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IV.4 Respiration and growth

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I. Introduction

As early as 1922 it was observed that the uptake of glucose by *Aspergillus niger* is related to its growth (Terroine and Wurmser, 1922). Under a range of conditions the weight of the mycelium formed is about 45% of the weight of the carbohydrates consumed. From the observation that this percentage decreases with the age of the culture, it was concluded that another energy-requiring process occurs to keep the organism functioning. This process was calculated to require about 1% of the mycelium dry weight per hour. Tamiya (1932) and Tamiya and Yamaguchi (1933) were among the first to use and quantify the concepts "growth respiration" and "maintenance respiration" by measuring glucose uptake, mycelium dry weight, oxygen consumption and carbon dioxide production of a growing *Aspergillus niger* culture. These workers presented some interesting ideas about basic phenomena of dry matter production. This kind of study is continued in microbiology (Rippel-Baldes, 1952; Bauchop and Elsdon, 1960; Payne, 1970), but is very scarce in literature about higher plants.

Another approach to the relation between respiration and dry matter production considers the energy contents of compounds and the reactions by which these compounds are formed. It is used in animal physiology (Brody, 1945; Blaxter, 1962; Needham, 1964), but is also to be found in the older literature of microbiology (Terroine and Wurmser, 1922; Tamiya, 1932) and in more recent work. Forrest and Walker (1971) provide detailed information about the energy requirement during the synthesis of bacteria.

Since the forties much research and study has been devoted to respiration rates of organs and organisms as influenced by temperature,

oxygen and carbon dioxide tension, concentration of micro-elements, uncoupling agents and in relation to metabolism. Biochemical investigations have supplied detailed information about glycolysis, the TCA cycle, electron transfer and phosphorylation in mitochondria and related processes (Ducet and Rosenberg, 1962; Beevers, 1970).

Recently the fascinating topic of photorespiration has received much attention. Biochemical mechanisms have been suggested, but the meaning of this process for the plant is still uncertain (Jackson and Volk, 1970; Walker and Crofts, 1970).

Of the many aspects of plant growth only change in dry weight will be considered. Other aspects of growth (fresh weight increase, change form or volume) have at the most only a small direct influence on carbon dioxide production.

Since simulation models of crop growth have been developed, it has become increasingly evident that quantitatively little is known about respiration involved with crop growth (Canvin, 1970). In the model of de Wit *et al.* (1970) an approach was adopted in which respiration associated with synthesis of dry matter was calculated using biochemical knowledge on the conversion of glucose into plant constituents, and that concerned with maintenance was estimated from plant protein content and temperature. There have been previous attempts to link dry matter production and respiration to substrate use based on molecular conversions (Tamiya, 1932; Krebs and Kornberg, 1957; Schiemann, 1958; Blaxter, 1962), but their results were not detailed and cannot be applied in quantitative estimates of crop and plant respiration. It is, however, this approach that will be extended in this paper in order to elucidate problems concerned with respiration of plants and crops.

Little attention will be paid to the efficiency of energy transfer in the plant. The main reason is the very much easier way in which information is obtained (Krebs and Kornberg, 1957) and calculations are performed using weights of compounds.

II. Respiration and synthetic processes

Increase in plant dry matter is nearly always due to synthetic processes. Only where minerals are taken up or glucose accumulates in cells as an end product is dry weight increase not the result of synthesis other than photosynthesis. It is therefore logical to study synthetic processes in detail.

Biochemical pathways for the synthesis of the majority of organic constituents are known (Bonner and Varner, 1965; Dagley and Nicholson, 1970). From such knowledge the weight of a certain compound synthe-

sized from 1.0 g of a particular substrate was established theoretically. Both material conversions occurring during synthesis and the chemical energy to be supplied to the reactions in the form of ATP were taken into account. Results of such calculations are given in Table I. The theoretical derivation of these values will be considered elsewhere. The factor by which the weight of the organic substrate is multiplied in order to achieve the weight of a particular end product formed via a particular conversion pathway will be called the "production value" or "weight

Table I

Some characteristic values for the conversion of 1.0 g of glucose into plant components, using the most efficient biochemical pathways.

<i>End product</i>	<i>Weight of end product (p.v.)</i>	<i>Carbon dioxide production factor (c.p.f.)</i>	<i>Oxygen requirement factor (o.r.f.)</i>	<i>Energy efficiency</i>	<i>N and S supplied as</i>
Amino acids	0.80	0.11	0.047	0.79	NH ₃ and H ₂ S
Amino acids	0.54	0.55	0.003	0.68	NO ₃ ⁻ and SO ₄ ²⁻
Proteins	0.67	0.16	0.081	0.78	NH ₃ and H ₂ S
Proteins	0.45	0.58	0.036	0.67	NO ₃ ⁻ and SO ₄ ²⁻
Nucleic acids	0.77	0.33	0.394	—	NH ₃ and H ₂ S
Nucleic acids	0.57	0.62	0.081	—	NO ₃ ⁻ and SO ₄ ²⁻
Lipids	0.36	0.47	0.035	0.88	
Cellulose and					
Starch	0.855	0.07	0.051	0.93	
Sucrose	0.915	0.053	0.0385	0.96	
Carboxylic acids	1.43	-0.25	0.13	0.6	

