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Substrate utilization and respiration in relation to growth and maintenance in higher plants[1]

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Summary

The significance and regulation of respiration processes in plants are investigated to determine how much of the carbon fixed by photosynthesis gets lost by respiration. The major part of the respiration of field crops results from growth processes. The relations between growth, substrate utilization, and maintenance are calculated accurately on a theoretical basis. These are also experimentally confirmed. Another part of the respiration is caused by maintenance processes to keep cells unimpaired. These are still little studied. The magnitude of maintenance respiration is therefore not well known. Overall picture has been obtained of the processes involved.

This study gives an insight into the energy metabolism of organisms. It contributes therefore to understanding of many quantitative biological problems.

Introduction

The recent development of simulation techniques to study growth of field crops actualized the question how much of the carbon fixed by photosynthesis gets lost by respiratory processes (de Wit et al., 1970). A coherent picture can hardly be constructed from literature data on carbon dioxide production and oxygen consumption of different organs in various conditions, and certainly none that allows extrapolation to other situations. This study tries to answer this question by the investigation of the significance and regulation of respiratory processes in plants. Although this problem is focussed to higher plants it is of a much broader nature.

Five groups of processes were recognized in which carbon dioxide evolution and oxygen uptake are involved:

1. Processes related to the biochemical conversion of substrate into the compounds found in organisms, or shortly: growth processes. The central question is how many grams of carbon dioxide are produced and how many grams of oxygen are consumed if 1.0 gram of glucose is converted into biomass. The question how many grams of biomass are formed simultaneously is closely related, but the answer to the second question does not follow from the answer to the first because also water is involved.
2. Processes related to maintenance of already existing cells and their structures. Energy for these processes is provided by respiration. From respiration measurements

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[1] This paper is a summary of the author's Ph. D. thesis by the same title.

it appears that the intensity of maintenance processes in plants is low compared to animals and micro-organisms. In many situations, however, these processes do consume an important fraction of the assimilates.

3. Processes related to active transport of organic compounds across cell membranes and in phloem vessels. Nearly all substrate for growth is transported, because substrate production usually does not occur in growing cells. Water transport is a passive process, which active regulation requires very little respiratory energy.
4. Processes without usefull outcome. A considerable fraction of the carbon dioxide evolution in plants has often been ascribed to 'uncoupled respiration': a process without any (known) use. It is pressupposed for this study that these processes are unimportant, and this is demonstrated in a few cases. To decide that these processes are also absent in other conditions, simultaneous measurements are lacking of rates of respiration, protein turnover and ion fluxes across membranes.
5. Photorespiration. The calculation of carbon dioxide assimilation of a canopy is usually based on the carbon dioxide assimilation light respons curve of a single leaf in similar conditions. A possible decrease of the rate of assimilation due to photorespiration is already included in this curve, and photorespiration is not important any longer for such calculations. Because in general photosynthesizing cells do not grow and none or little photosynthesis occurs in growing cells, photorespiration does not contribute to formation of any other product than sugars and amino acids, which amount is known already.

The energy consumption in other active processes in plants is negligible.

In this way the initial problem is restricted and clarified considerably. It is now very similar to that of production microbiologists, but is still new for many plant physiologists.

Methods

To determine the amount of biomass formed from a certain amount of substrate and the concomitant respiration, the 'reaction equation' of the biochemical conversions may be calculated. For example, if lysine is the end product and glucose and ammonia are substrates, handbooks of biochemistry indicate that in plants this conversion can be represented by the reaction equation:

$$\begin{gathered}1 \text{ glucose} + 2\ NH_3 + 2\ NADH_2 + 2\ ATP \rightarrow \\ 1 \text{ lysine} + 4\ H_2O + 2\ NAD + 2\ ADP + 2P_i\end{gathered}$$

Heterotropic cells obtain the hydrogen ($NADH_2$) and energy (ATP) required by oxidation of glucose. The maximum efficiency of substrate and energy utilization is always used, so that the total conversion process, expressed in grams, is represented by the equation:

$$\begin{gathered}1.000 \text{ g glucose} + 0.156 \text{ g } NH_3 + 0.039 \text{ g } O_2 \rightarrow \\ 0.671 \text{ g lysine} + 0.255 \text{ g } CO_2 + 0.269 \text{ g } H_2O\end{gathered}$$

