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RESEARCH PAPER

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Respiration estimation of a plant community through primary values (leaf area and phytomass)

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Abstract

Quantitative analysis of growth represents the first step in the analysis of primary production, being the link between the mere registration of plant productivity and the study of this by physiological methods. In classical growth analysis, most papers on this subject and applications do not provide evidence for the estimation of cellular respiration. This last factor, in ecophysiology and crop physiology, means loss of dry matter or phytomass, and is very different from a definition of a purely physiological point of view, which means oxidation of complex organic plant compounds in mitochondria. In this way, the full knowledge of the analysis of destructive growth, with estimation of respiration of monoculture plants or plant communities is crucial. It may represent a "tool" of great importance for understanding the functionality of an agroecosystem and improving productivity, especially the economic one, with an increase in harvest index and even in the quality of the final product and coproducts.

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Introduction

To understand how a plant and a biosystem work, interact and produce, it is necessary to know the variables involved and what responses are originated in this complex process of interaction. Aspects concerning ecophysiology, and knowledge of the physiological bases of vegetable production, which basically involves the production of energy (photosynthesis), energy use (breath), partition of assimilates and carbon balance are essential to understanding them. Primary productivity can be defined as the efficiency of conversion of radiant energy in substances, that is, the primary production designates the quantity of organic matter that is produced by autotrophs from solar energy (photosynthetic organisms).

Primary productivity is limited by two categories of "ecological restrictions". The first restriction concerns the quality of solar radiation that reaches the earth's surface. Only about 45% of this energy is comprised in the region of the spectrum of radiation that is effective for photosynthesis (PAR = photosynthetic active radiation comprised in the range of wavelengths between 400 nm and 700 nm). The remaining 55% of the spectrum are not converted into chemical energy and do not form biomass. Thus, the measure of the growth flow and senescence of leaf tissues within a plant population has allowed to estimate the proportion of primary production that can be considered as harvestable.

Plant growth analysis is an explanatory, holistic and integrative approach to interpreting plant form and function

Magalhães (1986) discusses the quantitative analysis of growth as the method that describes the morphophysiological conditions of the plant at different intervals of time, and proposes to follow the dynamics of photosynthetic production. Quantitative analysis of growth can be used to investigate the ecological adaptation of crops to new environments, the competition between species, the effects of management and crop husbandry and identification of the production capacity of different genotypes.

Despite the complexity involved in the growth of plant species, the quantitative analysis of growth is still the most accessible and a very accurate way of evaluating growth and inferring the influence of different physiological processes on the plant behavior. Among the studies that involve quantitative analysis of growth, this study cites Mahon (1990), regarding planting density.

Calculations for dry matter utilization during growth and development show that respiratory loss is substantial. In this way, it is truly relevant an approach on cellular estimation respiration in order to explain these loses. Although there are many articles available about this kind of literature, most of these papers do not provide evidence on that. The mitochondria gets from the cell that hosts it the supplies of oxygen and substrates derived from glucose, amino acids and fatty acids and converts them into a molecule called adenosine triphosphate (ATP). This molecule is responsible for energy storage, besides the formation of intermediate compounds that are precursors of important substances for the whole plant metabolism, such as cytochrome, chlorophyll, carotene, etc. (Taiz *et al.*, 2015) These intermediates are organic acids, derived from the glycolytic phase (glycolysis) and the citric acid cycle (Krebs cycle).

Estimation of respiration may provide data for a better rational management of this agroecosystem in order to reduce the metabolic cost. For instance, we can get net photosynthesis increment using cover crops to reduce the temperature, or intercropping systems to foster a greater use of solar radiation. Thus, the estimation of respiration can allow us to obtain an optimum ecological for the development of the crops. This work aims to provide information on classic growth plant analysis, including the estimation of respiration, based on the primary values of leaf area and phytomass.

General considerations

Aerobic respiration is common to almost all eukaryotic organisms and, in general, the respiratory process in plants is similar to that found in animals and lower eukaryotes (Taiz *et al.*, 2015).