efficiency" for this conversion (p.v.). Each combination of substrate, pathway and end product has its own p.v., but it appeared in most cases that the resulting p.v. depends little on the pathway chosen. It is therefore unlikely that the p.v. varies between species. The factor by which the weight of the organic substrate is multiplied to give the weight of the CO₂ produced will be called the "carbon dioxide production factor" (c.p.f.). The factor necessary to calculate the weight of oxygen required in the conversion of the initial weight of substrate will be termed the "oxygen requirement factor" (o.r.f.). To compare the "weight efficiency" (p.v.) of the conversions with the "energy efficiency" (the combustion value of the

end product per decrease of the combustion value of the substrate used) approximate values for the latter are presented in Table I. These are considerably more uniform than the p.v. of the conversions.

For the composition of the amino acid mixture and proteins in Table I, data for alfalfa (Mertz *et al.*, 1952) were used. Nucleic acids are assumed to consist of equal amounts of RNA and DNA. The lipid fraction was taken to be merely glycerine tripalmitate. Carboxylic acids are assumed to consist of equal weights of malic and citric acid. As the *in vivo* pathway of synthesis of carboxylates is not well established it is assumed that the carboxylation of pyruvate is an intermediate reaction, so that during their synthesis carbon dioxide is taken up instead of being produced.

From Table I it is seen that the p.v. of glucose for carbohydrates and carboxylic acids is considerably higher than its p.v. for lipids, amino acids, proteins and nucleic acids. The p.v. for synthesis of nitrogenous compounds is higher when reduced nitrogen and sulphur are supplied instead of nitrate and sulphate, due to the relatively large amount of energy required for reduction. The p.v. for protein synthesis depends upon the composition of its amino acid mixture. For 13 different plant and animal proteins the p.v. for synthesis from glucose and nitrate was calculated to vary between 0.446 (arachin) and 0.496 (gliadin), the c.p.f. being 0.588 and 0.522 and the o.r.f. 0.028 and 0.013 respectively.

The figures in Table I depend little on the assumptions made, the most important ones being that the plant uses what are believed to be the most efficient biochemical pathways, that these are common for all species at any time and that the P/O ratio of ATP production is 3 (Beevers, 1961, p. 127; Hadjipetrou *et al.*, 1964).

Provided that the chemical composition of the plant is known, the p.v.'s of Table I allow the amount of glucose required to synthesize 1.0 g of plant material to be calculated. An example of this is given in Table II, where the chemical composition refers to 25-day old maize plants. The fraction "organic N compounds" is assumed to consist of proteins (75%) and amino acids (20%), having a composition similar to alfalfa (Mertz *et al.*, 1952), and nucleic acids (5%). "Carbohydrates" consist of starch and cellulose (80%), sucrose (15%) and glucose (5%). For "lipids" and "carboxylic acids" the same suppositions as in Table I were made. Nitrogen and sulphur are taken to be supplied in the oxidized form.

Plant tissue contains minerals, which are taken up actively into cells with energy derived from glucose. It may be assumed from data collected by Beevers (1961) and Stein (1967) that 1.0 g of minerals can be taken up actively into cells with energy achieved from approximately 0.05 g glucose. Lehninger (1965) derived similar values on a thermodynamic basis.

As a rule a source of glucose is not present in growing cells and therefore carbohydrates have also to be imported. Assuming that all import is active, that passage of two cell membranes requires the energy of 2 ATP molecules per glucose molecule and that costs of translocation over distances less than 1 m are negligible (Weatherley and Johnson, 1968), it was calculated that for both the unloading and loading of the phloem by 1.0 g of glucose 0.05 g has to be respired. Costs of intracellular transport

Table II

The amount of glucose required to synthesize 1.0 g of plant material

<i>Compound or process</i>	<i>Weight of compounds (g)</i>	<i>p.v.</i>	<i>Glucose required (g)</i>	<i>c.p.f.</i>	<i>Carbon dioxide produced (g)</i>	<i>o.r.f.</i>	<i>Oxygen consumed (g)</i>
Organic N compounds	0.23	0.48	0.478	0.57	0.272	0.031	0.0148
Lipids	0.025	0.36	0.070	0.47	0.033	0.035	0.0025
Carbo- hydrates	0.64	0.87	0.735	0.064	0.047	0.047	0.0345
Carboxylic acids	0.04	1.43	0.028	-0.25	-0.007	0.13	0.0036
Mineral uptake	0.065	20	0.003	1.47	0.005	1.07	0.0035
Glucose uptake	—	—	0.070	1.47	0.103	1.07	0.0750
Total	1.00	—	1.384	—	0.453	—	0.1339

are neglected. The membrane transport mechanism of ionic and non-ionic compounds is not clear (Kaback, 1970), so that these figures are estimates.

