III.2 Substrate Utilization in Germinating Seeds

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INTRODUCTION

The rates of formation and consumption of substrate, and the resulting growth rate of the plant are much easier to observe separately in germinating seeds than are the analogous processes in autotrophic plants, but the major processes by which substrate is released and utilized in seeds are not really different from those in autotrophic plants. Therefore, seeds which germinate in darkness provide a suitable system to evaluate some aspects of a quantitative biochemical approach to utilization of substrates for synthesis and maintenance of biomass. With this approach, the increase in dry weight of a seedling can be predicted from the decrease of the weight of the seed. This approach is based on the use of biochemical reaction equations to determine the relative weights of substrate, oxygen and minerals, which are converted by the plant into biomass, carbon dioxide and water. From earlier experiments it was concluded that conversion and growth processes in higher plants operate at, or close to, their maximum efficiency; these studies included direct observations of dry-weight increase of a maize embryo growing on a glucose solution in darkness (Penning de Vries, 1974), and indirect observation of growth—through respiration—and of substrate consumption—through photosynthesis—in whole plants (Penning de Vries, 1975b). Further evidence is, however, desirable.

Only a few authors give the biochemical composition of seed and seedling beyond the first stages of germination. None of the reports contained sufficient information for a detailed comparison of the observed growth of the young plant and its predicted value, the latter being based on the decrease in weight of seed components and on the chemical composition of the seedling. Experiments were therefore carried out, using seeds of *Phaseolus vulgaris*, *Arachis hypogea* and *Zea mays*, these being important examples of the types of seeds which form bulk-storage products. In this paper, the maximum daily

biomass increase of seedlings is calculated from the daily dry matter decrease of the seed, and these are compared with observed growth rates.

QUANTITATIVE BIOCHEMISTRY OF GERMINATION PROCESSES

Germination involves the synthesis and activation of enzymes and hormones, and the formation of glucose or sucrose and amino acids by breakdown of seed components. Substances are translocated to the growing points to support growth, while some of the substrate is consumed in seed and plant maintenance processes. If the seedling is exposed to light, it becomes green and starts to photosynthesize. If the seedling is not exposed to light, it remains yellow, develops long and thin stems and petioles, and deteriorates after exhaustion of the seed.

In this section the breakdown processes in the seed, maintenance processes in all living cells, translocation of substrate to the seedling and seedling growth are described. The quantitative aspects of these processes have been reduced to formal schemes and integrated into a computer program. Also from these schemes, simplified biochemical reaction equations were derived and these are presented below.
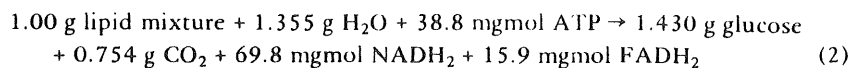
THE SEED

To calculate how much substrate is available to the young plant from its seed or cotyledons, the changes in biochemical components in the latter must be known. Textbooks describe in a sufficiently detailed manner how the major compounds are broken down and transformed into monosaccharides and amides (e.g. Dagley and Nicholson, 1970). These pathways have, mainly, been established in micro-organisms, but it is unlikely that they are much different in higher plants (Penning de Vries *et al.*, 1974).

In seeds, the breakdown of polysaccharides—mostly starch (Crocker and Barton, 1953)—into glucose occurs by hydrolysis and can be represented by the equation:
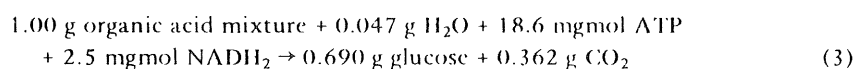
$$1.00 \text{ g carbohydrates} + 0.11 \text{ g } H_2O \rightarrow 1.11 \text{ g glucose} \tag{1}$$
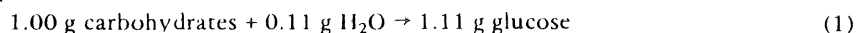
Fatty acids, resulting from hydrolysis of fats and oils, are broken down by β-oxidation into acetyl-coenzyme A molecules. By the glyoxylate pathway, phosphoenolpyruvate formation and the reversal of glycolysis, glucose-1-P is synthesized from these molecules (Beevers, 1961). Glycerol also contributes to gluconeogenesis. The degradation of a mixture of triglycerides of palmitic, stearic, oleic, linolic and linoleic acid (0.12, 0.03, 0.47, 0.33 and 0.05 $g\,g^{-1}$ respectively), may be summarized by the equation:

