BIOLOGIA PLANTARUM (PRAHA)

33 (6): 439–447, 1991

The Effect of Mineral Nutrition on the Growth and Maintenance Components of Respiration during Heterotrophic Growth of Barley Seedlings

P. SEKERKA*, L. NÁTR* and J. ČATSKÝ**

*Department of Plant Physiology, Faculty of Science, Charles University,
Viničná 5, 128 44 Praha 2, Czechoslovakia
**Institute of Experimental Botany, Czechoslovak Academy of Sciences,
Na Karlovce 1, 160 00 Praha 6, Czechoslovakia

Abstract. Spring barley seedling were grown in the dark for 21 d and respiration rates of the whole plant (including the seed), of the shoots, and of the roots were determined. A function describing the growth and maintenance components of respiration was interpolated through the experimental points and its parameters in plants under different mineral nutrition were compared. The plants grown in a complete nutrient solution showed the highest growth rate in the initial phase of development and thus reached the maximum respiration rate earlier than plants in the other variants. The highest proportion of substrate was respired in the shoot. Plants grown under deficiency of phosphorus and magnesium had a slower respiration rate than plants grown in the complete nutrient solution (NP), whereas the amount of respired substrate in plant parts was similar to that recorded in the NP plants. Plants grown in distilled water showed the lowest growth efficiency and respirated the highest proportion of substrate in the root.

The seed in the earliest phase of plant life is the sole source of saccharides and mineral substances. A limited saccharide reserve pool in the seed must support the growth of organs which then ensure full autotrophy of the plant, and simultaneously it must cover energy demands of the seedling connected with its heterotrophic growth and maintenance of its structures.

Energy usage by the plant shows two components (McCree 1970, Raven 1975, Thornley 1977): (1) the maintenance respiration rate, R_M (Penning de Vries 1975) represents energy used for the maintenance of cell structures, membrane potentials, and protein, phospholipid and RNA turnover, (2) the growth respiration rate (R_G), that corresponds to the energy necessary for the formation of new dry matter – macromolecules biosynthesis, uptake, transport and utilization of nutrients (Sinclair and De Wit 1975), and regulations associated with growth. In photosyntheticaly active plants, R_G is directly proportional to the rate of gross photosynthesis (P_G) (McCree 1970). In seedlings, P_G can be substituted with saccharide transport rate from reserve

---

Received September 20, 1989; accepted January 15, 1991

tissues (seeds) to growing tissues. Saccharide transport rate is dependent on the activity and the number of carriers, actual needs of the plant, the status of saccharide reserves, *etc.* (Humphreys 1987, 1988). The aim of this paper was to characterize respiration of etiolated seedlings grown under different mineral supply during the early stages of plant ontogeny.

Mathematical Model

The change in the structural dry mass of plant growing only from seed reserve substances in dependence on time is described in this paper by means of logistic function. When the saccharide transport from reserve tissues (provided they are not a part of the embryo) is continuous and its rate is directly proportional to growth rate, saccharides are not accumulated in the plant and their actual storage in root and shoot tissues is directly proportional to the structural dry mass of the plant. Under these conditions, the increase in total dry mass (W) can be described by a logistic (sigmoidal) function:

$$W = \frac{w}{1 + c\,e^{-dt}} \qquad (1)$$

The coefficients c and d determine the position of the inflexion point, w stands for the theoretical dry mass to which the real dry mass approaches, and t indicates time. This model can be applied to plants which are in the heterotrophic phase of growth entirely dependent only on seed reserve substances.

The simulation of the components of respiration (R) is based on the assumption that maintenance respiration (R_M) is directly proportional to dry matter content, whereas the growth respiration (R_G) to the change in dry matter content in time (McCree 1970, Barnes and Hole 1978, Lambers 1985):

$$R_M = b\,W \qquad (2)$$

and

$$R_G = a\,\frac{d\,W}{d\,t} \qquad (3)$$

where a and b are the coefficients of proportionality.