The result of the refinements included in Table II is that the maximum relative yield of 1.38 g glucose available from the phloem is 1.0 g of tissue and that 0.453 g of carbon dioxide is produced and 0.134 g of oxygen consumed.

Table III presents the results of an experimental test of the above hypothesis. Kandler (1953) cultivated maize embryos in darkness on a solution containing glucose and nitrate. Dry weight increase and glucose consumption were measured. The chemical composition of the young plant was estimated from the observed amount of nitrogen in the embryo.

The requirements for glucose and ion uptake were taken to be two times higher than the ones in Table II to account for uptake by the roots and transport into growing cells from vascular tissue. The lower p.v. for "organic N compounds" compared with Table II was calculated assuming that all amino acids are synthesized in the roots and that half of them are translocated to support shoot growth.

The experimentally established glucose consumption (75.4 mg) is 10% higher than was expected (68.0 mg). Causes of this discrepancy may be

Table III

The amount of glucose required to synthesize 47.5 mg maize embryo. Measured glucose uptake: 75.4 ± 2.4 mg

<i>Compound or process</i>	<i>Weight of compounds (mg)</i>	<i>p.v.</i>	<i>Glucose required (mg)</i>	<i>c.p.f.</i>	<i>Carbon dioxide produced (mg)</i>	<i>o.r.f.</i>	<i>Oxygen consumed (mg)</i>
Organic N compounds	5.6	0.44	12.8	0.60	7.7	0.080	1.0
Lipids	2.4	0.36	6.6	0.47	3.1	0.035	0.3
Carbo-hydrates	34.7	0.87	39.9	0.062	2.5	0.045	1.8
Carboxylic acids	2.4	1.43	1.7	-0.25	-0.4	0.13	0.2
Mineral uptake	2.4	10	0.2	1.47	0.3	1.07	0.2
Glucose uptake	—	—	6.8	1.47	10.0	1.07	7.3
Total	47.5	—	68.0	—	23.2	—	10.8

an incorrect estimation of the chemical composition of the dry matter. It is also possible that the neglect of maintenance respiration or redistribution (p. 342) is not warranted because of the relatively unfavourable culture conditions, evident from its low nitrogen content (1.9% compared with 3–5% normally observed). This suggestion is supported by the observation that the relative yield of the glucose consumed decreases rather rapidly with increasing age of the plant. A maintenance respiration rate of 5% of the dry matter per day (three times the normal value) may cover the difference between experiment and hypothesis completely. It is also possible that a certain rate of turnover of the synthesized com-

pounds occurs, increasing the amount of substrate required for dry matter production. If this takes place it ought to be included in the calculation of the p.v.

A similar correspondence between theory and experiment was not observed in bacterial cultures where the experimental yield is about 0.3–0.5 of the theoretical value. The cause of this difference between higher and lower organisms is discussed by Forrest and Walker (1971).

III. Respiration and synthesis from photosynthate

Photorespiration will not be discussed because it does not affect processes after production of photosynthate; that it decreases the rate of photosynthate formation is not relevant here. Heath (1969) has given a review about the interrelationship of photosynthesis and respiration.

Except under laboratory conditions, the substrate for plant growth is not merely glucose and nitrate. The substrate for dry matter production in roots, stems and young leaves is phloem translocate, more mature leaves utilizing their own photosynthetic products. In both cases the substrate for growth is complex: photosynthesis generates a wide variety of compounds (Gibbs *et al.*, 1967) and phloem contains a mixture of carbohydrates and amino acids (Kursanov, 1963).

It was measured in maize plants that from the daily net carbon dioxide uptake about 0.62 g dry matter per g carbon dioxide was formed, or 0.90 g when carbon dioxide fixation is expressed in g CH_2O . In *Helianthus annuus* these values are 0.64 and 0.94 respectively (Eckhardt *et al.*, 1971). This ratio is determined by the chemical composition of the plant, which does not depend on the photosynthetic rate. However, it does not matter what part of the carbon dioxide assimilated by leaves in the light ends up in plant material and what part is lost by respiration of leaves in darkness and in the other plant organs. Important questions in understanding plant production are therefore, first: how much photosynthate is required to produce 1.0 g of plant dry matter, and second: how much carbon dioxide uptake by adult leaves corresponds with this. It will be derived that from 2.027 g (carbon dioxide) gross assimilate a maize plant may produce 1.0 g of plant dry matter, and a bean plant this same quantity, but with different chemical composition, from 1.923 (carbon dioxide) gross assimilate. The conversion respiration is 0.430 and 0.368 g carbon dioxide respectively.