$$1.00 \text{ g lipid mixture} + 1.355 \text{ g } H_2O + 38.8 \text{ mgmol ATP} \rightarrow 1.430 \text{ g glucose}$$
$$+ 0.754 \text{ g } CO_2 + 69.8 \text{ mgmol NADH}_2 + 15.9 \text{ mgmol FADH}_2 \tag{2}$$
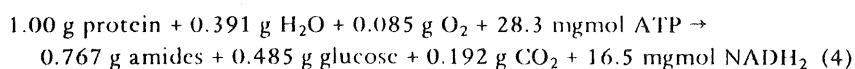
Equation (2) changes somewhat with the actual composition of the degraded lipids, but these changes are small.

Organic acids are present in small quantities in seeds. It is not clear whether these are converted into glucose during germination, while the accompanying cations are exported to the seedling, or whether they are translocated in their original form. It is assumed that the former process is the most important and this has little effect on the results of the germination computations. Glucose formation from a mixture of organic acids, consisting of oxalic, glyoxylic, oxaloacetic, malic, citric and aconitic acid (0.05, 0.05, 0.30, 0.10, 0.30 and 0.30 g g^{-1} respectively), may be represented by the equation:

$$1.00 \text{ g organic acid mixture} + 0.047 \text{ g } H_2O + 18.6 \text{ mgmol ATP}$$
$$+ 2.5 \text{ mgmol } NADH_2 \rightarrow 0.690 \text{ g glucose} + 0.362 \text{ g } CO_2 \qquad (3)$$

Proteins account for 5-35% of seed weight. They contain some 20 amino acids, in different proportions in the seed and the plant that grows from it. The amides glutamine and asparagine are the predominant nitrogen carriers from storage to growing points (Mayer and Poljakoff-Mayber, 1963), and are formed by hydrolysis of proteins and transformation of amino acids. The carbon skeletons not used for amide formation contribute to gluconeogenesis (Steward and Beevers, 1967). Often, some amino acids remain unchanged. It is supposed that cysteine and methionine are not transformed and are translocated as such. The formation of a mixture of 54.4% (by weight) of glutamine, 42.0% of asparagine, 1.0% of cysteine and 2.6% of methionine from zein, the main storage protein of *Zea mays*, can be represented by the equation:

$$1.00 \text{ g protein} + 0.391 \text{ g } H_2O + 0.085 \text{ g } O_2 + 28.3 \text{ mgmol ATP} \rightarrow$$
$$0.767 \text{ g amides} + 0.485 \text{ g glucose} + 0.192 \text{ g } CO_2 + 16.5 \text{ mgmol } NADH_2 \quad (4)$$

To derive equation (4) the amino acid composition of the transported mixture was chosen so that carbon loss is minimal. Again, equation (4) is only an approximation, because the composition of the transported mixture of amino acids and of storage protein differs between species, but equation (4) is considered to approximate to many situations.

The summation of equations (1)-(4), weighted according to the disappearance of compounds from the seed, gives an equation for the supply of substrates to the plant. Because $NADH_2$ and ATP are recycling intermediates, the final equation should not contain these compounds. Remaining $NADH_2$ is oxidized to NAD, yielding ATP. The ratio of moles of ATP formed per oxygen atom absorbed, the P/O ratio, is assumed to be 3.0 which is its maximum value. It is shown on p. 227 that the rate of ATP production in germinating seeds can be large, particularly in fat-rich seeds, and can exceed the rate of energy

consumption by the seed. If this occurs, the P/O ratio must decrease, to match supply and demand.