Aerobic respiration is the biological process in which reduced organic compounds are mobilized and subsequently oxidized in a controlled manner. During respiration, free energy is released and temporarily stored in a compound, the ATP, which can be readily used for the maintenance and development of the plant. The function of the process is to obtain energy that is necessary for growth activities, maintenance of living plant tissues, the activities of absorbing water and nutrients, and the synthesis of complex reserves such as starch, cellulose, protein, oil, DNA, RNA, etc.

Although the respiratory activity is a loss of plant biomass, it is essential to growth and normal development of plants. However, any factor that promotes a reduction in respiratory activity of leaves and other organs will cause an increase in plant productivity (Larcher, 2003). At first, with a higher photosynthetic balance and depending on the harvest index (coefficient of migration) and the scores of productivity, it increases economic productivity.

According to Larcher (2003), there is a clear relationship between increase in dry matter and nitrogen and carbon assimilation by the plant because the carbon that is not consumed by respiration and that increases the dry matter of the plant can be applied to growth and/or reservation.

The analysis of plant growth is a method that describes the morphophysiological conditions of the plant at different intervals of time, between two successive samples within the cycle. Growth analysis allows evaluating the final growth of the plant as a whole and the contribution of different organs to total growth. Based on the growth data, one can infer physiological activity, i.e., quite accurately estimate the reasons of variations in growth between genetically different plants.

The amount of metabolically active tissue that makes up a plant community is called phytomass, although some parts of the plant cannot be strictly considered as living tissue, like the xylem and a part of the bark of stems and roots, which are not commonly separated for calculation of dry matter. The phytomass is the living tissue of plants, that is, the symplast, without considering the apoplast (dead tissue), and according to the ecophysiological point of view, the phytomass is the mass (P = ma) of the plant, and is one of the primary values of classical growth analysis, and is destructive (Magalhães, 1986).

One of the main characteristic growth factors is the ratio of leaf area, which consists in specific leaf area, leaf weight ratio, leaf area index and leaf area duration. Little use of growth analysis techniques has been observed in Plant Genetics and Plant Breeding. However, this method can has be value in evaluating the interplant and interspecific differences of the various characteristics that define the productive capacity of the plant (Magalhães, 1986).

Based on the foregoing, the objective of this work was to present methods for determining estimates of assimilation and respiration rates of plant communities, according to the values of leaf area and total plant phytomass. This method can also be applied to any experiment of cultural management. In order to reach this achievement, the researcher predicts the size of parcels and has specific lines for the interval that will depend on the crop cycle, besides collecting the material, primary values, phytomass and leaf area. They must observe the cooperative and competitive interactions between the population plants and only remove plants in each biological crop that are in ecophysiological conditions, i.e., next to their competitors. At least five samples of the biological material must be collected at intervals that are regular and well established, according to the crop cycle. Thus, for example, for a cultivar of castor bean (*Ricinus communis* L.) with a 100-day cycle, in order to collect at least five samples, each one must be collected with an interval of 20 days between each other, and in each one there must be a sample of plants that will represent the experimental unit (plot) well. In general, 3-5 plants are chosen per plot in each crop, in which leaf area per plant and total phytomass (dry matter) are measure. Based on them, the growth characteristics and plant respiration are estimated.

The most appropriate measure for the evaluation of plant growth, which depends on the amount of material that is being accumulated, is the relative growth rate (Magalhães, 1986), according to equation 1.

$$K = \frac{\ln P_2 - \ln P_1}{t_2 - t_1} = RGR \qquad (1)$$

K = relative growth rate (RGR)

P_1 and P_2 = growth (dry weight or phytomass) at time periods of t_1 and t_2, respectively.

The result is expressed in units of produced plant material by the available plant material, during the preset time interval. If the relative growth rate is calculated in terms of dry weight, the unit may be $g.g^{-1}.day$. This can also be applied to the growth of leaf area, stem diameter and plant height, according to what is described in the work of Beltrão *et al.* (2000).

The sum of the relative growth rates of each of the components of the plant must be equal to the relative growth rate of the whole plant. The partitioning of the assimilated compounds during growth can be calculated by determining the growth rates of each part of the plant separately, by comparing them to the growth of a component that is more directly affected by the considered climate variations.