For the derivation of the above figures it is assumed that the plant is separated into a photosynthesizing part with hardly any permanent dry matter accumulation, and a non-photosynthetic growing part. The substrate for the formation of dry matter has to be transported from the productive sites to leaves that are not yet able to photosynthesize, to roots

and to other organs. Figures 1 and 2 represent an organ converting phloem translocate into new structural material and a photosynthesizing leaf respectively. In both Figures the types of compounds involved are given in blocks and the numbers represent the corresponding weights in grams.

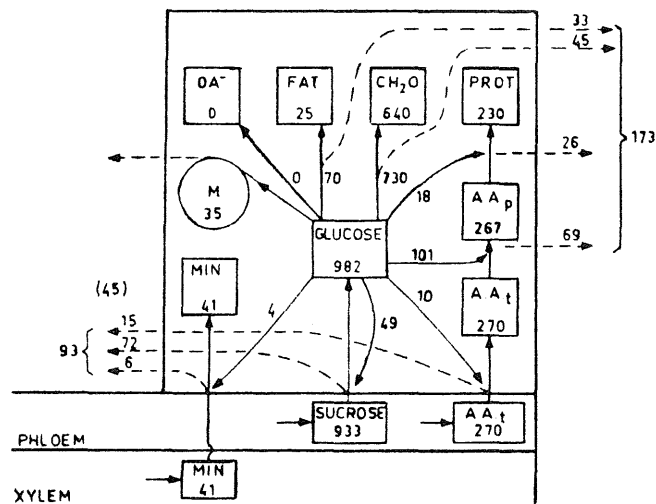


Fig. 1. A simple representation of a growing organ.

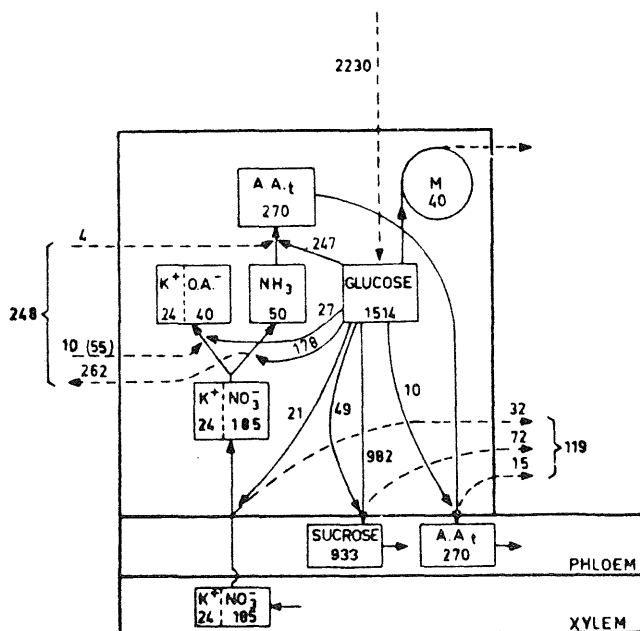


Fig. 2. A simple representation of a photosynthesizing organ.

Full drawn lines represent conversion and transport processes, dashed lines represent carbon dioxide exchange, and oxygen is not considered. The chemical composition of vegetative maize plants and the data of Table I were the basis for the calculations.

It is shown (Fig. 1) that $(230 + 640 + 25 + 41 =) 936$ g tissue may be synthesized from 41 g of minerals (MIN) supplied by the xylem, and $(933 + 270 =) 1203$ g phloem translocate, consisting of 77.5% of sucrose, and 22.5% of a mixture of amino acids (A.A._t), including 4.7% amides. After uptake, some sucrose is transformed via glucose into lipids (FAT), carbohydrates (CH₂O) and some is used to provide energy for uptake processes and protein (PROT) synthesis from amino acids. Glucose is also a source of carbon and energy for the transformation of amino acids of the translocated mixture (A.A._t) into a mixture (A.A._p) ready to synthesize the plant proteins. The composition of A.A._t was chosen to be the sum of the amino acids usually not formed via aspartic and glutamic acid and a large enough quantity of aspartic and glutamic acid to produce the amino acids synthesized from these. The carbon dioxide production amounts to $(33 + 45 + 26 + 69 =) 173$ g due to conversions and $(15 + 72 + 6 =) 93$ g due to membrane transport. The circle with M represents the maintenance processes and the number in it an estimation of its daily glucose requirement. It is not included in the calculations.

Figure 2 shows very simply what may be formed by a photosynthesizing leaf when it is supplying the substrate for the organ of Fig. 1. Considerable amounts of energy are involved in NO₃⁻ reduction (NO₃⁻ stands for both NO₃⁻ and SO₄²⁻). Some carbon dioxide is taken up during amino acid and carboxylic acid synthesis. Not all dry weight increase occurs in the "growing" organ: the formation of $(40 + 24 =) 64$ g of carboxylates takes place in the adult part and is coupled with NO₃⁻ reduction (Dijkshoorn, 1962). Like perennial ryegrass (Dijkshoorn *et al.*, 1968) maize exports most of its carboxylates formed to the roots, where the carboxylate group is exchanged with NO₃⁻. The carboxylate remaining in the leaf consists of an organic anion (OA⁻) and an inorganic cation (K⁺), the latter being part of the plant mineral content. It should be mentioned that in Figs 1 and 2 the net process of carboxylate formation is represented. Some non-photosynthetically absorbed carbon dioxide is transported to the roots as carboxylic acid and exchanged. The carbon dioxide involved in this process is given within parentheses in both figures. It appears that approximately 3% of the leaf carbon dioxide uptake is "pumped" from the air into the root medium, the exact percentage depending upon the mechanism of carboxylate formation. Part of the carbon dioxide uptake during photosynthesis is therefore not related to carbon dioxide reduction.