Such equations can be made for all important conversions. To do so only a basic knowledge is required of the well known processes that are the direct cause of carbon dioxide formation and oxygen consumption. When synthesizing complex products the reaction equations of the constituting monomers are added according to their relative importance, and cost of polymerization are accounted for. In this way a conversion reaction can also be constructed for synthesis of a complex end product, such as biomass. The equation contains only weights of glucose, oxygen, minerals, the end product, carbon dioxide and water. In addition, the active uptake of glucose and minerals requires respiratory energy. Finally, the computations were extended to include also some processes that require little energy.

Much of the basic information for such calculations has been obtained from microorganisms, but it seems correct to conclude that differences in this respect between various kinds of organisms are unimportant.

The above calculations can be applied in principle to higher plants, because heterotrophic, growing cells are generally separated from autotrophic non-growing cells. The substrate for growth mostly consists of sucrose and amino acids.

Costs of maintenance processes are calculated from the intensity of these processes and their specific costs. The latter concern mainly costs of (re)synthesis and are fairly well known, but their intensity has been determined only in a few cases. There are also still remarkable few measurements of maintenance respiration in plants.

Conclusions

A first question is whether the yield of growth processes calculated in this way agrees with what is found in plants, or that it is of purely theoretical value. A simple experiment by Kandler (1953) answers this. He grew maize embryos in darkness at 27 °C in a petri dish with a nutrient solution containing glucose and nitrate, and determined the weight increase of the embryos and the amount of glucose consumed over a five-day period. On basis of an estimate of the composition of the biomass synthesized a simplified calculation of how much glucose is required theoretically for synthesis is made (Table 1). In addition to 66 mg glucose needed for the synthesis of 47.5 mg dry matter, uptake of glucose and minerals consumes the energy of 3.7 mg glucose. Maintenance of the material already formed consumes 2 to 5 mg glucose, so that the total glucose consumption is calculated to be 71.5 to 74.5 mg glucose. This is almost identical to the experimental result (75.4 ± 2.4 mg). The ratios of the volumes of carbon dioxide and

Table 1. A calculation of the amounts of glucose, CO_2 and O_2 involved in synthesis of 47.5 mg of maize plant in darkness. Meaning of the columns: 1) weight increase (mg) of the fraction considered (only 'total' and 'nitrogenous compounds' have been observed); 2) amount of the fraction considered (g) formed from 1.0 g of glucose; 3) mg glucose required for biosynthesis; 4) amount of CO_2 (g) released during conversion of 1.0 g of glucose into the fraction considered; 5) mg CO_2 released; 6) amount of O_2 (g) required for conversion of 1.0 g glucose into the fraction considered; 7) mg O_2 required. The figures in the columns 2, 4 and 6 are standard values.

Fractions of the biomass formed	1	2	3	4	5	6	7
Carbohydrates	32.6	0.826	39.50	0.102	4.02	0.082	3.23
Nitrogenous compounds	5.6	0.404	13.85	0.673	9.35	0.174	2.42
Organic acids	3.0	1.104	2.71	-0.050	-0.14	0.298	0.81
Lignin	2.4	0.465	5.16	0.292	1.51	0.116	0.60
Minerals	2.4	-	-	-	-	-	-
Lipids	1.5	0.330	4.54	0.530	2.41	0.116	0.53
Total	47.5	-	65.76	-	17.15	-	7.59

oxygen involved in the calculation (1.35-1.29) and the experiment (1.2 ± 0.1) also agree fairly well. It is therefore concluded that the reaction equation derived from basic biochemical data reflects reality at least under good growing conditions, and that enzymatic conversions and transport processes in plants occur at almost maximum efficiency. Because the cost of synthesis and transport are independent of temperature, the result is almost independent of temperature.

A computer program has been formulated to execute these detailed calculations. A sensitivity analysis indicated that the rough chemical composition of the end product (as indicated in Table 1), and the form in which nitrogen was supplied (as nitrate or ammonia), have the most effect on the amount of biomass formed and the respiration. Much less important are more precise data on the composition of the end product (such as the amino acid composition of protein), cellular compartmentation of processes, maintenance cost of used enzymes, and even the efficiency of oxidative phosphorylation between 100 % and 50 % of its maximal value is of minor importance. Consequently a simplified scheme was derived to calculate the reaction equation of conversions (Penning de Vries et al., 1974).