According to Magalhães (1986), the growth of leaf area (A) and of biomass (P) can be directly associated to each other, or the relationship may be more complex. The general relationship between A and P can be expressed by equation 2:

$$P = a + bA^{\alpha} \quad (2)$$

In which *a* and *b* are constants.

If the value of a is considered negligible, α indicates the relationship between relative growth rate of biomass (RGRB) and relative growth rate of leaf area (RGRLA), according to equation 3.

$$\alpha = \frac{RGRB}{RGRLA} \qquad (3)$$

This ratio describes the allometric relationship between A and P and shows how the relative proportion of assimilatory tissue changes during growth.

The value of relative growth rate results from the contribution of two components. The first one refers to the rate of increase in growth per unit of time and per unit of leaf area, which is called apparent assimilation rate (AAR). The second one is defined by the ratio between leaf area and dry weight of the plant, which is called leaf area ratio (LAR).

The AAR shows the size of the assimilatory system that is involved in the production of dry matter, i.e., on an estimate of net photosynthesis (Magalhães, 1986), according to equation 4.

$$AAR = \frac{P_2 - P_1}{A_2 - A_1} x \frac{\ln A_2 - \ln A_1}{t_2 - t_1} \qquad (4)$$

The result is expressed in units of growth (weight) per surface of leaf area (area) per unit of time: $g.dm^2.day$.

Considering that P and A increase exponentially, the equation AAR can be used only if both variables grow with the same exponent, and continuously, in the considered time interval between two successive samplings. The discontinuity between the two variables may be caused by loss of leaf area, due to drought or insect attack, for example, followed by renewal of leaves.

The AAR depends on environmental factors, especially solar radiation. Due to the effect of self shading, the AAR decreases as leaf area increases, and hence decreases during the growth of the plant community.

The leaf area ratio (LAR) is defined as the ratio between leaf area and dry weight of the plant, and can be represented as the division between specific leaf area (SLA), which is equal to leaf area divided by leaf weight, and leaf weight ratio (LWR). This last parameter is calculated by the relationship between the dry weight of leaves and total dry weight of plants, according to equation 5. The SLA shows leaf thickness and the relative proportion of assimilatory surface and the mechanical and conductive tissues of the leaf.

$$LAR = \frac{A}{P} = \frac{A}{Pt} \text{ x } \frac{Pf}{P} \qquad (5)$$

In which Pf is the weight of leaves.

The leaf area ratio is the measure of the relative size at the assimilatory apparatus, and is an appropriate parameter for evaluation of the genotypical and climatic effects and the management of plant communities.

The relationship between leaf area ratio, apparent assimilation rate and relative growth rate, according to Magalhães (1986), is described by equations 6 and 7:

$$RGR = AAR \text{ x } LAR$$

Hence:

$$\frac{1}{P} \text{ x } \frac{dP}{dt} = \frac{1}{A} \text{ x } \frac{dP}{dt} \text{ x } \frac{A}{P}$$

The equation above indicates that the growth rate of a community can be altered by factors that affect the efficiency, or the size of the assimilatory system, or both. The LAR is usually calculated for each sample of plant material, separately. Thus, the change in LAR during the period of time between two samples cannot be calculated by using the ratio LAR = RGR/AAR, unless an exponential variation of A and P as the same exponent is considered.

The ratio of average leaf area during the time intervals of t_1 and t_2 can be obtained, according to Magalhães (1986), by equation 8:

$$\overline{LAR} = \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} \frac{A}{P} dt \qquad (8)$$

Integration can be done when a linear relationship between A and P occurs, in the same way in which it was considered for the calculation of the AAR.

The variation of the leaf area index during the course of a given culture is an important information to determine the date of sowing and transplanting. If the intervention of other factors is not taken into consideration, the crops should be sown so that the maximum values of leaf area index (LAI) are equal to the ones from the period of high radiation, when net photosynthesis is maximum. The leaf area and consequently the leaf area index (LAI) represent the unit of leaf area per unit of land area, and is therefore dimensionless. Its variation throughout the cycle of a culture is extremely important to allow modeling the growth (increase in mass or volume of a certain organ or plant as a whole, within a time interval) and the development (appearance of a plant phase) of plants and, consequently, productivity and total production of the culture (Teruel *et al.*, 1997).