MAINTENANCE

Seeds and seedlings require energy for maintenance processes, which include protein turnover and maintenance of ion gradients across membranes. It was estimated for leaf tissue (Penning de Vries, 1975a) that ion-gradient maintenance requires an energy of about 4 mg glucose g^{-1} dry matter day^{-1} at $25°C$, which value doubles for each $10°C$ temperature increase. Protein turnover in green leaves was found to consume an amount of energy, equal to that released by respiration, of 30-60 mg glucose g^{-1} protein day^{-1}, and is assumed to have a temperature response similar to that of ion-gradient maintenance processes. It is likely that about half this cost is brought about by daily degradation and resynthesis of ribulose-diphosphate-carboxylase, a process which presumably does not occur in etiolated leaves. It was also found that the intensity of maintenance respiration is related to the general metabolic activity of the plant, i.e. the rate of growth or of substrate consumption. The energy required for seed and seedling maintenance are thus calculated at $25°C$ as 4 mg glucose g^{-1} dry matter day^{-1} plus 20 mg glucose g^{-1} active proteins day^{-1} plus 0.04 of the dry weight exported and imported. All seedling proteins, and 10% of the seed proteins initially present, are supposed to be actively involved in metabolism.

Experimental data collected by McCree (1974, see also Section III.1, this volume) and Penning de Vries (1975a) indicate that there may be a 2-3 fold variation in maintenance respiration rates of different species. Due to lack of data on these respiration rates or on the rates of the basic processes, the cost of maintenance processes was calculated in the same way for all species. When ATP remains after rapid lipid breakdown, the maintenance energy requirement may be partly or completely met from this surplus. Synthesis or reactivation of enzymes in the seed requires little of the substrate produced, and its cost is supposed to be covered by the energy expenditure for maintenance processes.

TRANSLOCATION

A large group of seeds, including those of *Phaseolus* and *Arachis*, have most of their reserves stored in the cotyledons, which become the primary leaves. Sucrose, amides and minerals are translocated to the growing points within the plant. In another large group of seeds, which includes the Gramineae, the plant embryos absorb substrates mainly from their exterior, because the endosperm is not a part of the plant. Monomers released from the endosperm are absorbed by a transformed leaf, the scutellum. These uptake processes must be active in order to be effective. It will be assumed that all import processes--namely those into
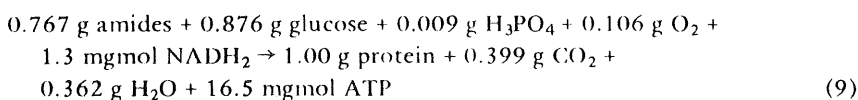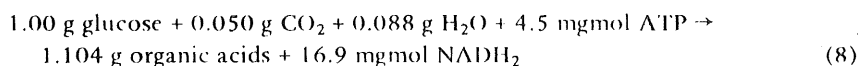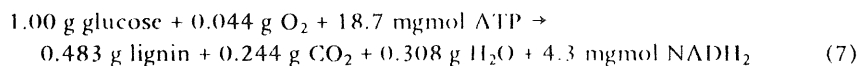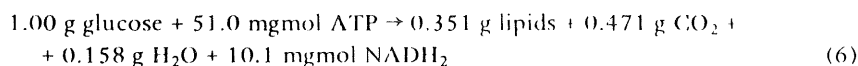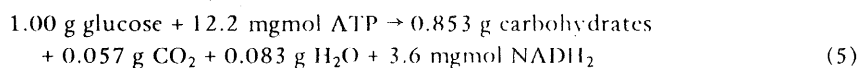
the scutellum, into the transport system and into growing cells—require energy, and that export is a passive diffusion process. Cost of import is assumed to be 1 molecule ATP per glucose molecule, 3 molecules ATP per sucrose molecule (which includes the energy required to synthesize sucrose from glucose) and 0.3 molecule ATP per amino acid, allowing no energy for translocation within the phloem (Penning de Vries, 1975b). Import costs cannot be covered by an eventual surplus of ATP in cells with a rapid degradation, because ATP is not transferred between cells.