When similating changes in R in dependence on time, dry matter content in Eq. 3 was substituted with R_M.

$$R_G = A\,\frac{d\,R_M}{d\,t} \qquad (4)$$

At the beginning, we implied the existence of a logistic function for the dependence of dry matter on time. After the substitution of dry matter with R_M, we obtain the relationship

$$R_M = \frac{r}{1 + c\,e^{-dt}} \tag{5}$$

which, after derivation, represents a relationship for the description of the dependence of R_G on time:

$$R_G = \frac{r\,c\,d\,e^{-dt}}{1 + c\,e^{-dt}} \tag{6}$$

The course of R in dependence on time can be obtained by summing the Eqs. 5 and 6.

$$R = R_G + R_M \tag{7}$$

In these equations, r is the theoretical maximum R_M, that is approached by the measured rate of maintenance respiration from below and by the measured rate of the total respiration from the above relations. The magnitude of r is directly proportional to w and depends on the magnitude of the coefficient b. The values of r differ according to varying environmental conditions (temperature, mineral nutrition).

The coefficients c and d determine the position of the inflexion point of the Eq. 5, and the position of the peak of Eq. 6, but they do not determine the position of the peak of the Eq. 7.

$$t = \frac{\ln c}{d} \tag{8}$$

R reaches its peak later than R_G (*cf.* Fig. 1). At the time of the R-peak the first observable symptoms of photosynthate deficiency appear – slacking up of growth and decrease of the respiration rate. The beginning of starving leads to the manifestation of regulatory responses resulting in reduced growth. This may be a passive mechanism caused by the shortage of photosynthates, or an active regulatory process. Sopanen (1984) reported that amino acids released from aleurone cells were transported across scutellum according to the actual need of the seedling. A similar mechanism may also exist in the photosynthate transport. Photosynthate deficiency manifests itself in reduced photosynthate reserve pool and in this way in reduced growth (Hànsen 1977, Moldau and Karolin 1977, André 1982). From the R decrease after transfer of the green plant to continuous darkness (Ruget 1981) or after cutting the kernel from germinating etiolated plants (*cf.* Fig. 3), R_G and R_M were interpolated.

The total amount of respired CO_2 and thus also the amount of substrate used for respiration, and the two respiration components can be calculated from the mathematical model by means of integral.

MATERIAL AND METHODS

Spring barley (*Hordeum sativum* L., cv. Korál) plants were grown from seeds with a mass of 46 to 50 mg per kernel in the dark at 20 °C in three variants differing in mineral nutrition. In the NP variant, plants were grown in a complete Hoagland 3 nutrient solution, in the N variant plants were grown in a solution without P and Mg salts, and the 0 variant plants were grown in distilled water; always twenty plants were grown in 1500 cm^3 vessels. Nutrient solutions were replaced in five-day intervals.

The respiration rate (R) was determined as CO_2 output in a closed gas exchange system of a small volume (65 cm^3). The application of Grubb Parsons optical filter for cutting off the absorption bands of water vapour (Janáč 1971) in an IRGA measuring cell (Infralyt IV, Junkalor, Dessau) allowed to maintain a high relative humidity in the system (Kaše and Čatský 1984); in this way sample wilting which results in inaccurate results in the systems with a freezing water vapour trap was prevented.

The respiration rate (R) was measured in 2 to 21 d-old plants. The values obtained were processed using a computer; the Eq. 7 was interpolated through the means of the method of mathematical network by gradually defining the parameters in more precise terms.

R and R_M of the whole plant (including the seed) shoot respiration rate, and root respiration rate were determined as a function of time (Fig. 2 and 4). The function coefficients, the position of the inflexion point, and the integral were calculated. The mean error of calculation was in the range 1 to 8 %.

RESULTS

Plants of the NP variant (complete nutrient solution) respired during the experimental period the highest amount of substrate (higher by 9 and 16 % than the N and O plants, respectively). The highest proportion of substrate was respired in the shoot (55 % of the whole plant [including seed] R). The root R represents 26 % of the whole plant R. This relatively high value is the result of a high R in the initial phase of seedling growth. Plants of the NP variant were the first in reaching maximum R, and in the first 150 h of cultivation showed the highest whole plant and plant part R values. The pattern of the R curve was more pronounced in the NP variant than in the other variants, with the peak showing both a steeper ascent and sharper descent.

Plants of the N variant (P and Mg deficiency) differed from plants of the NP variant above all in the shift of the peak of R to a later stage. Shoot R accounted for 55 % of whole plant R, root R represented 15 % of whole plant R. The root R curve showed only a low peak. Average dry shoot mass was 16.16 mg at the end of experiment (16.72 mg in the NP variant), average dry root mass 3.89 mg (4.8 mg in the NP variant).