The rate of dry matter production of a community or growth rate of community (GRC) depends on the LAI and the AAR, and can be calculated by using equations 9 and 10:

$$GRC = AAR \text{ x } LAI$$

$$\frac{dP}{dt} \text{ x } \frac{1}{At} = \frac{dP}{dt} \text{ x } \frac{1}{A} \text{ x } \frac{A}{At} \qquad (9)$$

In which *At* represents the area of land that was occupied by the plant community.

The LAI is therefore the main factor determining the productivity of a culture. LAI increases during growth of the community and reaches an optimum value when GRC is maximum (Fig. 1). The optimum LAI is different from the one that determines the maximum economic productivity, which is estimated by grain yield.

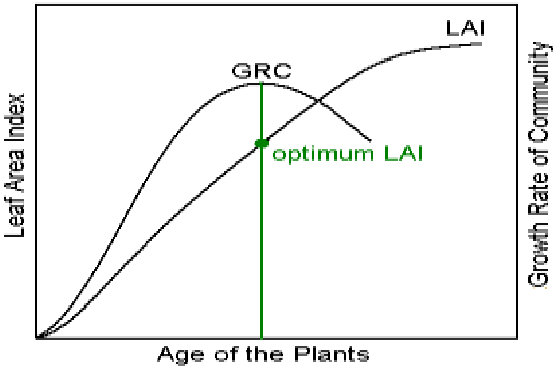


Fig. 1. Relationship between growth rate of community (GRC) and leaf area index (LAI), with an indication of the optimum LAI value (adapted from Magalhães, 1986).

The photosynthetic efficiency of a canopy is affected by the photosynthetic rate per unit of leaf area and by the way the solar radiation is intercepted. The interception of radiation depends on the characteristics of the canopy, like its structure and size. The leaf area index and the leaf area duration (D) are the most important factors in determining the dry matter production and hence growth. The plant growth is decisively influenced by the time in which the plant keeps its leaf surface active. This characteristic is defined by the leaf area duration (D) and can be represented by equation 11:

$$D = \int_{t_1}^{t_2} A\,dt \qquad (11)$$

The simplest solution to the equation is to use the graphical method, by measuring the area under the curve representing the variations in leaf area over time (Fig. 2).

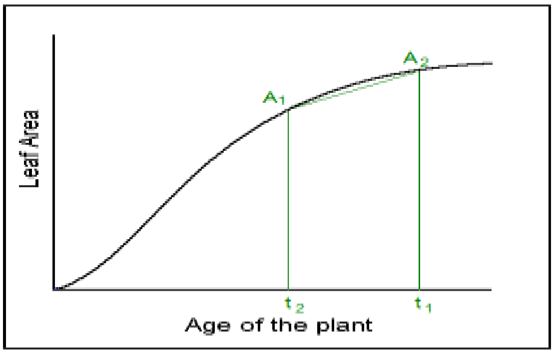


Fig. 2. Graphic determination of leaf area duration, calculated by the trapezoidal area: (adapted from Magalhães, 1986).

$$D = \frac{1}{2}(A_1 + A_2)(t_2 - t_1)$$

Growth characteristics directly related to economic and primary productivity, primary coefficient and productivity score

In classic destructive growth analysis, several features of growth can be estimated via measurement of the primary values, leaf area and phytomass. Among these features, the following stand out: the ones that are directly related to primary productivity, to net assimilation rate and to leaf area index, which together determine the growth rate of the crop, according to equation 12:

$$c = \int_{t_1}^{t_2} \frac{d_p}{d_t} c'\,dt = \frac{1}{S}(t_2 - t_1)\int_{t_1}^{t_2} \frac{d_p}{d_t}\,dt = \frac{(P_2 - P_1)}{S}(t_2 - t_1) \qquad (12)$$

t_1 and t_2 being the time of measurement of P_1 and P_2 (phytomass values), and S is the soil surface in which P_1 and P_2 are estimated.

