PBIO*3110 – Crop Physiology

Lecture #2

Fall Semester 2008
Lecture Notes for Tuesday 9 September

How is plant productivity measured?

Introduction: *Growth analysis and crop dry matter accumulation*

Learning Objectives

1. To learn what are the most relevant methodologies to measure the daily performance of crop canopy.
2. Why does plant-to-plant variability make the measurement of plant productivity so difficult?
3. To know what is radiation use efficiency (RUE).

Introduction

According to the yield equation, productivity of crop canopies is analyzed in terms of total incident radiation solar radiation (Q), the proportion of the incident solar radiation that is intercepted by the crop canopy (I_A'), the efficiency of conversion of intercepted radiation into plant dry matter (i.e., ϵ), and the partitioning of dry matter among various plant/crop components (i.e., ρ). Historically, the methodologies used in the study of the productivity of crop canopies have been dependent on available technology. In the 1950s, crop canopies were analyzed in terms of weight, weight distribution, and leaf area. This is called growth analysis. In general, growth analysis is the study of crop canopies over periods of weeks across areas of 0.1 to 10 m^2. In the 1960s, the infrared gas analyzer (IRGA) enabled quick measurements of CO_2 exchange rates and leaf photosynthetic rates (or leaf carbon exchange rate, CER) of field-grown crop canopies were studied. Leaf photosynthesis is measured on cm^2 leaf area over minutes. Although leaf photosynthesis does give an instantaneous measure of "plant growth", photosynthetic rates vary with leaf age, leaf position in the canopy, recent “light history” (i.e., sunlit vs. shaded leaf area), and time of the day. In the 1970s, whole-canopy crop enclosures were developed to alleviate some of the problems associated with single-leaf photosynthetic measurements. Canopy photosynthesis is measured over periods ranging from minutes to days for crop canopies covering 0.5 to 2 m^2 of ground area. Canopy photosynthesis represents an instantaneous measure of the canopy response to a change in environmental variables, but the measurement system is cumbersome and inflexible. Chlorophyll-fluorescence technology became available during the 1990s and chlorophyll fluorescence enables very quick and easy measurements of photosynthetic parameters of leaves. However, the measurements are made on very small pieces of leaf and it is extremely challenging to obtain values that represent the canopy.

Usually, a thorough analysis of the productivity of crop canopies would use two or more of the methods described above in combination and, most importantly, the results should represent the canopy as a whole and should therefore account for spatial variability (e.g., plant-to-plant variability). The magnitude of plant-to-plant variability in crop canopies consisting of plants that have the same genotype is one of the most difficult concepts to get across to biologist who are not familiar with crops. In carefully conducted experiments in research plots with a maize hybrid, for instance, the range from plants with the lowest dry matter to the plants with the highest dry matter at maturity is fourfold at low plant densities and tenfold at high plant densities. Under “normal” commercial conditions that range from lowest to highest plant weight will probably be much higher. The correct sample size is the sample size that will represent the canopy as a whole (i.e., in the example describe above, a few plants would certainly not suffice; possibly, 40-50 randomly selected plants would be a representative sample). The best method to analyze a crop canopy is always a compromise between the accuracy of the measurement (i.e., how good is the measurement) and the precision of the measurement (i.e., how repeatable is the measurement when we use another plant or set of plants). The difficulty to measure plant productivity accurately and precisely is probably the greatest challenge in any effort to improve the efficiency of production in agriculture, irrespective whether it involves traditional plant breeding, biotechnology, cropping systems research, or organic agriculture.

Growth analysis

Total crop dry matter is the spatial and temporal integration of all plant processes and, therefore, crop dry matter is the most relevant parameter in the study of crop canopies. Rate of dry matter accumulation varies across the life cycle of a crop and dry matter and leaf area are sampled at intervals ranging from days to weeks to quantify effects of environmental influences or to analyze genotypic differences between crop cultivars. In growth analysis two basic measurements are made, dry weight and leaf area, and a large number of parameters are derived from these measurements. Some of the important parameters have been listed below.

