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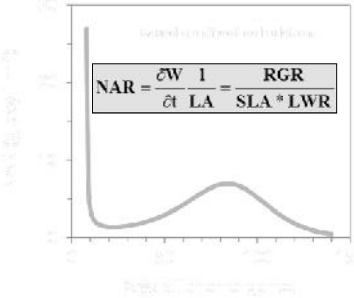
LECTURE 06: PLANT GROWTH ANALYSIS II: NAR, LAR, LWR & SLA



Automation applied to an efficient operation will magnify the efficiency, but automation applied to an inefficient operation will magnify the inefficiency. Bill Gates

LEARNING OUTCOMES

After the completion of this lecture and mastering the lecture materials, students should be able

1. to explain the relationship between biomass production and leaf are
2. to explain the initial concept of unit leaf rate or net assimilation rate (NAR)
3. to derive a model used to estimate NAR
4. to apply NAR model to estimate the efficiency of leaf area to produce biomass per unit time
5. to apply several growth indices in the quantitative analysis of plant growth

LECTURE OUTLINE

1. NAR
1.1 Initial Concept
1.2 Applied NAR Model
1.3 Dilemma NAR

2. LEAF CHARACTERISTICS
2.1 LAR
2.2 LWR
2.3 SLA

Chapter 5:
Sitompul, S.M. (2016).

1. INTRODUCTION

1. The difference in the production of biomass is due largely to the difference in the capacity of leaves through phososynthsis to produce karbohydrate that is used for the formation of biomass as leaves are the major photosynthetic organ.
2. Thereby analysis hereinafter important to do to elucidate the growth or yield difference between plants due to the difference in genotypes or environments, after the analysis of biomass production as a function of the initial biomass of plants, is the nature of leaves associated with this.
3. The capacity of leaves to produce biomass can be split into two components: the capacity of leaves per unit leaf area to produce photosynthate and total leaf area.

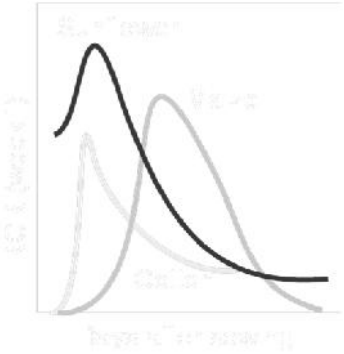
4. The capacity of leaves to produce biomass per unit LA (leaf area) is called unit leaf rate (ULR), often expressed as ‘E’ (Evans, 1972).
5. Instead of ULR, the term of NAR (net assimilation rate) is widely used which is actually amiss as ULR is not directly related to CO_2 assimilation.
6. However NAR, with the involvement of ∂W/LA, may represent a plant’s net photosynthetic effectiveness in capturing light, assimilating CO_2 and storing photoassimilate.
7. Variation in NAR can derive from differences in canopy architecture and light interception, photosynthetic activity of leaves, respiration, transport of photoassimilate and storage capacity of sinks, or even the chemical nature of stored products.

1. NAR

1. Initial Concept

- As shown previously, the relative growth rate is never constant for more than very short periods.

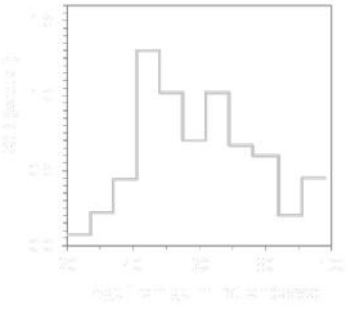
The general trend of RGR in Sunflower, Maize, and Cotton



Source: Modified from Evans (1972)

- Clearly in such cases, RGR as a grand overall index is going to be a most difficult one to handle in relation to environmental changes. When the ontogenetic drift is so marked,
  - how is one to disentangle this from effects of changing environment?
  - How to decide what the relative growth rate would have been in a given week, if the weather had been different?
- The first steps towards answering these question were taken almost at once.
- A remarkable body of data on the growth of maize, collected by Kreusler and a number of co-workers at the Agric. Res. Station at Poppelsdorf near Bonn, was analyzed by Briggs, Kidd and West in 1920.