The growth characteristics called indexes by some authors, which are more related to the primary economic productivity, in addition to the retro-mentioned ones that define the production rate of the crop, are the harvest index (HI) or coefficient of migration or emissivity (equation 13):

$$HI = \frac{\text{Economical Yield}}{\text{Biological Yield}} \times 100 \qquad (13)$$

The derivation is the score of productivity (SP), which is the sum of the harvest index, the primary productivity of the agroecosystem and the economic productivity of the crop.

For example, for a castor bean field that produces 2.26 tons of grains.ha^{-1}, 12.65 tons ha^{-1} of biological productivity and has a harvest index of 36, the EP is 53.7, which is important to describe the relationships between the yields of plants and the amount that is actually harvested and marketed.

Estimation of assimilation and respiration rates in communities

The apparent assimilation rate (AAR) results from the contribution of two components: the rate of gross assimilation (RGA) and respiration rate (RR) (Magalhães, 1986), according to equation 14.

$$AAR = n\,RGA - RR \qquad (14)$$

In which *n* is the number of days during which the plant performed photosynthesis.

Considering that the RGA is proportional to the assimilative surface, assimilation, and that RR is proportional to total biomass, the following equation can be applied (equation 15):

$$dP = \delta\,Adt - \rho\,pdt$$

In which:
P = total biomass (total plant dry weight);
A = assimilative surface (leaf area);
☐ = rate of gross assimilation (g.m^{-2}.day^{-1});
☐ = respiration rate (g.g^{-1}.day^{-1});
The coefficients ☐ and ☐ represent the mean values obtained during an indefinite period.
Solving the equation 16:

$$P_2 - P_1 = \delta\int_{t_1}^{t_2} Adt - \rho\int_{t_1}^{t_2} Pdt \qquad (16)$$

The expression represents the leaf area duration (D);

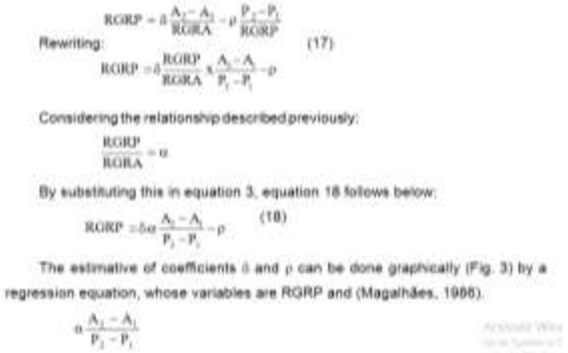
$$\int_{t_1}^{t_2} Adt$$

The expression is the accumulated biomass (Pt).

$$\int_{t_1}^{t_2} Pdt$$

Thus, the increase of dry weight (P_2 - P_1) is proportional to the coefficient ☐ and leaf area duration (D) represents the rate of gross assimilation. The amount of biomass that is lost by respiration, which is proportional to the coefficient ☐ and is accumulated biomass (Pt), is subtracted from RGA.

The values of D and Pt can be estimated by integration or by graphic method, by calculating the areas under the curves of A and P, in relation to time. Whereas, in the time period t_2-t_1, A and P grow exponentially, the relative growth rates of assimilative surface and total biomass (RGRA and RGRP) must be included in the calculation, according to equation 17:



$$RGRP = \delta\frac{A_2 - A_1}{RGRA} - \rho\frac{P_2 - P_1}{RGRP}$$

Rewriting:

$$RGRP = \delta\frac{RGRP}{RGRA}\times\frac{A_2 - A_1}{P_2 - P_1} - \rho \qquad (17)$$

Considering the relationship described previously:

$$\frac{RGRP}{RGRA} = \alpha$$

By substituting this in equation 3, equation 18 follows below:

$$RGRP = \delta\alpha\frac{A_2 - A_1}{P_2 - P_1} - \rho \qquad (18)$$

The estimative of coefficients δ and ρ can be done graphically (Fig. 3) by a regression equation, whose variables are RGRP and (Magalhães, 1986).