THE SEEDLING

The yields of conversion processes of carbohydrates into classes of different compounds were calculated earlier (Penning de Vries et al., 1974), and are summarized in equations (5)-(8):

$$1.00 \text{ g glucose} + 12.2 \text{ mgmol ATP} \rightarrow 0.853 \text{ g carbohydrates}$$
$$+ 0.057 \text{ g } CO_2 + 0.083 \text{ g } H_2O + 3.6 \text{ mgmol NADH}_2 \tag{5}$$

$$1.00 \text{ g glucose} + 51.0 \text{ mgmol ATP} \rightarrow 0.351 \text{ g lipids} + 0.471 \text{ g } CO_2 +$$
$$+ 0.158 \text{ g } H_2O + 10.1 \text{ mgmol NADH}_2 \tag{6}$$

$$1.00 \text{ g glucose} + 0.044 \text{ g } O_2 + 18.7 \text{ mgmol ATP} \rightarrow$$
$$0.483 \text{ g lignin} + 0.244 \text{ g } CO_2 + 0.308 \text{ g } H_2O + 4.3 \text{ mgmol NADH}_2 \tag{7}$$

$$1.00 \text{ g glucose} + 0.050 \text{ g } CO_2 + 0.088 \text{ g } H_2O + 4.5 \text{ mgmol ATP} \rightarrow$$
$$1.104 \text{ g organic acids} + 16.9 \text{ mgmol NADH}_2 \tag{8}$$

$$0.767 \text{ g amides} + 0.876 \text{ g glucose} + 0.009 \text{ g } H_3PO_4 + 0.106 \text{ g } O_2 +$$
$$1.3 \text{ mgmol NADH}_2 \rightarrow 1.00 \text{ g protein} + 0.399 \text{ g } CO_2 +$$
$$0.362 \text{ g } H_2O + 16.5 \text{ mgmol ATP} \tag{9}$$

Equation (9) specifies the glucose consumption when the transported mixture of amino acids is converted back into protein. It is derived from basic conversion reactions (Dagley and Nicholson, 1970). The amino acid composition of the protein was again chosen identical to that of zein. Because synthesis of plant proteins occurs from small monomers, equation (9) is not affected whichever specific protein amino acid composition is chosen.

The reaction equations leading to equations (1)-(9) are not influenced by temperature, and it is therefore expected that the efficiency of conversion processes is also unaffected by temperature.

The "energy charge" has been suggested to be an important regulator of the synthetic activity of cells. The "energy charge" has been defined as (ATP +0.5 x ADP)/(ATP + ADP + AMP) where ATP, ADP and AMP represent the concentrations of adenosine triphosphate, diphosphate and monophosphate

in the cells. Hoffmann and Krause (1975) recently demonstrated interesting
courses of the "energy charge" in germinating wheat plants. An approach to the
prediction of the chemical composition of biomass synthesized may be to follow
this "energy charge" at the points of growth.

GERMINATION EXPERIMENTS

Viable seeds of *Phaseolus vulgaris* (cv. Berna) with protein-rich cotyledons,
Arachis hypogea with fat- and protein-rich cotyledons, and *Zea mays* (cv. CIV 7)
with starch-like endosperm were used in germination experiments, which were
conducted at $18°$ and $25°$ C, at $20°$ and $27°$ C and at $15°$ and $25°$ C respectively.
Groups of about 50 seeds were germinated in stone seedbeds (22 x 22 x 4 cm),
which were placed in a 2 cm water layer and were filled with fine porous stones,
the germination rate was > 90% in all seedbeds. In preliminary experiments
some seedbeds had to be discarded after a visible attack of fungi, but good and
uniform germination was attained in all experiments reported here.