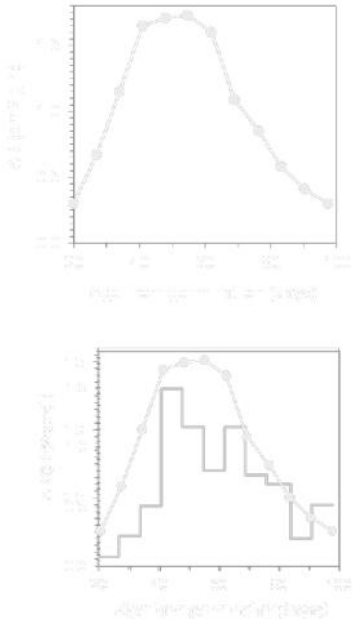
- Ontogenetic drifts of RGR, similar to that shown in the previous figure, are characteristic of these experiments.
- One of their concerns was to distinguish the effects of weather on plant growth from the effects of these ontogenetic drifts.
- At an early stage of their analysis they saw that the ratio of leaf area to total dry weight **LA/W** (Leaf Area Ratio), also showed an ontogenetic drift broadly parallel to that of relative growth rate.



Maize, var. Badischer Fruch, grown at Poppelsdorf in 1876. Source: adapted from Evan (1972) acquiring Kreusler *et al*. (1877)

- This parallelism can be seen clearly when the Fig. of RGR is superimposed over that of LAR.
- As they were searching for some aspect of plant growth relatively free from ontogenetic drift, in order to make progress with the study of the effects of weather, this led them to investigate the properties of the ratio of the two

RGR/LAR



- A constant growth index was much expected due to the parallelism of the two indices. Over an infinitesimally short period of time, ∂T,

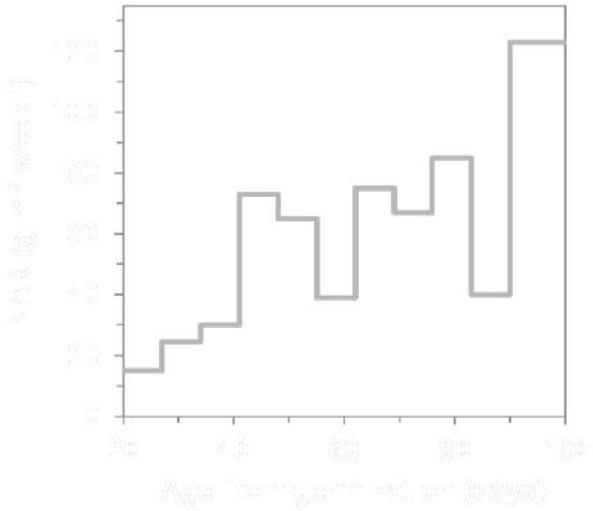
$$\frac{\mathbf{RGR}}{\mathbf{LAR}} = \frac{\partial \mathbf{w}/\partial \mathbf{t}}{\mathbf{LA}/\mathbf{W}} = \frac{\partial \mathbf{W}}{\partial \mathbf{t}} . \frac{1}{\mathbf{LA}} = \mathbf{ULR} = \mathbf{E} = \mathbf{NAR}$$

where W is total dry weight, ∂W is the increment of dry weight during the period ∂T, and L is leaf area.

- They gave the name 'unit leaf rate' to the quantity to which they had assigned the symbol E.
- The overall growth index, relative growth rate (RGR), was thus split into two as follows

RGR = NAR x LAR

- It can be seen that
  - leaf area ratio (LAR) is a morphological index of plant form (leaf area per unit dry weight of the whole plant), and
  - unit leaf rate (NAR) is a physiological index (rate of increase of dry weight of the whole plant per unit leaf area) closely connected with the photosynthetic activity of the leaves.
- Unfortunately, NAR is not a constant index and has its own ontogenetic drift making up with LAR the drift in RGR.
- The ontogenetic drift of LAR and NAR are quite different in form.
  - LAR has a grand march, rising to a maximum between 40 and 60 days, and with relatively small fluctuations.
  - NAR shows an early rise, and then marked fluctuations from week to week between days 42 and 90, but no marked upward of downward trend, during a period when LAR has dropped to a quarter of its value at day 42.



NAR of maize shows an early rise, and then marked fluctuations from week to week between days 42 and 90. Source: adapted from Evan (1972) acquiring Kreusler *et al*. (1877).