Parameter	**Symbol**	**Unit**
Crop Growth Rate	CGR	g (crop) m^{-2} d^{-1}
Leaf Area Index	LAI	m^2 (leaf) m^{-2}
Specific Leaf Area	SLA	m^2 (leaf) g^{-1} (leaf)
Relative Growth Rate	RGR	g (crop) g^{-1} (crop) d^{-1}
Net Assimilation Rate	NAR	g (crop) m^{-2} (leaf) d^{-1}

The pattern of rate of dry matter accumulation of a crop canopy is typically characterized by a sigmoid curve. Three more or less distinct phases can be distinguished (see Fig. 1): (i) a period of exponential growth during early development, followed by (ii) a period of more or less constant rate dry matter accumulation, and (iii) a period of declining crop growth rates during the final phase of development when green leaf area declines due to leaf senescence and leaf photosynthesis declines due to leaf aging. It is important to realize that the parameters SGR and NAR are only relevant during the first phase.

(i) Early phases of development. Rate of dry matter accumulation during early development is directly related to LAI and as LAI is closely associated with plant dry matter during this phase, rate of dry matter accumulation of a crop is a function of its own weight:

$$dW/dt = SGR \times W \qquad \textbf{[1]}$$

integrating Equation [1] gives:

$$W_t = W_o \times e^{SGR \times t} \qquad \textbf{[2]}$$

$$W_t / W_o = e^{SGR \times t} \qquad \textbf{[2a]}$$

where W_o and W_t are the crop weights at times t = 0 and t = t, and SGR is the slope of the natural log of crop dry matter vs. time, i.e.:

$$\ln (W_t / W_o) = \ln e^{SGR \times t} = SGR \times t \qquad \textbf{[3]}$$

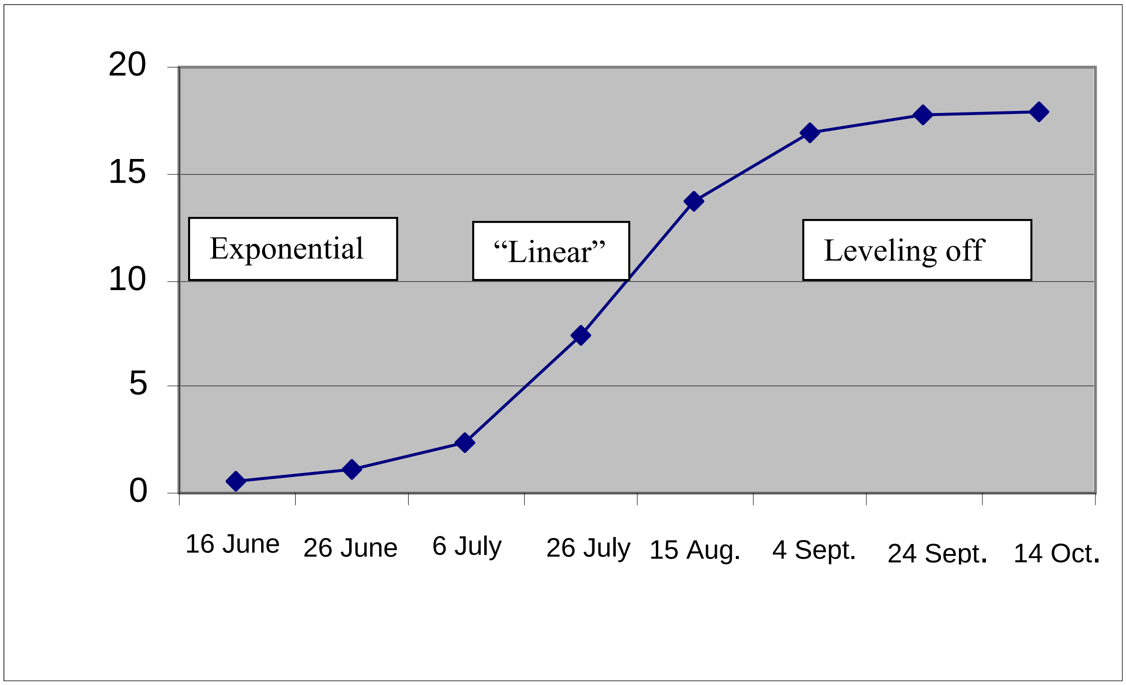

Fig. 1 Schematic representation of the three phases of dry matter accumulation (in Mg/ha) of a crop canopy. A logistic growth curve was applied to dry matter accumulation of a maize crop that was planted on 17 May and harvested on 14 October.

The increase in LAI, and, consequently, the increase in rate of dry matter accumulation, is proportional to rate of dry matter accumulation per unit leaf area (NAR). During this phase of development, an increase in leaf area leads to an increase in rate of dry matter accumulation (because light interception is directly related to leaf area during this phase of development) and an increase in dry matter accumulation leads to an increase in leaf area (because proportion of dry matter allocated to leaves remain fairly constant)..

Various equations are used to estimate mean net assimilation rate NAR_{mean}. NAR is the ratio of rate of dry matter accumulation and leaf area index and a mean ratio should take into account the rate of change of each of its components. During exponential dry matter accumulation, and assuming an equal exponential rate of increase for LAI and dry matter, mean NAR can be estimated as follows:

$$NAR_{mean} = [(W_2 - W_1) / (t_2 - t_1)] \div [(LAI_2 \div LAI_1) / (LAI_2 - LAI_1)] \qquad \textbf{[4]}$$

where NAR_{mean} is the mean net assimilation rate during a period from $t = t_1$ to $t = t_2$. The second part of Equation [4] expresses the inverse of mean LAI from $t = t_1$ to $t = t_2$. In contrast to mean NAR, instantaneous NAR can be estimated by calculating rate of dry matter accumulation at time t (i.e., by differentiating the "growth curve" at time = t) and measuring LAI at time = t.

Instantaneous NAR at time = t is rate of dry matter accumulation divided by LAI.
The NAR will decline once mutual shading among leaves in the canopy will occur. Rate of dry matter accumulation will become "constant" when a change in LAI will not influence absorptance of incident irradiance: the canopy has attained the phase of "constant" growth. Similarly, a crop will have attained the phase of "constant" growth when leaf-area expansion has been completed, even if PAR absorptance is less than 100%. Dry matter accumulation during this period is relatively unimportant in the context of dry matter accumulation during the growing season. For instance, a maize crop in Ontario will accumulate less than 15% of dry matter at maturity during this period.

(ii) The period of a relatively constant rate of dry matter accumulation. This period is the most important phase of development for dry matter accumulation and grain yield of most crops. For instance, maize in Ontario may accumulate up to 75% of its dry matter at maturity during this period and, consequently, this period contributes most to final yield. Rate of dry matter accumulation during this period is fairly constant and, consequently, CGR is the appropriate parameter to use. CGR will vary with incident solar irradiance and abiotic stresses may reduce CGR. Because CGR is relatively constant, total dry matter accumulated during this period is closely related to the duration of the period.

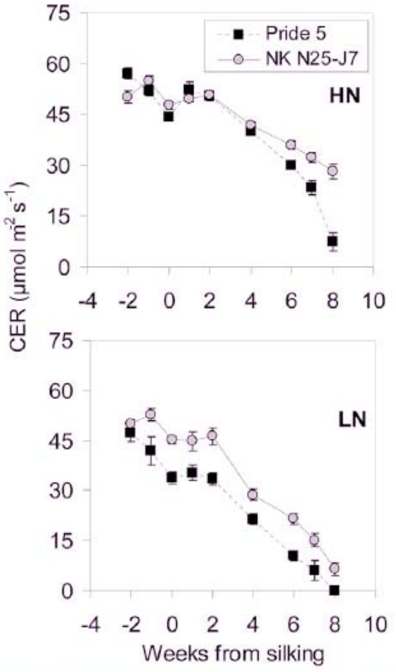

Figure 1. Leaf carbon exchange rate (CER) as a function of weeks from silking for an older ('Pride 5') and a newer ('NK N25-J7') maize (*Zea mays* L.) hybrid exposed to high N (HN) and low N (LN). Vertical bars represent ± SE and are not shown when smaller than the symbol size.

