while if K 1 then y is increasing faster than x. The value of k is called the <u>relative growth coefficient</u> or the <u>differential growth coefficient</u>, and is a useful index.

If $k \neq 1$, then the linear ratio between x and y will vary with their absolute sizes. Suppose, for example $y = 2x^{0.5}$

Thus when -

$x = 1$	$y = 2.0$	$\frac{y}{x} = 2.0$
$x = 2$	$y = 2.82$	$\frac{y}{x} = 1.41$
$x = 3$	$y = 3.46$	$\frac{y}{x} = 1.15$
$x = 4$	$y = 4.0$	$\frac{y}{x} = 1.0$
$x = 5$	$y = 4.48$	$\frac{y}{x} = 0.9$

This means, for example, that where $k \neq 1$ differences in shape of a plant organ may result simply from differences in absolute size. This is well shown for fruit-shape in certain gourds where an allometric relationship holds between the length (l) and width (W) of the fruits. Where $K \neq 1$ the shape of the fruit (which will be determined partly by the ration L/W) varies with its size.

Differences of fruit shape also arise between various races of gourd, due to differences in the value of K. Thus, where k 1 we may get very elongated fruits and where k 1 we get short squat fruits (Sinnott, 1936).

Crop Plants

The capacity of a plant to produce dry matter depends on leaf area and NAR. Generally the dry weight of a plant is proportional to the leaf area.

$W \times L$ (=A) - a capacity factor

where W = dry weight

L = leaf area

We already know that the Net Assimilation Rate (NAR)

$$\text{NAR} = \frac{dw}{L} \cdot \frac{1}{dt} \quad \text{- an intensity factor}$$

Then the Crop Growth Rate (C) will depend on the NAR and leaf Area Index (total leaf area per unit area of land)

$$C = \text{NAR} \times \text{Leaf Area Index}$$

To measure NAR, LWR $(\frac{L}{W})$ and RGR

Find leaf area (L) and dry weight (w) at intervals.

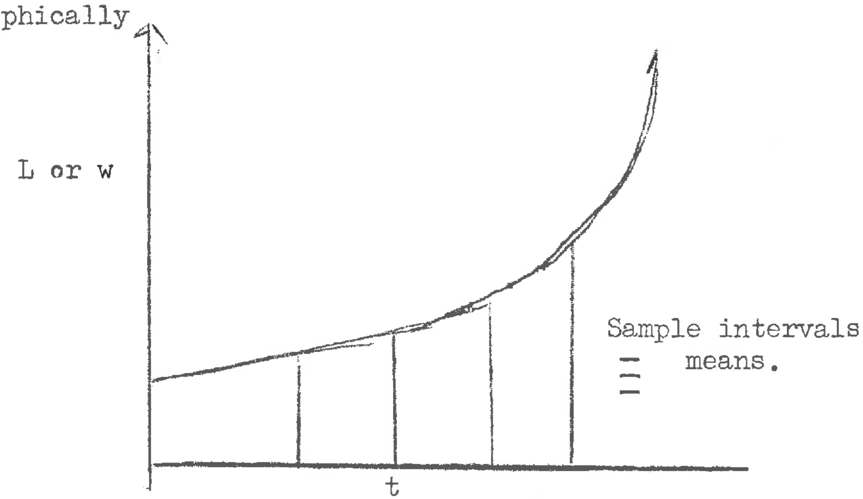
Now,

$$\text{LWR} = \frac{L}{W} = \frac{\text{leaf area}}{\text{total dry weight}}$$

and,

$$\text{NAR} = \frac{dw}{L} \cdot \frac{1}{dt}$$

Graphically



Since we are dealing with a curve and not a straight line, we cannot establish the mean by simple division.

$$\text{Mean dry weight} = \frac{W_2 - W_1}{\log_e w_2 - \log_e w_1}$$

Alternatively,

$$w_2 = w_1 \, e \, r(t_2 - t_1)$$

where r = percentage rate of increase

then,

$$\log_e w_2 = \log_e w_1 + r(t_2 - t_1)$$

thus,

$$RGR = \frac{\log_e w_2 - \log_e w_1}{t_2 - t_1}$$

since

$$NAR = \frac{dw}{L} \cdot \frac{1}{dt}$$

then

$$NAR = \frac{w_2 - w_1}{t_2 - t_1} \times \frac{\log_e L_2 - \log_e L_1}{L_2 - L_1}$$