The above calculations need not much change if applied to autotrophic plants: only the synthesis of many nitrogenous compounds consumes amino acids and sucrose instead of glucose and minerals, and cost of active transport has to be included. The transport cost for translocation over short distances is probably mainly that of passing membranes of the cell and phloem vessels, but transport over many meters may be much more expensive. A fair impression of the amount of substrate required for biosynthesis of 1 g of biomass in autotrophic plants can be obtained from the chemical composition of the tissue synthesized and the data for the various compounds of Table 1. About twice as much substrate may be involved in translocation as in the maize embryo example.

However, there is also an important difference: in most agricultural crops the majority of nitrate reduction occurs in the leaves in the light. If the light intensity is in the light-saturated part of the carbon dioxide assimilation light respons curve, the rate of carbon dioxide assimilation is limited by the rate of carbon dioxide diffusion into the leaf, and because then more energy is available in the green cell due to the high light intensity the other energy requiring processes do not decrease the carbon dioxide assimilation. This is important especially for an expensive process such as nitrate reduction. For this reason nitrate reduction in many field crops consumes much less energy from assimilates than is expected from its high reduction cost in darkness. Also other processes can use energy that has not been fixed in assimilates, but these are usually less important. Mainly due to nitrate reduction energy absorption by leaves is often 5 to 15 % higher than is expected according to the reaction: carbon dioxide plus water plus light energy gives glucose plus oxygen (Penning de Vries, 1974a).

Since formation of biomass from assimilates causes a predictable carbon dioxide production, it is possible to determine non destructively the rate of growth by measuring the rate of respiration. This is confirmed by experiments in which substrate utilization, respiration and growth of whole plants is known, as for example in constant conditions in the light, where the rates of carbon dioxide assimilation and of growth (and therefore that of dissimilation) are related. A comparison of measured and calculated ratios of assimilation to dissimilation of young plants of various species at some temperatures demonstrates that also these plants utilize their substrates at the biochemically maximal efficiency (Penning de Vries, 1974a). It seems thus impossible to increase the efficiency of plants in this sence by plant breeding.

Maintenance processes require an unimportant amount of energy in rapidly growing tissues, i.e. at a relative growth rate of 0.3 g $g^{-1}day^{-1}$ or more, but a considerable fraction in other cases (Penning de Vries et al., 1974, Penning de Vries, 1974b). Measurements of maintenance respiration indicate that these processes consume about 1 to 4 % of the weight of the dry matter in the form of carbohydrates per day. Knowledge of the individual maintenance processes indicates that the main part of it is used for continuous breakdown and resynthesis of proteins, while another important fraction is required to maintain ion concentrations in cells. To determine the amount of substrate required from the calculated energy consumption in these processes it is essential to know the efficiency of oxidative phosphorylation. However, due to technical difficulties this information is still very limited in plants.

The intensity of protein turnover, and therefore its cost, probably depends on the metabolic activity of the cells, which may be expressed as the daily carbon dioxide assimilation. The cost of maintaining ion concentrations depends mainly upon the environment. The first conclusion arises mainly from measurements of the maintenance respiration rate in leaves, and the few basic data do not support or oppose this. The second conclusion is derived mainly from basic data and was only indirectly confirmed. It seems worthwhile to investigate how to reduce protein turnover, a process that may have lost much of its importance in present agricultural conditions. Unlike increasing the efficiency of synthetic processes in plants, which is considered to be impossible, it seems feasible to control the rate of maintenance processes, and thus to influence the crop yield considerably (Penning de Vries, 1974b). Cost of maintenance processes probably depends on external conditions, such as temperature, salinity and water stress, but this cannot be quantified as yet.

Many minor questions have not been answered because of lack of basic data. Probably because the rate of synthetic processes in the investigated organ is unknown, quite some unexplained observations remain also. It is likely that many of such observations will not be explained before a better insight is obtained into the processes and factors that start, regulate and influence biochemical conversions and transport.

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