2. Applied NAR Models

- Several models (equations) of NAR that can be used for estimation of unit leaf rate (E or NAR) are shown below.

$$NAR = \frac{2(W_2 - W_1)}{(LA_1 + LA_2)(T_2 - T_1)}$$

$$NAR = \frac{(W_2 - W_1)}{(T_2 - T_1)} \frac{(\ln LA_2 - \ln LA_1)}{(LA_2 - LA_1)}$$

$$\overline{NAR} = \frac{W_2 - W_1}{LA(T_2 - T_1)}$$

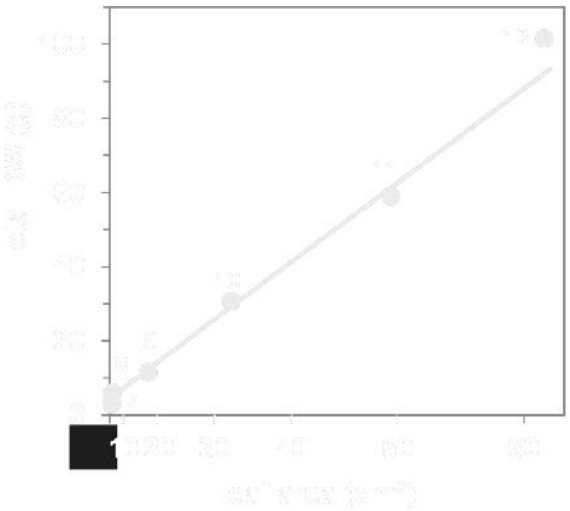
$$\overline{NAR} = \frac{2(W_2 - W_1)}{(T_2 - T_1)(LA_2 + LA_1)}$$

- The use of one among above equations is dependent upon plant condition which is not discussed here (see Sitompul, 2016).

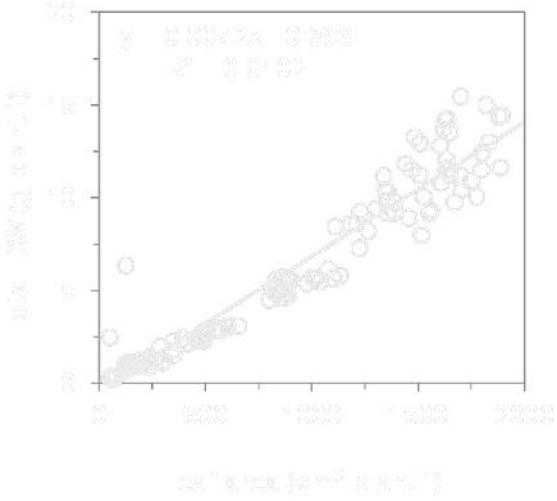
- The selection of one among above equations to be used is dependent upon plant condition which is not discussed all here (see Sitompul, 2016).
- The most frequently used model to estimate NAR is the second model above.

$$NAR = \frac{(W_2 - W_1)}{(T_2 - T_1)} \frac{(\ln LA_2 - \ln LA_1)}{(LA_2 - LA_1)}$$

- This model can be derived from the assumptions;
  - (I) NAR is constant and leaf area increases exponentially with time
  - (II) NAR is not constant and leaf area is linearly related to total dry weight (W).
- It should be remembered that NAR is never constant for more than very short periods.



Relationship between total DW (dry weight) and leaf area in sunflower (*Helianthus annuus* L.). Source: adapted from Evans (1972)



Relationship between total DW (dry weight) and leaf area in soybean [*Glycine max* (Merr.) L]. Source: adapted from Evans (1972)

- Therefore, the average NAR over a period under consideration (T_1-T_2) should be similar to the integration of NAR over the same period as follows.

$$\overline{E}(T_2 - T_1) = \int_{T_1}^{T_2} E\,\partial t$$

- While the general equation of NAR is

$$NAR = E = \frac{\partial W}{\partial t}\frac{1}{LA}$$

- So

$$\overline{E}(T_2 - T_1) = \int_{W_1}^{W_2} \frac{\partial W}{LA}$$

- The relationship between W and LA is linear

$$W = a + b.LA \rightarrow \partial W = b.\partial LA$$

As

$$\overline{E}(T_2 - T_1) = \int_{W_1}^{W_2} \frac{\partial W}{LA}$$ then $$\overline{E}(T_2 - T_1) = b\int_{LA_1}^{LA_2} \frac{\partial LA}{LA}$$