There is evidence that in a well fertilized crop the bulk of the NO₃⁻

reduction occurs in the leaves during photosynthesis (Beevers and Hageman, 1969). This means that the source of NADPH_2 for NO_3^- reduction (from carbohydrate oxidation or active chloroplasts) is irrelevant to this study because a certain measured photosynthetic carbon dioxide uptake would result in both cases in the same amount of reduced nitrogen and reduced carbon. The problem of channelling of energy may be of interest for a plant production approach because, if NO_3^- reduction is competitive with carbon dioxide reduction or utilizes carbohydrates, plants sub-optimally supplied with NO_3^- may have a higher carbohydrate production rate. It is also questionable whether the energy for both transport and maintenance is always channelled via carbohydrates, or whether it is directly available from active chloroplasts as suggested by Ried (1970). The value of 2230 g carbon dioxide in Fig. 2 represents the total of carbon dioxide to be reduced if all hydrogen for nitrate reduction and energy for the considered processes is derived from glucose. This value for carbon dioxide reduction is merely given to illustrate the relative magnitude of sinks of carbon and energy during photosynthesis, and not to suggest that glucose is the intermediate in these processes. Photorespiration, like nitrate reduction, could have been represented in Fig. 2 by an additional amount of carbon dioxide that is reduced and subsequently re-oxidized.

Gross carbon dioxide assimilation may be defined as the sum of assimilation in light and dissimilation as measured shortly after a period of long enough duration to establish an equilibrium between photosynthesis and respiration; the leaf should have a normal rate of nitrate reduction. The gross carbon dioxide assimilation, equal to the apparent gross photosynthesis, of the above maize leaf during production of $(936 + 64 =) 1000$ g biomass is $2230 + 4 + 55 - 262 - 119$ (assimilation in light) $+ 119$ (dark respiration) $= 2027$ g, while the plant dissimilation amounts to 430 g carbon dioxide, of which $(119 + 93 =) 212$ g due to transport, 173 g due to conversions and 45 g due to exchange. The overall net carbon dioxide uptake by the entire plant is $(2027 - 430 =) 1597$ g, which does agree with the expected value of $(1000/0.62 =) 1610$ g. In this calculation it is assumed that nitrate reduction and carboxylate formation occur in light only, and that export continues still at the same rate when dissimilation is measured; maintenance is neglected. It can be concluded that of a gross assimilation of 1.00 g carbon dioxide, equivalent to 0.68 g CH_2O , 0.49 g maize plant dry matter can be synthesized.

This set of calculations is evidently oversimplified. The calculated yield of the conversion may be slightly too low, as cells in nearly adult leaves supply substrate for their own growth, for which no translocation costs are incurred. In maize plants the factor 0.51 may therefore be used to

calculate vegetative dry matter production from the gross assimilation expressed in g carbon dioxide, or the factor 0.75 if expressed in g CH_2O .

For species not exchanging the carboxylate group with nitrate in roots it was calculated in a similar manner that of an apparent gross photosynthetic carbon dioxide uptake of 1923 g carbon dioxide 1000 g biomass may be synthesized, consisting of 46.5% carbohydrates, 22.0% proteins, 15.6% carboxylates, 12.1% minerals and 3.8% lipids; the associated respiration is 191 g carbon dioxide due to transport and 177 g due to conversion. Similar values of carboxylate and mineral content are reported by van Egmond and Houba (1970) in sugar beet plants. Thus in these plants, from 1 g of CH_2O apparent gross photosynthesis (1.47 g carbon dioxide), 0.77 g of plant dry matter may be synthesized. As in the previous

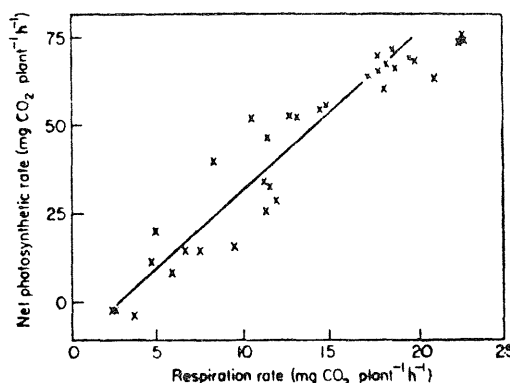


Fig. 3. Measured values of net photosynthetic and respiration rate of maize plants. The slope of the line is determined theoretically.

analysis this is probably an underestimate and the factor 0.80 may be more appropriate to calculate dry matter production from apparent gross photosynthesis expressed in CH_2O .