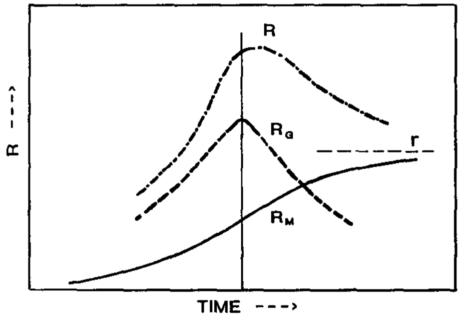

Fig. 1. Illustration of the mathematical model used for the description of changes in the respiration rate of seedlings grown in the dark. Solid line represents the logistic relationship (R_M), dashed line derivation (R_G), and dash-and-dot line is the sum of the above two relationships (R). The value approached by both the solid line and the dash-and-dot line is the coefficient r.

Plants grown in the O variant (distilled water) differed in many features. Whereas the pattern of the whole plant R curve was similar to that recorded in the N variant, the root R curve and the shoot R curve patterns markedly differed. Shoot R and root R reached 35 and 41 % of the whole plant R, respectively. Shoot and root dry masses were only 8.65 mg and 5.37 mg, respectively. The dry matter respired in the shoot decreased to 53 % NP, the shoot dry mass decreased to 51 % NP. The dry matter respired in the root increased to 132 % NP but the root dry mass increased only to 112 % NP. This indicated a lower growth efficiency in the root when compared with the shoot, or exactly for the growth and function of the root more energy on the biomass unit was depleted (Hansen and Jensen 1977, Szaniawski and Kietkiewicz 1982, Johnson 1990).

A comparison of the positions of inflexion points showed that in the N and NP variants the inflexion points occurred earlier in the root than in the shoot. Thus the shoot grew in these variants for a longer period than the root system. By contrast, in the O variant the inflexion point occured earlier in the shoot than in the root.

DISCUSSION

The conditions and the course of seed germination have a marked influence on the subsequent plant growth, in cereal crops it also influences yields (Frank 1980). Whereas the effect of mineral nutrition on photosynthesis is well understood (*e.g.* Nátr 1972), the nature of the effect of mineral nutrition on respiration and on heterotrophic growth is more complex. Nutrient deficiency induces growth reduction owing to reduced photosynthetic rate and shortage of photosynthates and other metabolites, and the following reduced R_G.

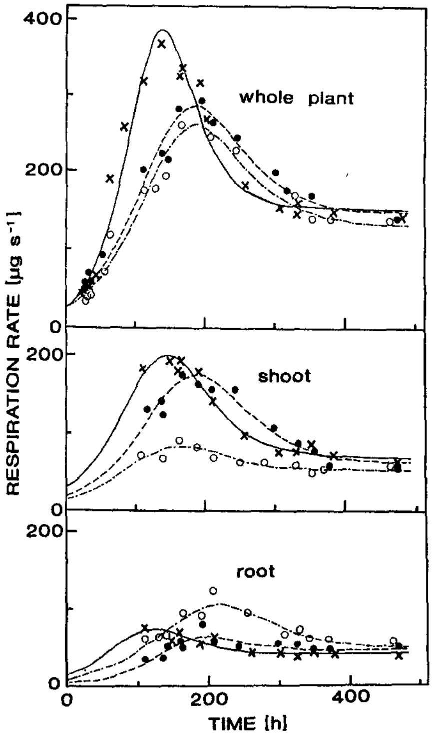

Fig. 2. Respiration rates of the whole barley plant including seed, of the shoot, and of the root in dependence on time. Solid lines (×) represent the NP variant (complete nutrient solution), dashed lines (●) the N variant (solution deficient P and Mg), dash-and-dot lines (○) the 0 variant (distilled water). The plants were grown in the dark at 20 °C; the seed was the sole source of saccharides. One point is average from three measurements.

On the other hand, however, energy expenses associated with the growth and formation of new structures involved in nutrient uptake or reutilization can simultaneously increase. This results in a reduction in growth efficiency. Simultaneously, R_M increases owing to enhanced turnover rate (Trewavas 1975), which results in a high energy consumption in the cell (Ryle *et al.* 1976).

In spite of high level of mineral nutrients in the seed, their deficiency is manifested already in early growth phases. Nátr (1988) found a significant effect of mineral nutrition on the mass of barley seedlings grown in the dark. Differences in the amount of respired substrate were also significant. They ranged from 49 to 52 % of utilizable substrate of the seed, whereas the content of the not utilizable seed dry matter was around 14 %, which is consistent with values presented in this paper.