Groups of 50-300 seeds were harvested at regular intervals until the seeds
were exhausted. The plants were dissected into "seed" and "seedling" by cutting
the cotyledons from the young plant, and the dry weight and the content of
proteins, lipids, organic acids and minerals were determined. Proteins were
estimated by multiplying the amount of nitrogen found by Kjeldahl analysis by
6.25 (although this is some 5% too high for many plant proteins); minerals were
estimated by multiplying the weight of the oxide-ash by 0.6, and the organic
acids by multiplying the weight of the oxide-ash by 0.4. Lipids were determined
by boiling the sample with hydrochloric acid, the addition of ethanol, extraction
with carbon tetrachloride and weighing the residue after evaporation of the
solvent. With dry matter divided into six classes of components (Penning de
Vries *et al.*, 1974), the subtraction of these four fractions from the total dry
weight leaves only lignin and carbohydrate. The lignin content in the young
sprouts is negligible; that of the seeds does not change during germination
because it is not degraded. Thus, the total dry weight change of seed and
seedling, minus the determined fractions, gives the change in the carbohydrate
content. Actually, the content of reducing sugars "after inversion" and the
"cellulose + hemicellulose" content were determined as well. Summing all
fractions, however, always left 10-30% of the dry weight unaccounted for. In
view of the analytical techniques used, these fractions consist, most likely, of
various carbohydrates (H. Vertregt, personal communication).

The weight of chemical fractions of seed and seedling are presented in Figs
1-6. The amount of nitrogen in groups of 50 seeds plus their seedlings fluctuates
only slightly in these experiments (cf. Mayer and Poljakoff-Mayber, 1963),
presumably due to differences in seed size before germination. The sudden
setbacks of the germination process, such as at Day 18 in Fig. 1, are artefacts,

caused by the uneven rate of germination in different seedbeds. Because stages of germination are compared to the initial stage, the weight of each seed and seedling sample is multiplied by a factor, such that the amount of nitrogen in "seed + seedling" equals that of the sample taken before germination. This factor ranges from 0.95 to 1.05.
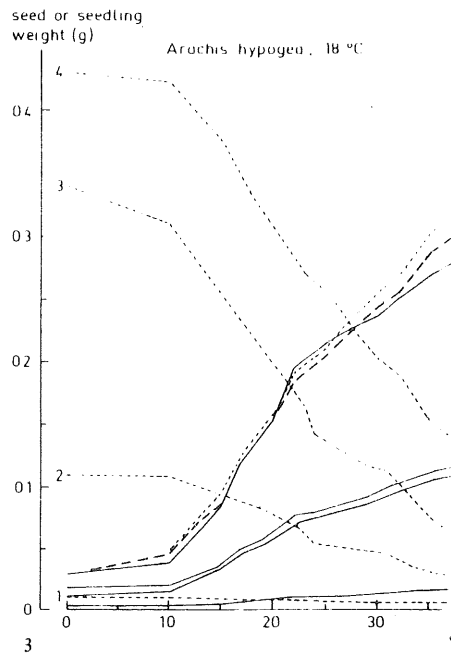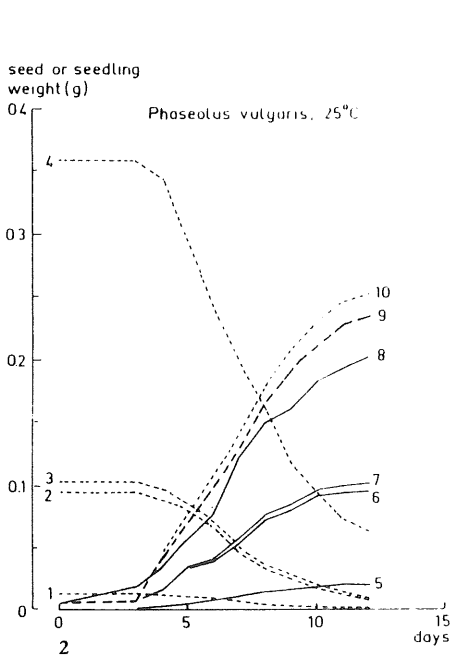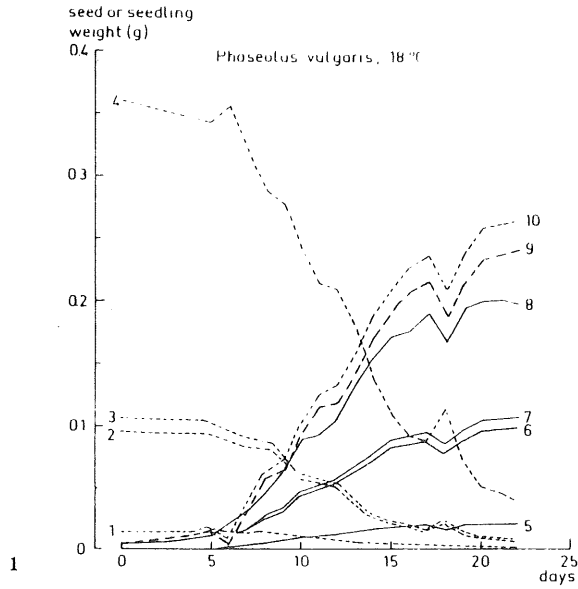
PREDICTED AND OBSERVED SEEDLING GROWTH