$$\alpha\frac{A_2 - A_1}{P_2 - P_1}$$

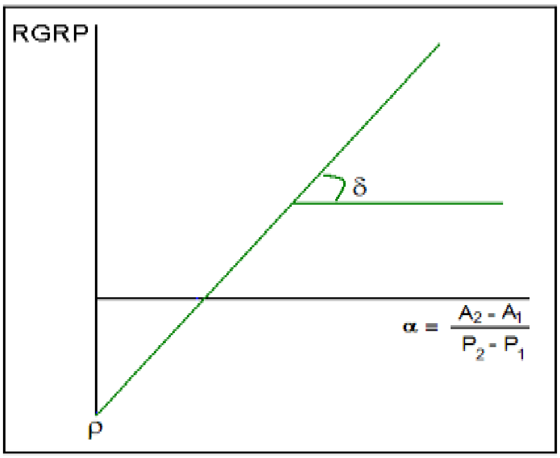


Fig. 3. Estimative of coefficients ☐ (rate of gross assimilation, expressed in g.m^{-2}.day^{-1} and ☐ (respiration rate, expressed in g.g^{-1}.day^{-1}) through relative growth rate of total biomass (RGRP) variations (adapted from Magalhães, 1986).

The relationships between the characteristics of growth and respiration rate are ecophysiologically defined as a loss of phytomass. It is proportional to formed biomass, and based on the component of maintenance and growth. In this way, Beltrão *et al.* (2000) estimated graphically the respiration for two varieties of cotton: perennial cultivar 7MH, under ecophysiological conditions of Seridó (Paraíba), Brazil, in two populations of plants (20,000 plants and 33,333 plants), at 100 days after emergence, and found the values that were described on Fig. 4, respectively for 33,333 plants.ha^{-1} and 20,000 plants.ha^{-1}. The respiration of the plant community of 7MH, defined as loss of phytomass, was much greater at the higher population – 33,333 plants.ha^{-1}.

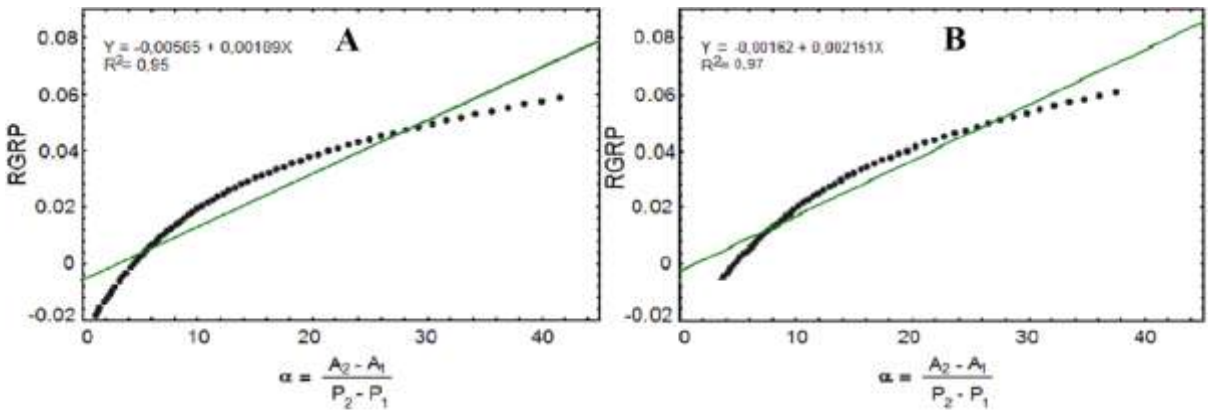


Fig. 4. Estimation of cotton respiration, cultivar 7MH, at the configuration of 1.0 m × 0.3 m, with 33,333 $plants.ha^{-1}$ (A) and at the configuration of 1.0 m × 0.5 m, 20,000 $plants.ha^{-1}$ (B). Patos, PB, Brazil, 1997 (adapted from Beltrão *et al.*, 2000).