Which results in

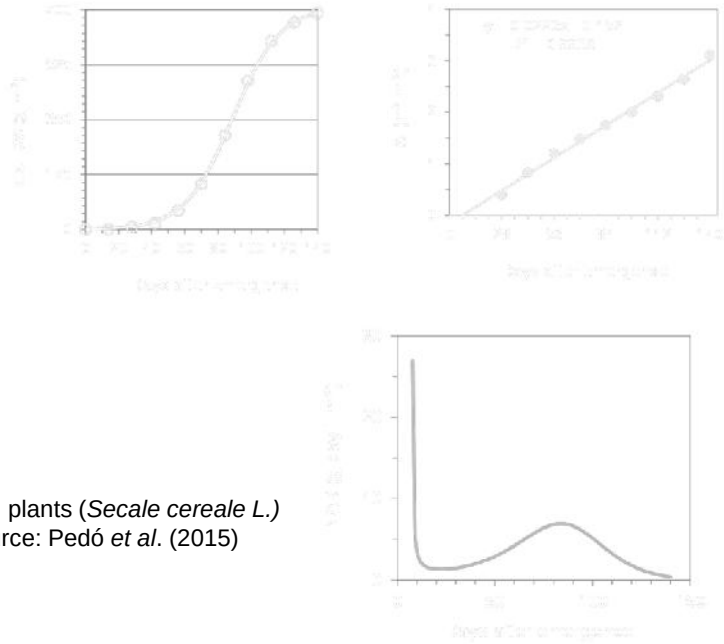
$$\overline{E}(T_2 - T_1) = b(\ln LA_2 - \ln LA_1)$$

The value of parameter 'b' can be solved as follows
$(W_1 = a + b.LA_1) - (W_2 = a + b.LA_2)$
and

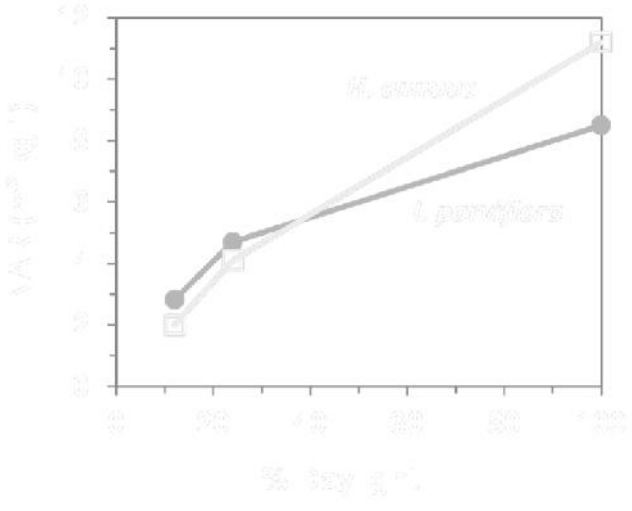
$$b = \frac{(W_2 - W_1)}{(LA_2 - LA_1)_1}$$

- Finally,

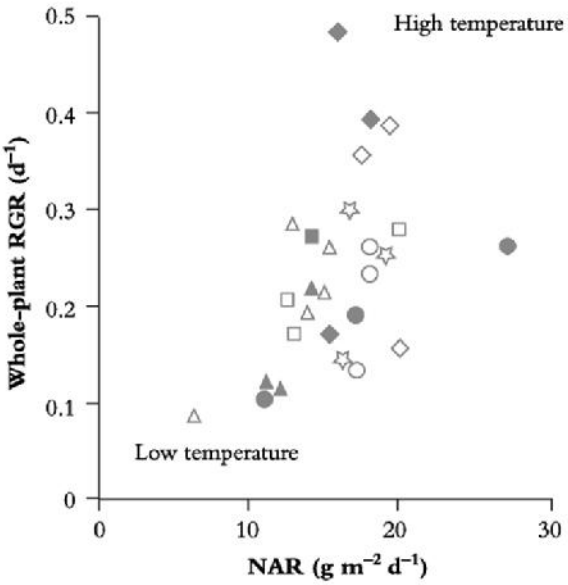
$$E = \frac{(W_2 - W_1)(\ln LA_2 - \ln LA_1)}{(LA_2 - LA_1)(T_2 - T_1)}$$



Rye plants (*Secale cereale L.)*
Source: Pedó *et al*. (2015)



Based on Blackman and Wilson 1951b; Evans and Hughes 1961)



Based on Potter and Jones, 1977

EXCERCISE

- **Case**. An experiment was conducted to study the growth of maize in the field, and plant samples were harvested on day 15, 20, 25, 30, and 35 after emergence resulting in leaf area (LA) of 30, 76, 172, 430, and 839 cm^2 per plant, and total dry weight of 0.40, 0.82, 2.74, 6.21, and 16.35 g per plant respectively.
- **Question**. What is the best model of NAR to calculate the value of unit leaf rate, and how are estimated values of NAR with that model.
- **Answer**. As the plants grew in the field with a fluctuating environment, then NAR should be assumed not constant. The relationship between total dry weight and leaf area should be analyzed to determine the proper model to use.