To compare theory with observations, the daily production of sucrose and of amino acids from the seed were calculated for the six experiments described above. Daily maintenance requirements were subtracted from the carbohydrate production, and then the weight of seedling which could have been synthesized was computed. To do so, the rate of nitrogen removal from the seed was taken to be the rate of nitrogen import into the seedling, rather than the observed value. This tends to increase the difference between the observation and prediction of seedling growth rate, but enables thorough checking of computed reaction balances. The amounts of lipid, organic acids and minerals calculated to be synthesized or taken up into the seedling, are taken as the observed values. The substrate remaining after subtraction of that required for synthesis and maintenance of the seedling, is converted into carbohydrates (equation 5). If the computation procedure simulates the germination process correctly, the calculated weight of the carbohydrates in the seedling will be equal to that observed, and the predicted total plant weight will also be equal to the observed values. In Figs 1-6, the lines numbered 9 represent the predicted total plant weight; the lines 8 represent the observed total plant weight. To demonstrate how much carbohydrates are consumed during germination for maintenance purposes, the computations were repeated with maintenance cost set at zero. The plant weights so predicted are represented by the lines numbered 10 in Figs 1-6. Some conclusions from comparisons of predicted and observed seedling weight are as follows. The results with *Phaseolus* and *Arachis* strongly support the hypothesis that conversion and maintenance processes can be considered at the biochemical level, and that plants utilize their substrates efficiently in growth processes. Temperature does not alter the efficiency of conversion processes.

Accurate experiments with six species by Terroine *et al.* (1924) yielded similar results, although they could not be assessed thoroughly because the chemical composition of the seeds was not determined in sufficient detail. Terroine *et al.* (1924) demonstrated that the increase in seedling weight per unit of decrease of seed weight, was independent of temperature over a range much wider than applied in the experiments described here.

When the seed approaches exhaustion, seedling weights increased less than calculated, and finally decreased. The oldest parts of the seedling deteriorate,

seed or seedling
weight (g)

0.4

Phaseolus vulgaris, 18 °C

0.3

0.2

0.1

0

        4

        10
        9
        8

        3
        2

        7
        6

        1
        5

0   5   10   15   20   25
                                days

1

seed or seedling
weight(g)

0.4

Phaseolus vulgaris, 25°C

0.3

0.2

0.1

0

        4

        10
        9
        8

        3
        2

        7
        6

        1
        5

0   5   10   15
                        days

2

seed or seedling
weight (g)