The highest relative yields from photosynthetic products observed in rapidly growing plants are about 0.8 (Warren Wilson, 1967). More direct evidence for the reliability of the calculations is presented in Figs 3 and 4. The slope of the line relating net photosynthetic rate to respiration rate of 10-day old maize plants (Fig. 3) and of 17-day old bean shoots (*Phaseolus vulgaris*, Fig. 4) will be derived theoretically. Both correspond well with the experimental data (crosses).

In the maize experiment plants were exposed to a regime of 7 h light followed by 1 h darkness in an assembly as described by Louwerse and van Oorschot (1969). At the third repetition of the light cycle, an equilibrium was reached between the net photosynthetic rate and respiration rate

and only measurements of these situations are represented. After the third cycle another value of light intensity in the range from 0 to 300 W m^{-2} visible radiation was applied. Assuming that synthetic processes in the growing organs and transport continue at the same rate in light and darkness because of a buffering capacity of the producing leaves, it was calculated from Figs 1 and 2 that a carbon dioxide production rate of 430 g per unit of time should correspond with a net photosynthetic rate of $(2027 \times 8/7 - 430 =) 1890$ g carbon dioxide per unit of time. The factor 8/7 is introduced to take into account that photosynthesis occurs during only a fraction of the time and respiration continuously. When the maintenance respiration rate is independent of the rate of dry matter production the theoretical relationship between net photosynthetic rate

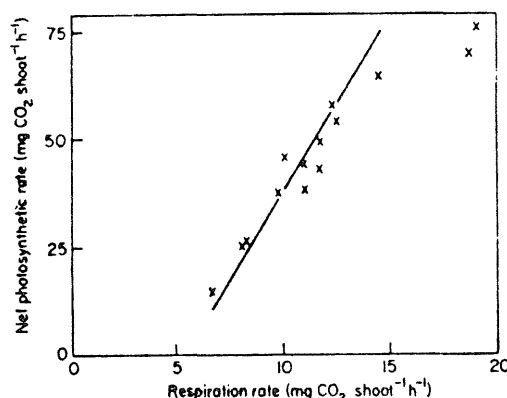


Fig. 4. Measured values of net photosynthetic and respiration rate of bean shoots. The slope of the line is determined theoretically.

and conversion respiration rate of maize is given by the line in Fig. 3. Only the intercept of the line, representing maintenance respiration, is adjusted to the position of the crosses.

A corresponding relationship for bean shoots was computed in a similar manner and is presented in Fig. 4 with a line. The experimental conditions were slightly different.

In Figs 3 and 4 there is a good correspondence between theory and experiment, although the experiment is not sensitive enough to detect minor changes in the assumptions. At the highest light intensities this correspondence does not hold. It is not clear in these cases whether substrate (carbohydrate) induced respiration occurs or that a shift of processes takes place to the dark period due to water stress in the light. Figs 3 and 4 do not support the suggestion (p. 332) of an intensive turn over of compounds during synthesis.

IV. Respiration and maintenance

Maintenance consists of processes to compensate for the degradation of existing structures and organization. The respiration originating from energy production for maintenance is called maintenance respiration. Resynthesis of hydrolysed proteins is likely to be part of maintenance processes, but also dry matter accumulation on one level of organization may sometimes be seen as a part of maintenance on a higher level, e.g. the formation of a new leaf on a plant when it replaces a lost one. It may be stated that maintenance very often comprises synthesis, but also other kinds of processes may participate. Both the factors causing and those influencing the rate of degradation processes, and thus the rate of re-growth, are still largely unknown. It is therefore as yet not possible to derive the rate of maintenance respiration theoretically.

According to Pirt (1965), Ducleaux (1898) was the first to distinguish energy for maintenance and energy for growth. Terroine and Wurmser (1922) estimated it to cause 26% of the fungi mycelium dry weight per day to be combusted. Tamiya (1932) and Tamiya and Yamaguchi (1933) reported similar high values and Pirt (1965) even higher ones for bacteria. McCree (1970) estimated by extrapolation maintenance respiration rates of intact clover plants to be as low as 1.5% of the plant dry matter per day, which is in close agreement with the author's measurements (Table IV). Maintenance respiration has been taken to be the rate constant during 12 h at the end of a dark period which lasted from 1 to 4 days, depending on plant type and pretreatment. De Wit *et al.* (1970) concluded from results obtained with a simulation model for crop growth that this maintenance respiration rate is a reasonable estimate for vegetative tissue. The respiration rate of storage tissue (Norton, 1963) and woody tissue (Yoda *et al.*, 1965) is much lower. Maintenance respiration rates appear to be more uniform when expressed on the basis of soluble nitrogenous compounds, which suggests a direct or indirect relationship.