The most frequently reported range of the coefficient b in green plants is 1 to 4% of dry matter per 24 h (Moldau and Karolin 1977). Our values were somewhat higher, plants of the O variant respired at the end of the experiment 5.6 % of dry matter per day, plants of the N and NP variants 5.1 %. The coefficient b of each treatment is considered to be constant in our model during the whole experimental period.

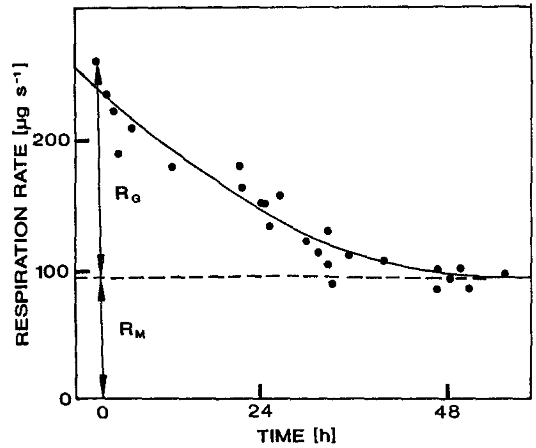

Fig. 3. Respiration rate of the whole barley plant (NP variant) in dependence on time. The seed of a 120-h-old plant was cut. The respiration rate decreased during 48 h and reached a constant value, maintenance respiration rate, R_M. R_G – growth respiration rate.

Plants of the O variant utilized the highest proportion of energy in the root, where it was measurable as the growth component of root respiration. This energy was utilized mostly in functional processes of the root and to a lesser extent in root growth processes (*cf.* the discussion on difficult interpretation of the growth and maintenance respiration components at a lower level than the whole plant or plant canopy (Kaše and Čatský 1984)). The measured R_G includes both the root growth (its dry mass increase), and the uptake, metabolism and transport of nutrients utilized in shoot growth (Johnson 1990). The latter component is associated with a high energy consumption which is not reflected in a marked increase in root mass. Thus R_G of roots also involves a portion of R_G of shoots (Szaniawski and Kietkiewicz 1982, Lambers 1985).

Changes in the positions of inflexion points of the R of the shoot and the root in the variants differing in mineral nutrition indicate the existence of regulation mechanisms of the distribution of photosynthates between roots and shoots. Brower (1962) deduced similar conclusions from growth analysis of plants growing under different mineral nutrition. However, the nature of such regulation mechanism is so far unknown.

Acknowledgement

The authors wish to thank colleagues of the Department of Photosynthesis of the Institute of Experimental Botany, Czechoslovak Academy of Sciences, especially Dr. J. Václavík for useful assistance during experimental measurements, and Professor B. Sekerka from the Faculty of Science, University of Maiduguri, Nigeria for computer processing of data.

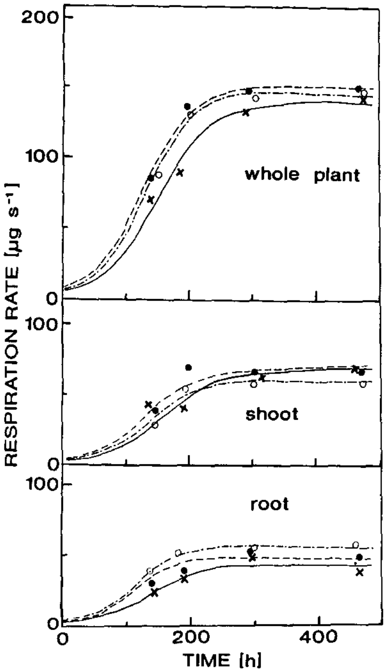

Fig. 4. Maintenance respiration rate (respiration rate 48 h after cutting off the seed) in dependence on time. The description and experimental conditions are described in Fig. 2.

REFERENCES

André, M., Massimino, J., Dagnenet, A., Massimino, D., Thiery, J.: The effect of day at low irradiance of maize crop. II: Photosynthesis, transpiration and respiration. – Physiol. Plant. **54**: 283–288, 1982.

Barnes, A., Hole, C. C.: A theoretical basis of growth and maintenance respiration. – Ann. Bot. **42**: 1217–1221, 1978.