0.4

Arachis hypogea, 18 °C

0.3

0.2

0.1

0

        4

        3

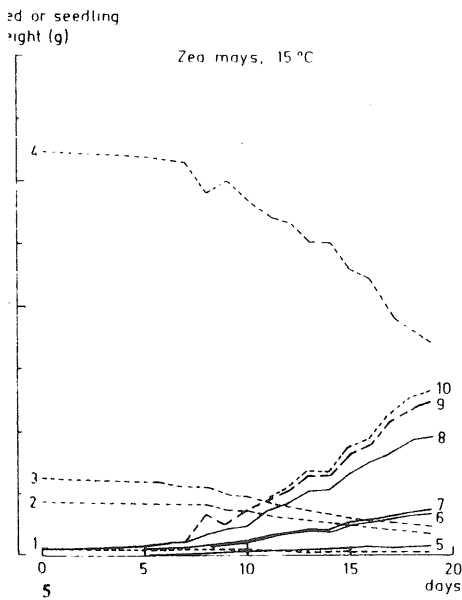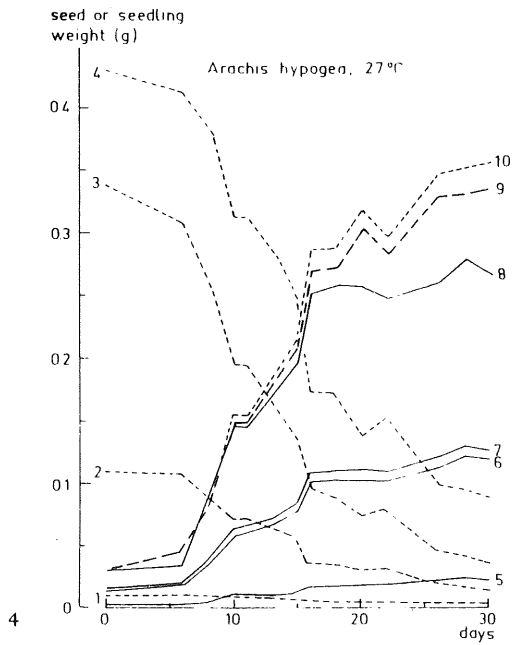   2

        1

0   10   20   30

3

Figs 1-6. The amounts of organic acids plus minerals, proteins, lipids and carbohydrates in
the seed are presented in sequence. The distance between line 1 and the base line of the
figures at a certain moment represents the amount of organic acids plus minerals at that
moment; the distance between lines 1 and 2, the amount of proteins, between lines 2 and 3,
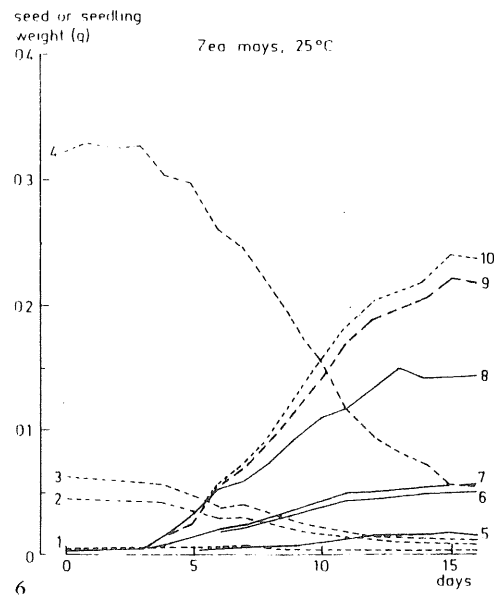
the lipids; and between lines 3 and 4, the carbohydrates. The composition of the seedling is presented similarly by lines 5, 6, 7 and 8. Line 9 presents the predicted total weight, and line 10 seedling weight if maintenance cost would have been zero. For further explanation, see text.

and presumably supply amino acids to the parts that are still growing. This process favours continuous growth at the growing point, but decreases net plant growth. Finally, disintegration of cells starts because of absence of substrate for maintenance. Rotting begins and organic matter is lost. Such processes are different in their nature from those studied here, and discrepancies between predicted and observed weights in the final germination stages received little attention.

For *Zea mays*, seedling growth is overestimated by 20-30% at 15°C and at 25°C. Since Cooper and MacDonald (1970) and Donaldson and Blackman (1974) observed that the maize scutellum gains no weight, or very little, during early germination and loses weight afterwards, the yield depression is not due to unobserved growth in the seedling. The low growth-rate could be due to a low efficiency of phosphorylation in the plant or a high rate of maintenance respiration.