since

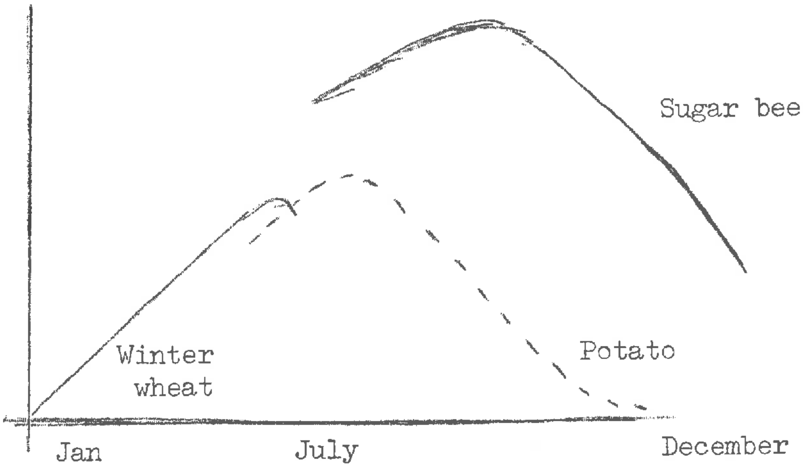
$$LWR = \frac{L}{W}$$

then

$$LWR = \frac{L_2 - L_1}{\log_e L_2 - \log_e L_1} \times \frac{\log_e w_2 - \log_e w_1}{w_2 - w_1}$$

WATSON worked on this topic using crop plants under field conditions and has developed the study of "Crop Physiology".

He considered the photosynthetic ability (NAR) of various crops under field conditions.



This reflects variations in light intensity and temperature.
The NAR increases with:-

(1) increasing day temperature
(2) decreasing night temperature

(i.e. a wide diurnal temperature range)

This may be due to the fact that the high day temperature increases photosynthesis. Cool nights reduce respiratory losses of photosynthesis. Also, the optimum temperature coefficient for carbohydrate translocation from the leaves is low. However, insugar beet this is favoured by high night temperatures.
WATSON believes that mineral nutrition has little effect on the NAR except in extremes of Nitrogen.
WAREING, working on trees, disagrees with this.
Drought affects the NAR, perhaps by decreasing CO_2 uptake through the stomatrd.

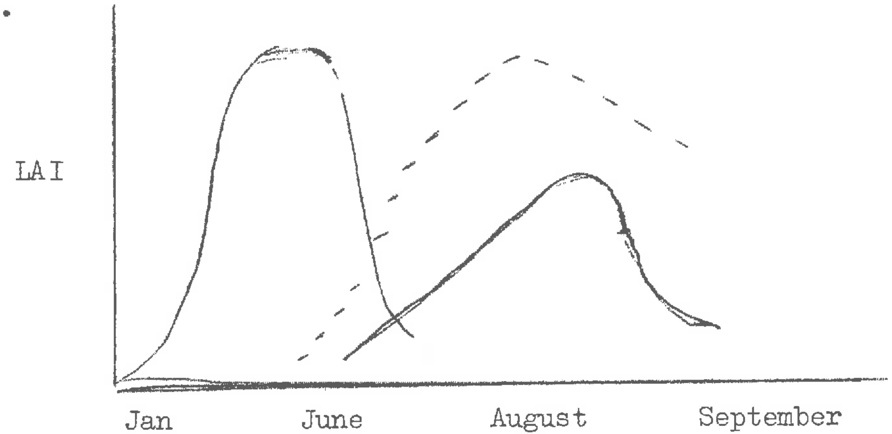
NAR of different species

GREGORY once claimed that there was very little differences in the NAR of various species e.g. the NAR of cotton growing in Egypt was equal to that of wheat growing in U.K. This does not appear to be true.

wheat, barley
(50% lower than beet)
increasing NAR
Potato, kale
sugar beet

Leaf Area Index

WATSON looked at the PHOTOSYNTHETIC CAPACITY as indicated by the Leaf Area Index (LAI), and noted that the LAI can vary from 0 to 9. Thus, the area of leaf in a field of corn in the later stages of development is much larger than that of the land, but much less when in the first stages of growth. WATSON noted that there was a large LAI for only a relatively short length of time and the peak often differed in time from species to species.



Note that the LAI of cereals corresponds with optimal photosynthetic conditions. Also, there is a good LAI for only half the available time. In potatoes and sugar beet the situation is even worse, for although they have a good LAI for a longer time, this occurs when photosynthetic conditions are declining. An efficient crop should have a high LAI throughout those times favourable for photosynthesis.

Arable plants have low productivity compared with perennial evergreen forests and grassland pastures, both having a reasonable LAI throughout the year. Deciduous trees do not photosynthesise until April, but rapidly form a dense canopy for the remainder of the photosynthetic period.