3. Dilemma NAR

- NAR Model developed on the basis of assumption that NAR is not constant with total dry weight and leaf area linearly or quadratically related is the most widely used.
- In many cases, sufficient data is not always available to determine the right NAR to use. Thereby one of two models is selected randomly.
- This, of course, raises a question as to the degree of deviation (error) when the improper model is used
- A detail analysis showed that the ratio of NAR values obtained with the two models was dependent upon the ratio LA_2/LA_1. As long as $\mathbf{LA_2/LA_1}$ á **2**, the error would not be more than 4% providing W and LA are related linearly or quadratically.

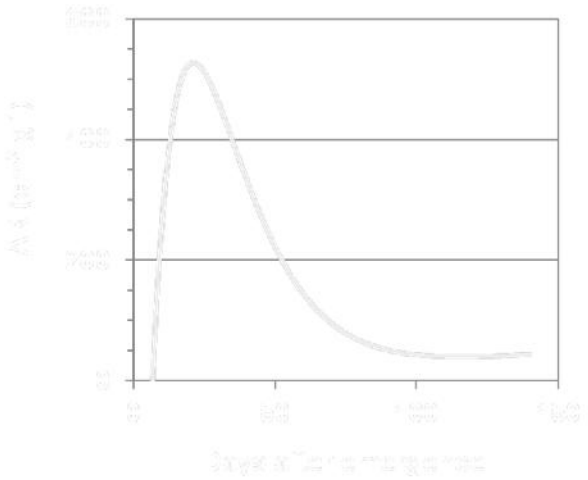
2. LEAF CHARACTERISTICS

1. LAR

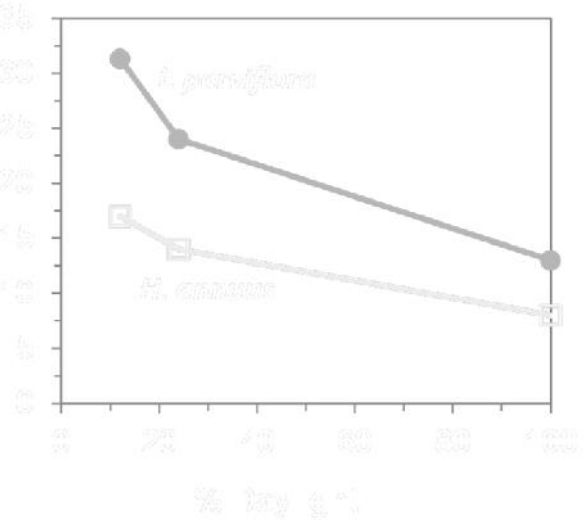
- Suatu parameter pertumbuhan yang dapat digunakan untuk mencerminkan morfologi tanaman yang berhubungan dengan hal diatas adalah nisbah luas daun (LAR) yaitu hasil bagi dari luas daun dengan berat kering total tanaman (LA/W).
- Harga LAR dapat juga diperoleh dari hasil bagi laju pertumbuhan relatif (RGR) dengan harga satuan daun (NAR atau E) seperti ditunjukkan berikut ini.

$$\mathbf{LAR} = \frac{\mathbf{RGR}}{\mathbf{NAR}} = \frac{(\partial \mathbf{W}/\partial \mathbf{t})(1/\mathbf{W})}{(\partial \mathbf{W}/\partial \mathbf{t})(1/\mathbf{LA})} = \frac{\mathbf{LA}}{\mathbf{W}}$$

- As LAR is an integration of RGR and NAR, it is a very complex index of plant growth.