Green plants have a substance, the chlorophyll, which is capable of absorbing light radiation. The absorbed energy is used to transform carbon dioxide from the air (CO_2) and water (absorbed by the roots) into glucose (a type of sugar) through a process called photosynthesis. The production of organic matter can also be expressed in energy units, considering that solar radiation is ultimately transformed into biomass. The calorie or the joule are the most commonly used units for calculating the energy content of the incident radiation, and also the energy stored in organic matter. In general, the energy content of one gram of biomass varies from 3.500 kcal to 4.800 kcal, which corresponds to 14.650 J and 20.100 J (1.000 cal $\cong$ 4.186 J). The herbaceous plants have, on average, values around 4.000 $kcal.g^{-1}$ (16.744 $J.g^{-1}$), while woody species have energy values of approximately 4.700 $kcal.g^{-1}$ (19.674 $J.g^{-1}$) (Lieth, 1969).

The estimation of conversion efficiency of solar energy (E_s) can be done by equation 19, which was proposed by Kamel (1959):

$$E_S = \frac{BP \; x \, QE}{SR \; x \, 0.45} \qquad (19)$$

In which:

BP = biological productivity = change in dry matter production per unit of land, per unit of time ($g.m^{-2}.day^{-1}$);

QE = quantity of energy contained in dry matter ($kJ.g^{-1}$ or $kcal.g^{-1}$);

SR = solar radiation ($kJ.m^2.day$);

0.45 = fraction of total solar radiation, which can be used to carry out photosynthesis.

The value of Ec shows appreciable changes with the amount of incoming solar radiation and plant age.

Practical implications of knowledge of respiration and its control

In field conditions, at an ecophysiological level, particularly in the tropics where the temperature is high, which is generally above 25°C on average, being able to reach over 34°C, oxidative or mitochondrial respiration is high, substantially reducing the net photosynthesis, or photosynthetic balance, which was expressed by the simplified equation 20:

$$Y = \int_{t_1}^{t_2} (netP)\, dt \qquad (20)$$

In which:

Y is the total plant phytomass (dry weight), t is time and netP is the net photosynthesis rate of plants "stand", according to Baker & Meyer (1966), as previously mentioned.

In ecophysiology, respiration means loss of phytomass, which can represent up to more than 60% of what was already produced via chlorophyll assimilation, being very significant for the primary productivity of the agroecosystem, and depends on the partition of assimilates to reach its economic productivity. To increase the productivity of the plant community, besides the factors of production, input and appropriate cultural management, there must be mechanisms to reduce the respiratory process, that is, to increase the balance and thus the photosynthetic coefficient, and to make the CO_2 balance the most positive as possible (equation 21):

$$P_G = P_N + R \qquad (21)$$

i.e., P_G = gross photosynthesis, P_N = net photosynthesis and R = total agroecosystem respiration.

To increase primary productivity (equation 22), in case of C3 metabolism plants, such as castor bean, cotton, rice, wheat and others (mostly Spermatophyta), respiration must be reduced.

$$P = \frac{P_G}{R} = \frac{P_N + R}{R} = \frac{\text{PN} + (\text{Oxidative Answer} + \text{Photorespiration})}{\text{Total Answer}} \qquad (22)$$

In general, Primavesi (1980) recommends several practices to increase photosynthesis and reduce respiration under tropical conditions, such as these ones followed described. 1 – It is necessary provide adequate water supply for the plant to increment the efficiency of water use, to not be in water stress, due to deficiency or excess, and thus to not close their stomata during the day, so that CO_2 penetrates and is used in the photosynthetic process. 2 – The crops must be kept healthy, with no pests and diseases, through proper management of the agroecosystem, involving planting season, appropriate cultivation, absence of weeds, balanced fertilization, etc. 3 – It is important to decrease the respiration rates, by decreasing soil temperature. It can be achieved through soil protection, reducing the direct insolation, using intercropped crops and less spacing, besides other techniques. 4 – Finally, and not less important, it is essential to have water, dams and other reservoirs to reduce room temperature, and thus contribute to increase photosynthetic balance.

Conclusion

The full knowledge of the analysis of destructive growth, with estimation of respiration of monoculture plants or plant communities is crucial. It may represent a "tool" of great importance for understanding the functionality of an agroecosystem and improving productivity, especially the economic one, with an increase in harvest index and even in the quality of the final product and coproducts.

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