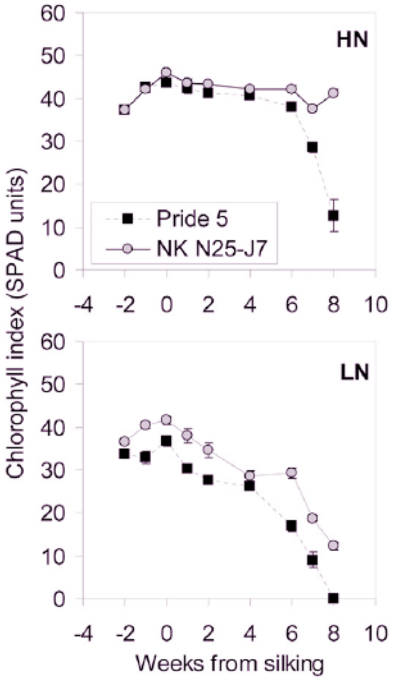

Figure 3. Leaf chlorophyll index (SPAD units) as a function of weeks from silking for an older ('Pride 5') and a newer ('NK N25-J7') maize (*Zea mays* L.) hybrid exposed to high (HN) and low (LN) N levels. Vertical bars represent ± SE and are not shown when smaller than the symbol size.

(iii) Final phase of development. Rates of dry matter accumulation per day start to decline due to aging during the final phase of development. The decline in the rate of dry matter accumulation during this phase is associated with functional and visual leaf senescence. Functional leaf senescence is the decline in photosynthesis per unit leaf area due to aging. Visible leaf senescence is the loss of chlorophyll in the leaf. Whereas no photosynthesis will occur in a leaf that has lost all its chlorophyll, a leaf that has retained all its chlorophyll does not necessarily maintain it rate of photosynthesis. For instance, Figs. 1 and 3 in a report by Echarte et al. (2008) depicted above show that leaf photosynthesis (CER) declines during the grain-filling period of maize, even if chlorophyll content remain constant under a high N fertilizer level. The sevenfold increase in grain yield of corn hybrid in North America during the last 70 years has been attributed, in part, to increased functional and visual "stay green".

Rate of crop dry matter accumulation

Rate of crop dry matter accumulation is the product of total incident solar radiation (**Q**, MJ m^{-2} d^{-1}), the absorptance of incident solar radiation by the crop canopy ($\mathbf{I_A}$', %), and the efficiency of conversion of absorbed solar radiation into plant dry matter (**€**, g dry matter MJ^{-1}). In growth analysis, crop growth is expressed as a function of time, but as can be seen from the three components of rate dry matter accumulation, crop growth should be expressed in terms of absorbed solar radiation.

Absorptance of incident solar radiation (I_A')

The penetration or transmission of radiation fluxes in a crop canopy of black leaves with homogeneously arranged leaves of uniform inclination can by approximated be the Lambert-Beer's law of absorption:

$$\mathbf{I_t / I_o = e^{-k \times LAI}} \qquad \mathbf{[5]}$$

where I_t is transmitted irradiance at the bottom of a canopy with a leaf area = LAI, I_o is the incident irradiance at the top of the canopy (e.g., incident solar radiation), and k is the extinction coefficient. The extinction coefficient (k) is a function of the leaf angle. It should be noted (a) that Equation [5] is for "black" leaves (i.e., no reflectance nor transmittance of irradiance by individual leaves) and (b) that leaf inclination will usually vary with age and/or leaf position in the leaf canopy (therefore, k should actually vary accordingly). Equation [5], however, is a very good first approximation of the interception and absorption of incident solar radiation by a canopy when the extinction coefficient (k) and LAI are known. For instance, the proportion of incident PPFD that is absorbed by a canopy with LAI = 2 and k =0.65 is 73 %, because:

Transmittance = $I_t' = I_t / I_o = e^{-k \times LAI} = e^{-0.65 \times 2} = 0.27$

Absorptance = $I_A' = 1 - \text{transmittance} = 1 - 0.27 = 0.73$

Note that transmittance (I_t') is transmitted radiation as a proportion of incident radiation (I_t/I_o) and absorptance (I_A') is absorbed radiation as a proportion of incident radiation (I_A/I_o). Alternatively, it is possible to estimate the LAI that is required to intercept 90% of the incident PPFD when k = 0.65 (when absorptance is 90%, then transmittance is 100% - 90% = 10%):

$I_t' = I_t/I_o = 0.1 = e^{-k \times LAI}$
$\longrightarrow \ln(I_t/I_o) = \ln(0.1) = \ln(e^{-0.65 \times LAI})$
$\longrightarrow \ln(0.1) = -0.65 \times LAI$
$\longrightarrow LAI = \ln(0.1)/-0.65 = 3.5$

Hence, absorptance (I_A') in the yield equation (Lecture #1, Equation [1]) can be estimated from LAI and the extinction coefficient of the leaf canopy.

Radiation use efficiency (RUE)

The efficiency of conversion of absorbed solar radiation into plant dry matter (Є) is related to the mean leaf net photosynthetic rate across the crop canopy. In growth analysis the mean leaf net photosynthetic rate is called net assimilation rate (NAR), which is estimated from rate of dry matter accumulation and mean LAI (Equation [4]). Rather than using mean leaf net photosynthesis, which is not very meaningful when part of the canopy is sunlit and part is shaded, we can use the increase in crop dry matter accumulation (or crop growth rate, CGR). Radiation use efficiency (RUE) is estimated empirically from the crop growth rate during a period of 2 weeks or more and the amount of photosynthetically active radiation intercepted by the crop canopy (PAR_i) during the period crop the growth rate is determined:

$$RUE = CGR / PAR_i \qquad [\mathbf{6}]$$

where CGR is in g m^{-2} d^{-1}, PAR_i is in MJ m^{-2} d^{-1}, and RUE is in g MJ^{-1} (note that the value of incident PAR is approximately 50% of the value of Q, see Lecture #5). The main variables that influence RUE are maximum gross leaf photosynthetic rate, crop respiration rate, stresses that affect leaf photosynthetic rate, and changes in leaf photosynthetic rates associated with phase of development. Other factors that can influence RUE are the level of incident radiation and the fraction of diffuse radiation. Sinclair and Muchow (1999) compiled results reported in the literature on RUE in number of crop species. Results reported in their paper showed that maximum values for RUE (in g dry matter per MJ intercepted photosynthetic active radiation) are about 4.0 for sugar cane, 3.3 for maize, 3.3 for potato, 3.1 for sunflower, 2.9 for wheat, 2.8 for rice, 2.6 for sorghum, 2.6 for barley, 2.1 for soybean and peanut, and < 2.0 for grain legumes. Differences in maximum RUE among crop species are attributable, in part, to differences in maximum net leaf photosynthetic rate (for instance, differences in maximum net leaf photosynthetic rate between C_4 and C_3 species) and to differences in respiration rate that are due to the composition of plant dry matter formed from the initial products of photosynthesis; these effects will be discussed in more detail in Sections II and III. Hence, RUE can be used as an estimate of Є in the yield equation after incident solar radiation (Q) is converted to PAR.

References

Echarte, L., Rothstein, S, and Tollenaar, M. 2008. The response of leaf photosynthesis and dry matter accumulation to nitrogen supply in an older and a newer maize hybrid. Crop Sci. **48**:656-665.

Sinclair, T.R. and Muchow, R.C. 1999. Radiation use efficiency. Advances in Agronomy **65**: 215-265.