Both are unlikely: *Zea* embryos without endosperm grow very efficiently on a glucose solution (Penning de Vries, 1974), and the rate of maintenance respiration of maize leaves is relatively low (Penning de Vries, 1975a). It has been observed that seeds of many plants, of Gramineae in particular, leak carbohydrates, amino acids and minerals when in contact with liquid water. In experiments with barley, Abdul-Baki and Anderson (1970) demonstrate that "the percentage of leaked glucose, even in a highly viable seed, is a significant portion of the total seed glucose". Maize seeds, in contrast to the cotyledons of *Phaseolus* and *Arachis* in our experiments, do remain in contact with liquid water in the seedbeds, and a considerable loss of glucose from the endosperm through the seed coat could have been expected. Because the nitrogen content of the "seed + seedling" in our experiments was constant during germination, re-absorption of leaked amino acids by the roots must have been very effective. Terroine et al. (1924) and Cooper and MacDonald (1970) recorded a seedling growth per unit of decrease of the endosperm weight close to that of our own experiments. It thus appears that in these experiments carbohydrate leakage has also been important.

Many seeds of cereal crop plants are low in protein (8-12%). Even with a considerable leakage of carbohydrates, the protein content of their seedlings is still lower than that of *Phaseolus* and *Arachis* (20-25% vs. 30-35%), and seedling demand for nitrogen still larger than that for carbohydrates. Leakage with effective nitrogen re-absorption is therefore not very disadvantageous for such seeds.

The amount of carbohydrates respired to provide energy for maintenance processes in seed and seedling, as indicated by the difference between the lines 9 and 10 in Figs 1-6, is always relatively small. Ten per cent or less of the reserves of the seed are spent for maintenance purposes, and 90% or more for growth and translocation. With changing temperature both the energy requirement g^{-1} dry

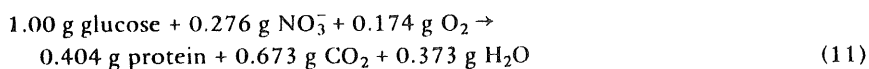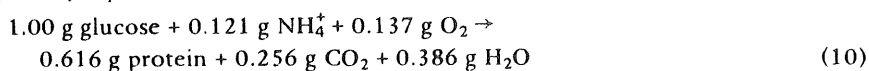matter day^{-1} and the rate of growth are modified in the same direction, so that the ratio of seedling weight formed to reserves consumed is hardly temperature-dependent (cf. Terroine *et al.* 1924).

In the cotyledons of *Arachis* the rate of ATP production from excess $NADH_2$ is such that for most of the time seed maintenance costs are completely covered from this source. Still, their P/O ratio must sometimes be as low as 1.5. Only cost of plant maintenance is to be paid, which is reflected in the small difference between the lines 9 and 10 in Figs 3 and 4.

Dark-grown seedlings are completely etiolated, and may behave somewhat different from green seedlings. The experiments were therefore repeated, on a smaller scale, with *Phaseolus, Arachis* and *Zea mays* at 27°C with continuous dark-red light of an intensity of about 10 W m^{-2}. This light is almost completely photosynthetically inactive, but caused their leaves to be green and the seedlings to be much shorter. Observed and simulated seedling weights followed the same pattern as that of the experiments in darkness. The germination process was somewhat quicker, and the prediction and measurement agreed even better than in the experiments described earlier.

Autotrophic plants consume reserve components for growth and maintenance at night and in other periods, so that substrate consumption exceeds its production by photosynthesis. The majority of these components, which are "reserves" by definition, are carbohydrates. Proteins are seldom "reserves". Equations (1) and (4) describe how much substrate can be formed from them. The equations (5) to (8) apply also in these cases, but equation (9) applies only if amides are supplied. Nitrate or ammonium, however, is also the usual source of nitrogen to plant cells. It was calculated elsewhere (Penning de Vries *et al.*, 1974) that for such situations the reaction for protein (i.e. zein) synthesis can be given by equation (10) and (11):

1.00 g glucose + 0.121 g NH_4^+ + 0.137 g O_2 →
0.616 g protein + 0.256 g CO_2 + 0.386 g H_2O (10)

1.00 g glucose + 0.276 g NO_3^- + 0.174 g O_2 →
0.404 g protein + 0.673 g CO_2 + 0.373 g H_2O (11)

For plant composition, transport of substrates and maintenance cost can be accounted with similar reasoning as for the germinating seeds.

ACKNOWLEDGEMENTS

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