Brouwer, R.: Distribution of the dry matter in the plant. – Neth. J. agr. Sci. **10**: 361–376, 1961.

Frank, R.: Grain yield and ear development of spring barley as influenced by environmental conditions during early stages of plant development. – Biol. Plant. **22**: 274–281, 1980.

Hansen, G. K.: Adaptation to photosynthesis and diurnal oscillation of root respiration rates for *Lolium multiflorum* L. – Physiol. Plant. **39**: 275–279, 1977.

Hansen, G. K., Jensen, C. R.: Growth and maintenance respiration in whole plants, tops and roots of *Lolium multiflorum* L. – Physiol. Plant. **39**: 155–164, 1977.

Humphreys, T. E.: Sucrose efflux and export from the maize scutellum. – Plant Cell Environ. **10**: 259–266, 1987.

Humphreys, T. E.: Anomalous kinetics of sucrose uptake in maize scutellum slices. – Plant Cell Environ. **11**: 525–534, 1988.

Janáč, J., Čatský, J., Jarvis, P. G., Brown, K. W., Eckardt, F. E., Fock, H., Schaub, H., Björkman, O., Gauhl, E.,Pieters, G. A.: Infra-red gas analysers and other physical analysers. – In: Šesták, Z., Čatský, J., Jarvis, P. G. (ed.): Plant Photosynthetic Production. Manual of Methods. Pp. 111–123. Dr W. Junk N. V. Publ., The Hague 1971.

Johnson, I. R.: Plant respiration in relation to growth, maintenance, ion uptake and nitrogen assimilation. – Plant Cell Environ. **13**: 319–328, 1990.

Kaše, M., Čatský, J.: Maintenance and growth components of dark respiration rate in leaves of C3 and C4 plants as affected by leaf temperature. – Biol. Plant. **26**: 461–470, 1984.

Lambers, H.: Respiration in intact plants and tissues: Its regulation and dependence on environmental factors, metabolism and invaded organism. – In: Douce, R., Day, D. A. (ed.): Higher Plant Cell Respiration. Pp. 418–473. Springer-Verlag, Berlin – Heidelberg – New York – Tokyo 1985.

McGree, K. J.: An equation for the rate of respiration of white clower plants grown under controlled conditions. – In: Prediction and Measurement of Photosynthetic Productivity. Pp. 221–229. PUDOC, Wageningen 1970.

Moldau, H., Karolin, A.: Effect of the reserve pool on the relationship between respiration and photosynthesis rate. – Photosynthetica **11**: 38–47, 1977.

Nátr, L.: Influence of mineral nutrients on photosynthesis of higher plants. – Photosynthetica **6**: 80–99, 1972.

Nátr, L.: Shoot/root ratio during early heterotrophic growth of barley as influenced by mineral nutrition. – Plant Soil **111**: 237–240, 1988.

Penning de Vries, F. W. T.: The cost of maintenance processes in plant cells. – Ann. Bot. **39**: 77–92, 1975.

Raven, J. A.: The quantitative role of "dark" respiratory processes in heterotrophic and photolitotrophic plant plant growth. – Ann. Bot. **40**: 587–602, 1976.

Ruget, F.: Respiration de croissance et respiration d'entretien: méthodes de mesure, comparaison des résultats. – Agronomie **1**: 601–610, 1981.

Ryle, G. J. A., Cobby, J. M., Powell, C. E.: Synthetic and maintenance respiratory losses of $^{14}CO_2$ in uniculm barley and maize. – Ann. Bot. **40**: 571–586, 1976.

Sinclair, T. R., de Wit, C. T.: Photosynthate and nitrogen requirements for seed production by various crops. – Science **189**: 565–567, 1975.

Sopanen, T.: Uptake of peptides and aminoacids by the scutellum of germinating barley grain. – In: Cram, W. J.: Janáček, K., Rybová, R., Siegler, K. (ed.): Membrane Transport in Plants. Pp. 365–370. Academia, Praha 1984.

Szaniawski, R. K., Kietkiewicz, M.: Maintenance and growth respiration in shoot and root of sunflower plants grown at different root temperatures. – Physiol. Plant. **54**: 500–504, 1982.

Thornley, J. H. M.: Growth, maintenance and respiration: a re-interpretation. – Ann. Bot. **41**: 1191–1203, 1977.

Trewavas, A.: Control of the protein turnover rates in *Lemna minor*. – Plant. Physiol. **49**: 47–51, 1972.