Estimated LAR of Rye plants (*Secale cereale L.).* Source: Pedó *et al*. (2015)

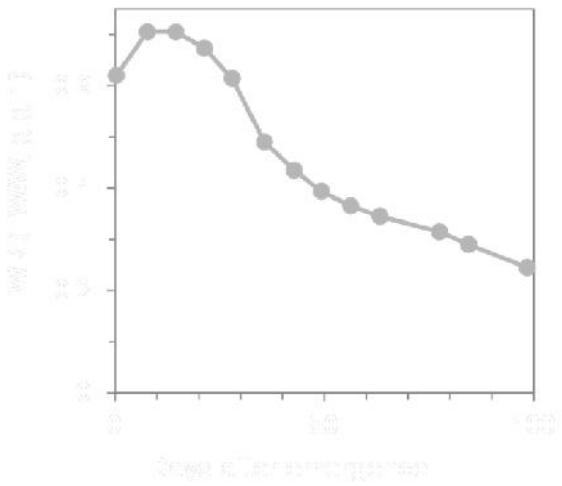


Based on Blackman and Wilson 1951b; Evans and Hughes 1961

2. LWR

- Leaf area is determined at first by the amount of substrate (carbohydrate) allocated the leaf organ.
- As leaves in the growth cycle of plants undergo senescence, then unproductive old leaves have to be replaced by newly formed leaves to able continue to produced carbohydrate.
- Therefore the partitioning of carbohydrate to leaf organ is highly determinant of plant development in the its growth cycle.
- This carbohydrate partitioning, therefore, can be regarded as the phenomenon of investment of plant capital to the productive part of plants.
- This can be seen in an index known as LWR (leaf weight ration) which is the ration LW/W.

$$LWR = LW/W$$



3. SLA

- Other process determining leaf area (LA), besides the partitioning of assimilate to leaf organ, is the efficiency of leaf area formation per unit of available assimilate.
- .
- This can be studied through an index called specific leaf area (SLA) which is the ratio of leaf area (LA) and leaf weight (LW) as shown bellow.

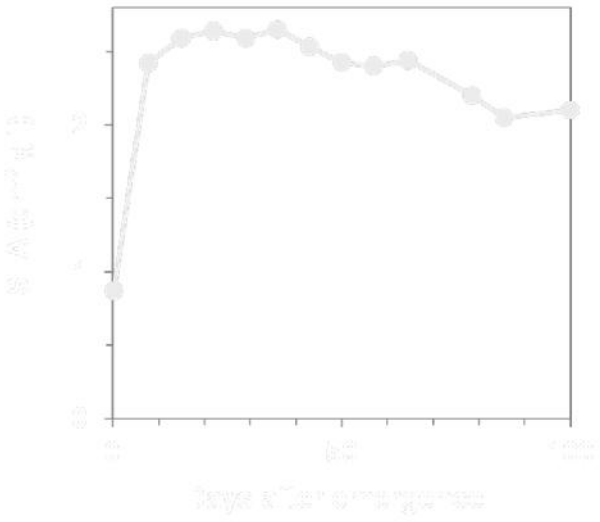
$$SLA = LA/LW$$

- The index can be also derived from the ratio of LAR and LWR as follows.

$$\frac{LAR}{LWR} = \frac{LA/W}{LW/W} = \frac{LA}{LW}$$

- This index contains physiological character with the information of leaf thickness reflected by this index that means the density of photosynthetic organelles and, hence, the rate of photosynthesis.
- For instance, thick leaves are expected to contain more chloroplasts per unit leaf area than thin leaves.

- Light interception would be high on the thick leaves which therefore have a high capacity of CO_2 reduction in comparison with thin leaves.
- The development of SLA with time in sun flower showed a sharp increase at the initial of growth. This was followed by a phase of SLA relatively constant, and a slight decrease was found at the end stage of growth.
- This means that the formation of leaf area per unit of dry weight allocated to the leaf organ was low at the initial of growth and increased thereafter.



The development of SLA with time in Sunflower (*Helianthus annuus*)

The relationship between SLA and total dry weight (W) in *Impatiens parviflora* grown in the field with different levels of shade at experiment I & II

WHAT HAVE YOU G0T?

1. What is the major plant factor having the highest contribution to the biomass production of plants.
2. What are the two main plant factors determining the quantity of photosynthate produced by plants.
3. How is the ontogenetic drift of LA/W known as LAR.
4. What is the first approach used to disentangle variation of RGR with time due to ontogenetic drift and environment.
5. What is the result of RGR divided by LAR.
6. What is the category of LAR and NAR as growth indices
7. How is the ontogenetic drift of NAR.
8. What is the most common model of NAR used to calculate the efficiency of plants to produce biomass per unit time per unit leaf area.
9. What is LWR and SLA.
10. How is the effect of increasing daylight on NAR.

http://leavingbio.net/TheStructureandFunctionsofFlowers%5B1%5D.htm