Various factors affect the LAI, especially mineral nutrition. Plant husbandry is often concerned with increasing the LAI via fertilizer treatment. When many plants develop large leaf areas then this may become shaded in part, thereby reducing photosynthetic activity and subsequently dry weight. Thus, there is a built-in compensating mechanism against an increase in LAI. Temperature may exert an effect at the shoot apex and affect leaf initiation and development besides influencing photosynthesis and other metabolic processes.

Prospects for increasing Dry Weights

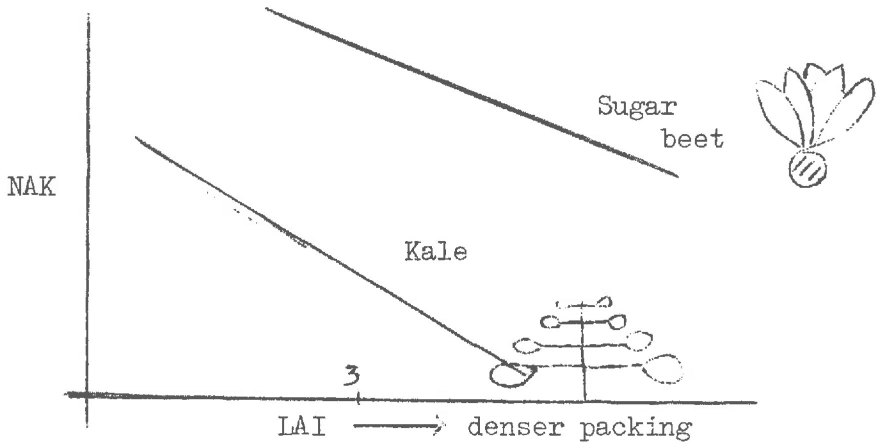
WATSON now finds that generally there are far bigger differences in the LAI between species than in the NAR. He believes that there are far better prospects for increasing production by increasing the LAI rather than the NAR. Thus, breeding of sugar beet has not increased the NAR and emphasis has been attached to the LAI. Forestry workers tend to disagree with this because of large variations in the NAR between clones.

Production by increasing Leaf Area

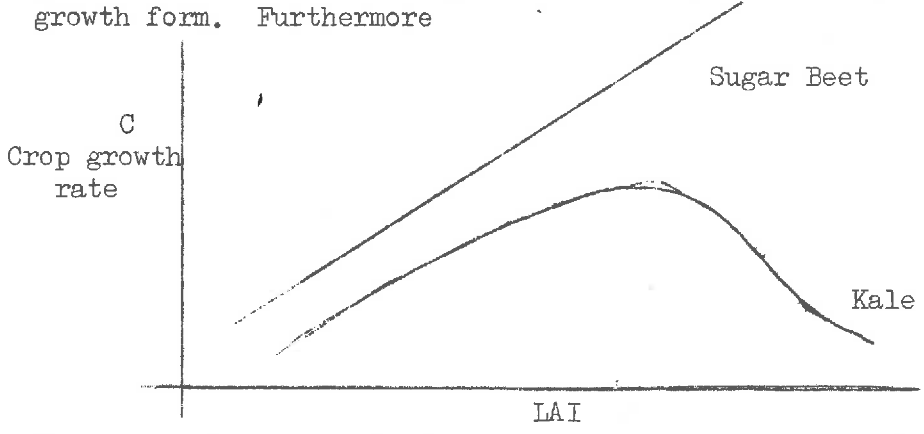
Fertilizers and irrigation must be at an optimum, but this has already been attained in many parts of the world.

If we increase the leaf area then we consider the LAI, NAR and Crop Growth Rate (C).

Thus, in sugar beet and kale, two plants which have different growth forms:-



Thus the NAR decreases in both plants due to SHADING. This effect is greater in kale than in sugar beet and may be directly related to the growth form. Furthermore



Thus, in kale, the LAI of 3 gives the madimum crop yield (C). After this value, an increase in LAI causes a drop in C due to the effect on the NAR. However, in sugar beet, a higher LAI gives a better crop growth rate, and it is therefore advantageous to have a dense leaf packing.
Hence, there is scope for increasing LAI in some species but not in others. At the moment there is little known about the regulation of the NAR. WATSON considers that it is better to obtain a good LAI earlier in the year. However, in e.g. sugar beet, early planting will lead to vernalization and premature bolting.

J.R. Hillman

Reference: F.L. Milthorpe and J. Moorby. An introduction to crop physiology. pages 152-179. Cambridge University Press. 1974.