It is questionable whether turnover rates of proteins, as measured by Holmsen and Koch (1964) are caused only by maintenance processes or also by redistribution of amino acids in the plant. It is therefore not realistic to calculate the maintenance respiration rate from these figures, giving a protein half-life time of seven days for tobacco plants.

It should be investigated whether the excess ATP produced during photosynthesis (Ried, 1970) or rapid growth (Forrest and Walker, 1971) may be used in processes such as maintenance, thereby reducing the amount of substrate required for these purposes. Uncoupled and idling respiration (Beevers, 1970; Tanaka, 1971) are not considered because of the lack of experimental information.

Table IV

Some maintenance respiration rates. Accuracy: $\pm 20\%$

Object	Respiration rate	
	$\text{g CH}_2\text{O g}^{-1} \text{ day}^{-1}$	$\text{g CO}_2 \text{ g}^{-1} \text{ day}^{-1}$
Maize, adult leaf, 25°C	0.011	0.015
Maize, adult leaf, 25°C ¹	0.008	0.012
<i>Phaseolus vulgaris</i> , adult leaf, 25°C ²	0.012	0.017
Maize, 20 day old plant, 15°C	0.013	0.019
Maize, 20 day old plant, 20°C	0.011	0.015
Maize, 20 day old plant, 25°C	0.013	0.019
Maize, 10 day old plant, 25°C	0.013	0.019
Maize, 10 day old plant, 25°C	0.022	0.032
<i>Lolium perenne</i> , 40 day old plant, 25°C	0.014	0.021

¹ Alberda, unpublished results² Louwerse, unpublished results

V. Respiration and temperature

No observations are known where temperature influences the pathway by which a compound is synthesized or the P/O ratio of energy production. In other words, p.v., c.p.f. and o.r.f. are expected to be the same in the range of temperatures normally encountered. It is therefore concluded that temperature affects the conversion respiration rate only indirectly, the rate of synthesis being intermediate.

The conclusion that the p.v. is independent of temperature is supported by the results of experiments with young organisms growing on glucose solution and seeds germinating at temperatures ranging from 11 to 38°C, presented in Table V. The relative yields of the growth processes are given in g plant formed per g substrate used and in some cases also in heat of combustion of the material formed per decrease in heat of combustion of the substrate used. The number of replicates and individuals per replicate are indicated. Significant differences in relative yield are not caused by temperature variation, but by differences in the chemical composition of the substrate. The different values in Table V for the relative yields within one species will at least partly be caused by the variable chemical composition of seeds. Kaufmann (1952) concluded that the relative yield of *Saccharomyces cerevisiae* depends on temperature but this does not agree with his data.

Table V

The influence of temperature and chemical composition of seed or substrate on the relative yield of growth processes

Species	Main storage compounds	Temp. (°C)	Relative yield g g ⁻¹ cal ⁻¹		Number of exp. and individuals	Duration of the experiment (days)	Refer- ence
Rice	carbohydrates	26	0.57	0.65	1 (50)	10	1
Rice	"	30	0.60	0.73	4 (25)	9	2
Rice	"	20-30	0.60	—	1 (1000)	5-15	3
Barley	"	22	0.64	—	8 (100)	3-7	4
Sorghum	"	17	0.78	0.74	2 (45)	12	2
Sorghum	"	33	0.54	0.74	3 (45)	4	2
Maize	"	22	0.60	—	2 (10)	10	5
Maize	"	15	0.50	—	1 (100)	17	6
Maize	"	25	0.51	—	2 (100)	13	6
Maize	glucose + NO ₃ ⁻	27	0.62	0.70	2 (16)	5	7
Lentils	carbohydrates and proteins	11	0.56	0.63	2 (3)	10	2
Lentils	"	18	0.57	0.63	3 (3)	6	2
Lentils	"	30	0.57	0.62	7 (3)	7	2
Peas	"	18	0.54	0.62	5 (3)	8	2
<i>Vigna</i> <i>sesquipedalis</i>	"	30	0.48	—	1 (?)	3	8
<i>Phaseolus</i> <i>vulgaris</i>	"	18	0.63	—	1 (50)	13	6
<i>Phaseolus</i> <i>vulgaris</i>	"	25	0.73	—	2 (50)	7	6
<i>Brassica</i> <i>napus</i>	lipids	11	0.83	0.52	2 (45)	17	2
<i>Brassica</i> <i>napus</i>	"	21	0.92	0.52	3 (45)	9	2
Groundnut	"	17	0.88	0.52	6 (1)	15	2
Groundnut	"	30	0.86	0.54	8 (1)	2-10	2
Groundnut	"	20	0.96	—	1 (50)	22	6
Groundnut	"	27	0.95	—	2 (50)	16	6
<i>Aspergillus</i> <i>niger</i>	glucose + NH ₃ (aerobic)	22-38	0.45	0.72	7-16 (—)	1-4	9
<i>Escherichia</i> <i>coli</i>	"	30	0.37	—	4 (—)	1-5 h	10

References:

1 Tang *et al.*, 19652 Terroine *et al.*, 1924

3 Tanaka, 1971

4 calculated from Barnell, 1937

5 Cooper and MacDonald, 1970

6 Penning de Vries, unpublished data

7 Kandler, 1953

8 calculated from Oota *et al.*, 1953

9 Terroine and Wurmser, 1922

10 calculated from Siegel and Clifton,
1950a, 1950b

It should be noted that "relative yield" includes the integrated maintenance requirement (Pirt, 1965). The relative yield is therefore not an accurate measure of the p.v. of a conversion process. The duration of the experiments is given in Table V.

The presumption that under unfavourable conditions synthesis proceeds less efficiently was rejected by Terroine and Wurmser (1922). Shemikato (1970) explains the lower relative growth rate and yield observed in these cases as due to a stimulation of maintenance processes. Rippel-Baldes (1952) and Forrest and Walker (1971) suggested that micro-organisms do not operate at the theoretical maximum efficiency in converting material and energy. It might be useful to investigate whether the low relative yield of micro-organisms as compared with higher plants is caused only by a lower p.v. of synthetic processes or also by a higher maintenance requirement.

VI. Respiration and net dry matter production

From the foregoing considerations about respiration (R , g carbon dioxide), apparent gross photosynthesis (P , g CH_2O), dry matter production (DMP) and maintenance, a formula can be given for respiration:

$$R = aP + bW$$

and also one for dry matter production, similar to the empirical one of McCree (1970):

$$\text{DMP} = cP - 30/44bW$$

in which a is approximately 0.31 or 0.28, and c is 0.75 or 0.80, depending on the plant type (p. 337). b is 0.0225 day^{-1} and W represents plant dry weight. The variables a and c are determined by the chemical composition of the material synthesized, which may change considerably with time, and b is likely to depend upon tissue protein content and temperature.

Plant dry matter production is the resultant of dry matter production of organs and of various kinds of losses. In the above equation only increase has been considered, except for decreases due to maintenance. An analysis of weight decrease due to loss of organs is beyond the scope of this paper. A third cause of weight loss is redistribution, consisting of breakdown, membrane passage, translocation and resynthesis of complex compounds. This process needs consideration especially during the reproductive phase of plant growth, but it occurs also within the vegetative plant. It is estimated that breakdown, conversion into transportable products, trans-

location and resynthesis may reduce the weight of the translocate by 15% when it consists of sucrose and by 30% when the translocate consists of amino acids (70%) and sucrose (30%). The substrate for the corresponding respiration is taken from the translocate. Thus respirational losses of crops may be 5 to 10% larger than those calculated from the above formula. From unpublished investigations carried out by the author it appeared that in a continued dark period redistribution in maize may be quite considerable, but little is known about the field situation.

VII. Concluding remarks

Not all processes concerning physiological aspects of respiration have been considered or even mentioned. An important and essentially unsolved problem in what is discussed remains the nature and intensity of maintenance processes, which were here only empirically treated. This process, however, is of crucial importance in understanding crop productivity. Data about the chemical composition and accurate methods to determine it are scarce. Such data as are usually reported concern special tissues or chemical fractions of the plant.

Respiration has been considered so far in a steady state. To understand and predict the conversion respiration rate of plants under non-steady-state conditions more information should be available about the effects of factors such as temperature, the relative amount of substrate for growth and the relative water content, on the rates of conversion processes.

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Discussion

Penning de Vries was asked if it were possible to measure maintenance respiration of higher plants directly by using growth inhibitors, as had been done in bacteria. He replied that he was not aware of such experiments; photosynthesis can be stopped by removing carbon dioxide but

this does not stop growth or the redistribution of products which together utilize much more energy than was likely to be consumed for maintenance purposes. In reply to another question on variation in maintenance respiration levels in different parts of the plant, he replied that maintenance respiration rates may be expected to depend on the amount of readily hydrolysable protein in the tissue. This will vary with the tissue and would change with time and temperature.

Scott Russell asked Penning de Vries to elaborate on how he estimated the energy consumption for salt uptake in his model. He replied that in higher plants energy was expended in transporting an ion across membranes at the site of uptake and again at the site of utilization. In animal cells (Stein, 1967) it had been found that the uptake of one ion across a membrane requires the energy of about one ATP molecule so that, extrapolating, in plants two ATP molecules would be required. But only one of the two ions of a salt has to be transported actively, the other entering to maintain electrical equilibrium, hence the uptake of one ion involves one ATP molecule, from which it can be calculated that approximately 8-10 g of minerals could be accumulated per 1 g of glucose. Sutcliffe thought that this interpretation was open to argument although these energy requirements were of the same order as calculated by Robertson for the maximum efficiency of ion uptake by the root. Scott Russell felt that the movement of ions throughout the plant would involve further energy expenditure.